



Winter mortality in the northern Yellowstone elk herd 1988-90
by Jane Park Roybal

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in
Biological Sciences
Montana State University
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Abstract:

Efforts to reestablish wolves in Yellowstone are underway. Elk constitute the largest proportion of ungulate biomass in the area and have served as the primary prey species for the reestablished wolf population. The northern Yellowstone elk herd is the single largest ungulate population in Yellowstone. Information on the extent and age/sex structure of early and mid-winter mortality within this herd would be potentially valuable in evaluating the effects of current and future management as well as the reintroduced wolf population. This study was initiated in January 1989 to evaluate Gardiner late hunt data and carcass survey information to determine the structure of early and mid-winter mortality in the northern Yellowstone elk herd. Elk harvest information from the 1982-83 to 1992-93 late hunts was obtained from the Gardiner check station, compiled and analyzed. Age structure of the harvest was estimated during 1988-89 and 1989-90, using tooth eruption/wear and cementum analysis. The two aging techniques were compared. A hunter survey was conducted to determine the effects of hunter selection on structure of the harvest. An index of winter severity was computed for 15-day intervals and used to assess the influence of weather on elk mortality. Carcass surveys were conducted during 1988-89 and 1989-90 in key elk wintering areas and along randomly located transects to determine the age and sex structure of natural mortality and spatial/temporal distribution of carcasses. Age structure of the harvest differed significantly between the two years. The majority of elk harvested during both (years) were female. Maximum ages for harvested elk were 21.5 years for cows and 13.5 years for bulls. The majority of elk were killed in Hunt Area 2 (closest to the Park boundary) in 1988-89 and 1989-90. Age structure of the harvest did not differ significantly from that of the live population when bulls were excluded from analysis. Overall frequency of differences in age estimation by eruption/wear compared to cementum analysis was 80%, with discrepancies between the 2 techniques increasing as age of the animal increased, resulting in overaging younger and underaging older class animals. Methods for improving accuracy of eruption/wear aging are discussed. Results of the hunter survey could not be used to interpret harvest data. Hunter and hunting characteristics and techniques for increasing the accuracy of survey responses are presented. Calves were over-represented in mortality surveys compared to the live population. Adult females constituted 70% of the estimated live population, but were under-represented in carcass surveys and overrepresented in the harvest.

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A thesis submitted in partial fulfillment
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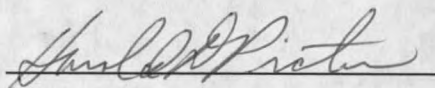
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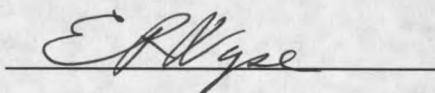
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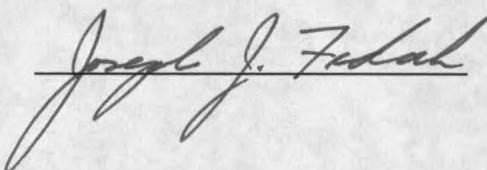
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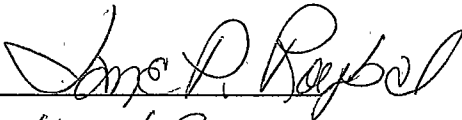
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TABLE OF CONTENTS

	Page
LIST OF TABLES	ix
LIST OF FIGURES	xiii
ABSTRACT	xv
CHAPTER	
1. INTRODUCTION	1
2. STUDY AREA	7
The Northern Range - Location, Size and Ownership	8
Climate	12
Vegetation	13
Fauna	14
3. HISTORY OF THE NORTHERN YELLOWSTONE ELK HERD	16
Winter 1988-89	18
Sex and Age Composition of the Northern Yellowstone Elk Herd ..	21
4. THE GARDINER LATE ELK HUNT	25
History of the Gardiner Late Hunt	25
1988-89 Gardiner Late Hunt	28
1989-90 Gardiner Late Hunt	32
Methods	32
Results	35
1988-1989 Gardiner Late Hunt	35
1989-1990 Gardiner Late Hunt	39
Comparison of Age Structure with Live Population	43

TABLE OF CONTENTS -- Continued

CHAPTER

4.	THE GARDINER LATE ELK HUNT — <u>Continued</u>	
	Comparison of Age Structure of Late Hunt Harvests from 1982-1993	45
	Discussion	49
	Comparison of Females Versus Males in Harvest	49
	Location of Kill	54
	Differences in Age Structure of the Harvest	55
	Comparison of Age Structure of Harvest with Live Population	57
	Comparison of Age Structure of Late Hunt Harvests from 1982-1993	58
5.	COMPARISON OF AGING TECHNIQUES	61
	Introduction	61
	Methods	64
	Results	67
	Discussion	75
6.	HUNTER SURVEY	82
	Gardiner Late Hunt 1990-91	83
	Methods	84
	Results	87
	Discussion	103
	Survey Coverage	103
	Validity of the Survey	103
	Hunt Characteristics	106
	Management Recommendations	107
7.	ELK CARCASS SURVEYS	109
	Methods	109
	Index of Winter Severity	116
	Results	117
	Winter Carcass Surveys 1988-89	117
	Winter Carcass Surveys 1989-90	122
	Time of Death	125

TABLE OF CONTENTS -- Continued

CHAPTER

7. ELK CARCASS SURVEYS — Continued

Correlation with Index of Winter Severity	129
Cause of Death	131
Carcass Location	134
Aspect	134
Landform	136
Slope	137
Cover Type	137
Discussion	140
Time of Death	141
Cause of Mortality	143
Carcass Location	146
Management Recommendations	147

8. CONCLUSIONS 148

REFERENCES CITED 152

APPENDICES 164

Appendix A -	
1988-89 Gardiner Late Hunt - Location of Kill by Hunt Area	165
Appendix B -	
1989-90 Gardiner Late Hunt - Location of Kill by Hunt Area	170
Appendix C - Hunter Survey Questionnaire	173
Appendix D - 1988-89 Carcass Survey Routes	177
Appendix E - 1989-90 Transect Lines	180
Appendix F - Cover Type Categories	188
Appendix G - Carcass Survey Data Forms	190

LIST OF TABLES

Table	Page
1. Summary/comparison of sex age composition of elk classified during early winter surveys on the northern range (Houston 1982, F.J. Singer unpublished data, Mack and Singer 1992)	23
2. Age distribution of 2409 elk harvested in the 1988-89 Gardiner late hunt based on eruption/wear age estimation (includes illegally harvested animals)	36
3. Location, distribution, and percent of total harvest for the 1988-89 Gardiner late elk hunt. Percentages are based on the 2,359 elk for which location of kill was known.	38
4. Age distribution of 432 elk harvested in the 1989-90 Gardiner late hunt based on eruption/wear age estimation (includes illegally harvested animals)	40
5. Location, distribution, and percent of total harvest for the 1989-90 Gardner late elk hunt. Percentages are based on the 421 elk for which location of kill was known	41
6. Comparison of cows, calves, and bulls harvested during the 1988-89 and 1989-90 Gardner late elk hunts including all known illegal kills. (number(percent of) total animals harvested)	42
7. Comparison of percentage of male and female elk in each age group for the 1988-89 and 89-90 Gardner late hunts based on eruption/wear age estimation. Percent is of total females or males harvested that year	44
8. Comparison of number (and percentage) of cows, calves, and bulls in the Gardiner late hunt harvest and estimated in the wild population in 1988-89	45
9. Age classification of elk harvested and aged in Gardiner late elk hunts 1982-83 through 1992-93 [number (percent of total)] and minimum prehunt population estimates based on census counts	46

LIST OF TABLES — Continued

Table	Page
10. Summary of the Gardiner late elk season, 1982-83 through 1988-89 (MTFWP. C. Simme, unpubl. data) and Chi-square values comparing 88-89 age distribution with previous years.	47
11. Summary of the Gardiner late elk season, 1989-90 through 1992-93 (MTFWP. C. Simme, unpubl. data) and Chi-square values comparing 89-90 age distribution with subsequent years.	48
12. Established certainty codes and associated accuracy limits used as reliability indicators for cementum analysis aging.	63
13. Error in age estimates for 699 elk harvested in 1988-89 and aged using the eruption-wear technique as compared to actual age determined from cementum analysis [number(percent of total in age group)].	69
14. Error in age estimates for 215 elk harvested in 1989-90 and aged using the eruption-wear technique as compared to actual age determined by cementum analysis [number(percent of total in age group)].	72
15. Comparison of age distribution of elk harvested in the 1988-89 and 1989-90 Gardiner late hunts based on eruption/wear age estimation (ErW) and cementum (Cem) analysis [number (percent of total carcasses aged)].	73
16. Contingency table analysis of tag type by sex of hunter.	88
17. Contingency table analysis on reason for participating in the hunt by sex of hunter	91
18. Contingency table analysis on reason for participating in the late hunt by tag type.	91
19. Contingency table analysis on reason for participating in the late hunt by state of residence.	91

LIST OF TABLES — Continued

Table	Page
20. Contingency table analysis of hunting method by sex of hunter.	94
21. Contingency table analysis of hunting method by tag type.	94
22. Contingency table analysis of hunting area by sex of hunter	95
23. Contingency table analysis of hunting area by tag type.	95
24. Contingency table analysis on whether participants hired a guide by sex of hunter	97
25. Contingency table analysis on whether participants hired a guide by tag type.	97
26. Rating scale for IWS values.	117
27. Age distribution of 349 elk located/reported during carcass surveys during 1988-89. Percentages are based on 349 elk	120
28. Age distribution of 17 elk located/reported during carcass transect surveys in 1989-90. Percentages are based on 17 elk	123
29. Comparison of number (and percentage) of cows, calves, and bulls observed in carcass surveys, the Gardiner late hunt harvest, and estimated in the wild population in 1988-89	125
30. Age distribution of carcasses located in 1988-89 surveys by time period	126
31. Sex and age distribution of carcasses located in 1988-89 surveys by time period	126
32. Age distribution of carcasses located in 1989-90 transect surveys by time period	127
33. Sex and gross age distribution of carcasses located in 1989-90 transect surveys by time period	127

LIST OF TABLES — Continued

Table	Page
34. Index of winter severity for the northern range 1988-90	129
35. Cause of death for elk located in 1988-89 and 1989-90 carcass surveys	131
36. Cause of death for calves and adult elk located in 1988-89 carcass surveys	133
37. Number (percent) of carcasses located on surveys during 1988-89 and 1989-90 by landform. Percentages are based on 314 elk in 1988-89 and 17 elk in 1989-90	138
38. Number (percent) of carcasses located on various landforms during 1988-89 by sex of elk. Percentages are based on 140 cows and 105 bulls including those where landform was unknown	138
39. Number (percent) of carcasses located on various landforms during 1988-89 by age class. Percentages are based on 162 calves and 125 adult elk including those where landform was unknown	138
40. Distribution of elk carcasses among gross sex and age classes located during 1974-75, 1975-76 (Houston 1978), and 1988-89 surveys.	141
41. 1988-89 Gardiner late hunt location of kill by hunt area	166
42. 1989-90 Gardiner late hunt location of kill by hunt area	171

LIST OF FIGURES

Figure	Page
1. Map of Yellowstone National Park showing the winter range (shaded) of the northern Yellowstone elk herd	9
2. Boundaries of the current versus late 1970's northern Yellowstone elk winter range (from Lemke et al. 1996)	10
3. Montana hunting district boundaries north of Yellowstone National Park	30
4. Late hunt administrative hunting areas for the 1988-89 season	31
5. Scatterplot of eruption/wear (Age_est) versus cementum age (Actual_A) for elk harvested in the 1988-1989 Gardiner late hunt	68
6. Scatterplot of eruption/wear (Est_Age) versus cementum age (Actual_A) for elk harvested in the 1989-1990 Gardiner late hunt	71
7a. Age distribution of elk harvested in 1988-89 late hunt as determined by eruption/wear versus cementum analysis	74
7b. Age distribution of elk harvested in 1989-90 late hunt as determined by eruption/wear versus cementum analysis	74
8. Respondent's reasons for hunting in the Gardiner late hunt	90
9. Respondent's reasons for hunting in the Gardiner late hunt by sex of hunter	90
10. Respondent's reasons for hunting in the Gardner late hunt by tag type	93
11. Respondent's indication of whether they hired a guide to locate elk	98
12. Number of years participated in Gardiner late elk hunt	100
13. Number of years participated in an elk hunt	100

LIST OF FIGURES — Continued

Figure	Page
14. Why respondents took elk that did not meet their specifications	102
15. Survey routes traversed on the northern range during the 1988-89 field season	110
16. Approximate location of elk carcasses located on the northern winter range during 1988-89 carcass surveys	118
17. Age distribution of 349 elk located/reported in 1988-89 carcass surveys	121
18. Age distribution of 17 elk located/reported in 1989-90 carcass surveys	121
19. Distribution of calves, cows, and bulls among elk carcasses, harvested elk, and the estimated live population	124
20. Percent distribution of elk by gross age/sex class that died in each 15-day time period based on date of death estimated during 1988-89 carcass surveys (n = 301)	128
21. Percent distribution of elk by gross age/sex class that died in each 15-day time period based on date of death estimated during 1989-90 carcass surveys (n = 17)	128
22. Percent distribution of elk that died in each 15-day time period as correlated with Index of winter severity (IWS) during 1988-89 carcass surveys	130
23. Cause of death for elk located in carcass surveys	132
24. Cause of death for calves and adult elk located in 1988-89 carcass surveys . .	132
25. Percent distribution of elk carcasses located in 1988-89 surveys by aspect . . .	135
26. Percent distribution of elk carcasses located in 1988-89 surveys by aspect . . .	135
27. Percent distribution of total carcasses located on surveys by landform	139
28. Percent distribution of total carcasses located on surveys by slope	139

ABSTRACT

Efforts to reestablish wolves in Yellowstone are underway. Elk constitute the largest proportion of ungulate biomass in the area and have served as the primary prey species for the reestablished wolf population. The northern Yellowstone elk herd is the single largest ungulate population in Yellowstone. Information on the extent and age/sex structure of early and mid-winter mortality within this herd would be potentially valuable in evaluating the effects of current and future management as well as the reintroduced wolf population. This study was initiated in January 1989 to evaluate Gardiner late hunt data and carcass survey information to determine the structure of early and mid-winter mortality in the northern Yellowstone elk herd. Elk harvest information from the 1982-83 to 1992-93 late hunts was obtained from the Gardiner check station, compiled and analyzed. Age structure of the harvest was estimated during 1988-89 and 1989-90, using tooth eruption/wear and cementum analysis. The two aging techniques were compared. A hunter survey was conducted to determine the effects of hunter selection on structure of the harvest. An index of winter severity was computed for 15-day intervals and used to assess the influence of weather on elk mortality. Carcass surveys were conducted during 1988-89 and 1989-90 in key elk wintering areas and along randomly located transects to determine the age and sex structure of natural mortality and spatial/temporal distribution of carcasses. Age structure of the harvest differed significantly between the two years. The majority of elk harvested during both (years) were female. Maximum ages for harvested elk were 21.5 years for cows and 13.5 years for bulls. The majority of elk were killed in Hunt Area 2 (closest to the Park boundary) in 1988-89 and 1989-90. Age structure of the harvest did not differ significantly from that of the live population when bulls were excluded from analysis. Overall frequency of differences in age estimation by eruption/wear compared to cementum analysis was 80%, with discrepancies between the 2 techniques increasing as age of the animal increased, resulting in overaging younger and underaging older class animals. Methods for improving accuracy of eruption/wear aging are discussed. Results of the hunter survey could not be used to interpret harvest data. Hunter and hunting characteristics and techniques for increasing the accuracy of survey responses are presented. Calves were over-represented in mortality surveys compared to the live population. Adult females constituted 70% of the estimated live population, but were under-represented in carcass surveys and over-represented in the harvest.

CHAPTER 1

INTRODUCTION

The gray wolf (*Canis lupus*) was essentially eradicated from most of the western United States by the 1930's (U.S. Fish and Wildlife Service (FWS) 1980). Control programs and U.S. government trappers extirpated wolves from Yellowstone National Park (YNP) between 1914 and 1926 as part of national program to eliminate all predatory animals from public lands (Weaver 1978, Houston 1982, FWS 1987).

In 1978, the gray wolf was listed under the Endangered Species Act of 1973 (ESA) (U.S.C. 1531 et seq.) as endangered in the conterminous United States, except Minnesota, where it was designated as threatened. With listing came legal protection and a mandate to recover the gray wolf. The FWS approved a revised recovery plan for the Northern Rocky Mountain wolf (*Canis lupus irremotus*) in 1987, identifying the need to reintroduce wolves into the Greater Yellowstone area and possibly central Idaho (FWS 1987). During the late 1980's and early 1990's, several wolf sighting reports were received annually from northwest Wyoming. However, pack or breeding activity was never confirmed (Cole 1971; Weaver 1978; FWS 1980, 1987, 1993).

The biological and social implications of restoring wolves in their former range in the Rocky Mountains has long been debated and has been reviewed at length

(National Park Service [NPS] 1975; Weaver 1978; FWS 1980, 1987; Yellowstone National Park (YNP) et al. 1990; Varley and Brewster 1992; FWS 1993). Aldo Leopold, as early as 1940, had proposed restoration of the wolf in Yellowstone National Park (Fritts et al. 1997). Between 1988 and 1991, the FWS and NPS, under Congressional direction, conducted or sponsored studies to evaluate the potential effects of wolf restoration to Yellowstone National Park and the surrounding area including impacts to the ungulate prey base and big game hunting (YNP et al. 1990, Varley and Brewster 1992).

In 1991, Congress directed the FWS to develop an Environmental Impact Statement (EIS) to analyze alternatives for and potential impacts of wolf recovery in Yellowstone and central Idaho. Approved and released in April 1994, the final EIS called for reintroduction of wolves into YNP and central Idaho, as experimental populations (Fritts et al. 1997). The final step in the process came in June 1994, with the signing of the Record of Decision by the Secretary of Interior. On January 12, 1995, some 70 years after their eradication, the first group of wolves arrived in Yellowstone. A second group of wolves was captured and translocated to Yellowstone and central Idaho in early 1996.

Of all the areas evaluated, Yellowstone's northern range has perhaps the greatest potential for sustaining a reintroduced wolf population year round. The region supports the area's greatest ungulate prey base, including elk (*Cervus elaphus*), bison (*Bison bison*), mule deer (*Odocoileus hemionus*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), and pronghorn (*Antilocapra americana*) (Houston 1982,

Singer 1990). The Rocky Mountain elk is the most abundant of eight ungulate species occurring in Yellowstone National Park. Eight elk herds summer or reside year-round within the Park, with numbers in summer reaching between 25,000 to 31,000 individuals (Houston 1982, Mack et al. 1990, Singer 1990). The northern Yellowstone elk herd, consisting of those animals wintering in the Yellowstone River drainage within and adjacent to the Park, represents the largest single ungulate population in the area. The winter range occupied by the northern Yellowstone elk herd is often referred to as the "northern range."

Controversy concerning the need to manage elk numbers within Yellowstone National Park has made the northern Yellowstone elk herd one of the most studied ungulate populations in the world. Several NPS biologists studied the northern range: Walt Kittams 1948-58, Robert Howe 1958-62; William Barmore 1962-69 (Barmore 1980); Douglas Houston 1969-79 (Houston 1982); and Francis Singer 1980-90 (NPS 1988). Erickson (1981) and Houston (1982) have summarized the history of elk population dynamics and management in the Yellowstone area. The merits of past and possible future management scenarios including winter feeding, predator control, removal of ungulates, and natural regulation have been debated and discussed by Skinner (1928), Cahalane (1943), Cole (1969, 1971), Beetle 1974), Cayot et al. (1979), Houston (1982), Chase (1986), Despain et al. (1986), and Boyce (1991).

Skinner (1928), Rush (1932), Kittams (1963), Ellis (1964), Craighead et al. (1972), Shoesmith (1979), Houston (1982), and Vore (1990) have documented the distribution and movements of the northern Yellowstone elk herd. Vales (unpubl. Ph.D

Diss.) investigated over-winter survival strategies of mature bulls. Changes and transitions in the condition of the northern range have been discussed by Despain (1973), Tyers (1981), Houston (1982), Kay (1985, 1987, 1990), Despain et al. (1986), Coughenour (1991), Frank and McNaughton (1992, 1993), and Merrell et al. (1994). Predation on elk and use of ungulate carrion by carnivore and scavenger species have been documented (Murie 1944, Cole 1972, Houston 1978, Craighead and Sumner 1982, Schleyer 1983, Knight et al. 1984, Harting 1985). Grizzly bear predation on elk calves in Yellowstone National Park was documented by Gunther and Renkin (1990) and French and French (1990). Green and Mattson (1987) and Green (1994) examined the availability of ungulate carcasses and subsequent use by grizzly bears during early spring on the northern range and other areas of the YNP. Long-term studies were initiated on Yellowstone's northern range in 1989 to look at coyote distribution and population dynamics and gather baseline information in anticipation of potential impacts resulting from wolf reintroduction (Crabtree and Varley 1995, Gese et al. 1995, Grothe et al. 1995, Hatier and Crabtree 1995(a,b), Sheldon et al. 1995, Slade et al. 1995, Stotts et al. 1995). Between 1987 and 1995, field studies were conducted to look at mountain lion abundance, home range size, food habits and predation (Murphy and Tischendorf 1988; Murphy et al. 1995; Murphy, unpubl. Ph.D Diss.).

Elk represent an important winter and spring food source for the existing predator/scavenger fauna of Yellowstone and may be especially important during periodic severe winters (Houston 1978). Ungulates once made up the bulk of the wolf's diet across North America (Mech 1970) and although resident wolf packs were

eliminated from Yellowstone, evidence suggests at one time elk were an important year-round food source for wolves (Weaver 1978). Because of their abundance in the Park today, elk would undoubtedly serve as the primary prey species for any reintroduced wolves.

Since Houston's studies, (1970-78), the northern Yellowstone elk population as well as vegetative communities within Yellowstone have undergone considerable change. Recent studies on carcass utilization by grizzly bears (Green and Mattson 1987, Green 1994), effects of the 1988 drought and fires (Lemke 1989, Singer et al. 1989, Merrill and Boyce 1991), the ungulate prey base for wolves, and potential impacts of wolves (Garton et al. 1990, Singer 1990, YNP et al. 1990) have provided information on elk population dynamics and mortality. However, no recent information is available on the extent and age/sex structure of early and mid-winter mortality within the northern Yellowstone elk herd. Such information will be essential in determining the current status and trends in the elk population, and evaluating effects of the current natural regulation policy, wolf reintroduction, winter severity, or future management strategies. With continuing predation on the elk herd by grizzly bears, coyotes, and other predators, this knowledge will also be helpful in accurately assessing the impacts of increased predation or utilization of the northern Yellowstone elk herd by wolves or humans.

This study was initiated in December 1988 to determine the age and sex structure of early and mid-winter mortality in the northern Yellowstone elk herd.

Primary objectives of the study were:

1. Estimate the age and sex structure of mortality in the northern Yellowstone elk herd during 1988-90;
2. Determine spatial and temporal distribution and availability of carcasses;
3. Determine, when possible, cause of mortality and degree of use of carcasses by various predators species;
4. Compare, where available data make it possible, current patterns of mortality with that from earlier periods including control periods (1950's through 1970's);
5. Compare sex and age structure of mortality associated with hunted segments of the populations with that of unhunted segments remaining in the Park;
6. Compare accuracy of traditional aging techniques (tooth eruption and wear) to that of cementum analysis; and
7. Evaluate current criteria used for aging by tooth eruption and wear technique to determine if recent changes in vegetational structure of habitat are producing noticeable changes in tooth wear patterns.

Field work was conducted on the Park's northern elk winter range from January 3 through March 18, 1989, and from January 17 through March 18, 1990.

CHAPTER 2

STUDY AREA

Yellowstone National Park occupies roughly 9,065 sq km (3,500 sq mi) including portions of Wyoming, Montana, and Idaho. Straddling the Continental Divide, the Park is characterized by several broad, forested volcanic plateaus ranging in elevation from 1,500 - 3,300 m (5,000 to 11,000 ft) and bounded by mountains on all sides (Houston 1982). Underlain by sedimentary strata, the area has a history of glacial, geothermal, and volcanic activity. Meagher (1973) provided a general description of the physiography of Yellowstone. Keefer (1972) described the geology of the region.

Natural fire has greatly influenced the vegetation of Yellowstone. Prior to 1988, roughly 79% of the Park was closed canopy forest, dominated by lodgepole pine (*Pinus contorta*) (81%), generally occurring between elevations of 2,300 and 2,600 m (7,500-8,500 ft). The lodgepole pine zone consists of primarily climax lodgepole pine or seral stages with little or no spruce-fir understory. Subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) account for 9% of the forest, generally at elevations above 2,600 m (8,500 ft). Engelmann spruce is the major climax species in the subalpine zone, with douglas-fir (*Pseudotsuga menziesii*) found at lower elevations

(Despain 1973, Houston 1982). Grassland and sagebrush (*Artemisia spp.*) are located on slopes and ridges interspersed throughout the forest at higher elevations, with mesic meadows occurring on moist sites. Subalpine meadows occur on the upper plateaus and mountain slopes, while nonforested rock and tundra dominate higher elevations above (3,048 m) 10,000 feet (Knight et al. 1984).

The Northern Range - Location, Size, and Ownership

Many elk in the northern Yellowstone elk herd are seasonally migratory, moving from summer ranges within YNP to wintering areas outside the Park or in the central and northern portions of Yellowstone. Elk utilize a much smaller range in winter (mid-November to April), occupying primarily lower elevation areas along the Yellowstone, Lamar, and Gardiner rivers (Lemke et al. 1996). The study area consists of those wintering areas that were utilized by the northern Yellowstone elk herd both within and outside of the Park from 1988 through 1990 (Figure 1).

Through the 1980's, the occupied northern winter range (Figure 2) was estimated to include approximately 100,000 ha (247,100 acres) with roughly 83% of the range lying inside YNP and 17% occurring outside (Houston 1982) on Gallatin National Forest (13,600 ha), State (400 ha), or privately owned (3,000 ha) lands. However, increases in the northern elk herd over recent years have resulted in increased numbers of elk migrating north out of the Park. As a result of this and other factors, managers have observed an expansion of the herd's winter distribution both

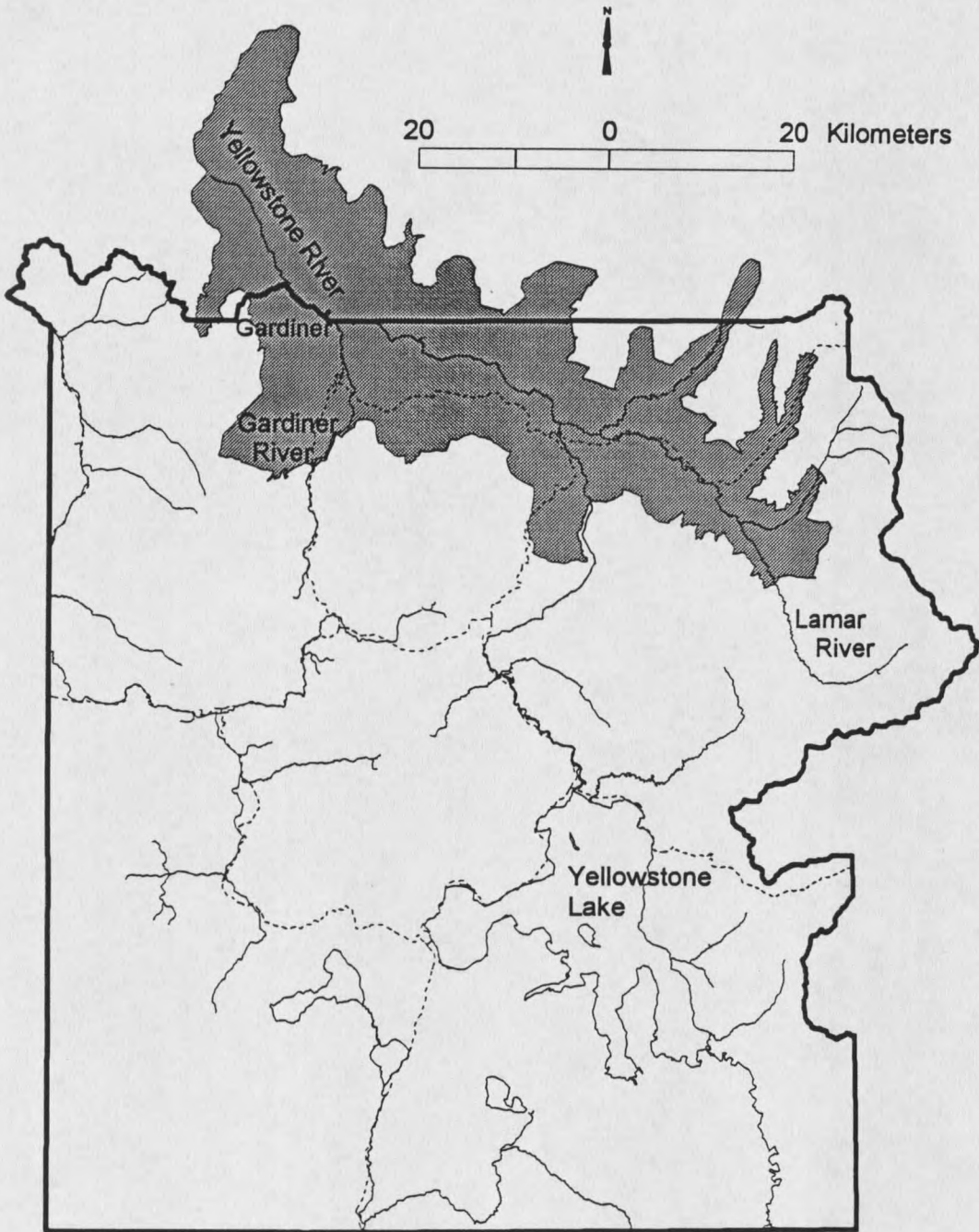


Figure 1. Map of Yellowstone National Park showing the winter range (shaded) of the northern Yellowstone elk herd.

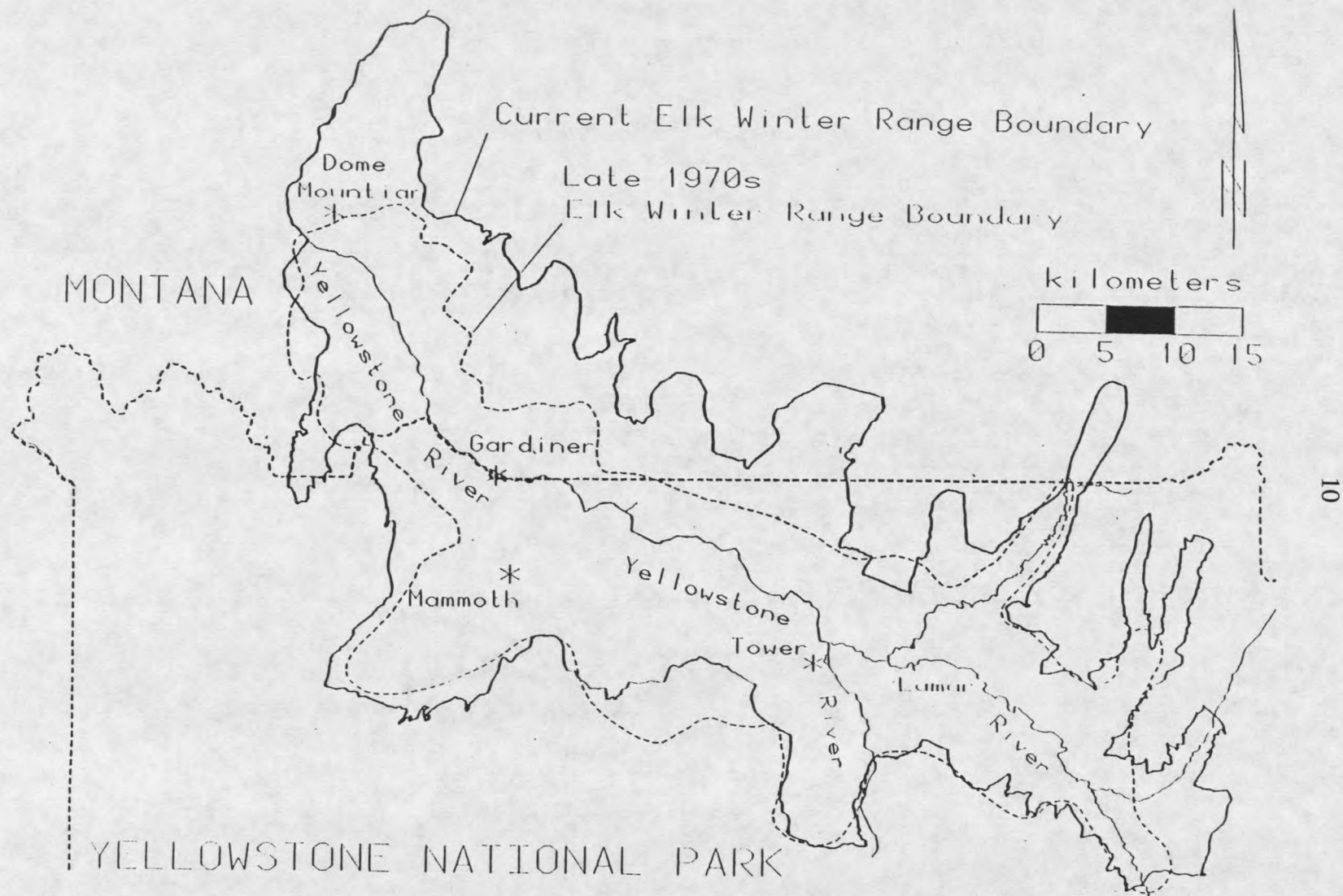


Figure 2. Boundaries of the current versus late 1970's northern Yellowstone elk winter range (from Lemke et al. 1996).

within and outside Yellowstone. Based on distribution data since 1988-89, the current occupied northern winter range area consists of 152,663 ha (377,077 acres) of primarily lower elevation areas, low-lying valleys, and high windswept ridges through portions of the Lamar, Yellowstone, and Gardiner river drainages extending from the upper Lamar River in the Park northeast to Sixmile Creek, 28 km north of YNP (Figure 2). This constitutes an increase in occupied winter range of approximately 41% including an increase in elk use north of the Park from 22,179 ha (54,800 acres) to 53,262 ha (131,610 acres) (Lemke et al. 1996). This range expansion was, in part, facilitated by the purchase private lands in historic wintering habitat north of the Park. In 1986, 1,200 ha (2,965 acres) were purchased by the State of Montana. Efforts were initiated in 1989 to protect additional winter range outside Yellowstone, resulting in the purchase of 3,500 ha (8,700 acres) by 1993, including 1,680 ha (4,148 acres) adjacent to Montana's Dome Mountain Wildlife Management Area and another 1,832 ha (4,524 acres) on the OTO Ranch and areas near Gardiner, Montana (Rocky Mountain Elk Foundation 1993).

The portion of the winter range along the Yellowstone/Lamar rivers and northern Park boundary (roughly 4,600 ha [11,367 acres]), is sometimes referred to as the "boundary line area" (BLA) (Houston 1982). Elevations on the northern winter range extend from 1,500 to 2,401 m (4,900-7,900 ft), with 52% of the range between 1,500 and 2,100 m (4,900-6,900 ft). While the majority of elk normally winter at elevations between 1,500 to 2,200 m (4,900-7,200 ft), some animals also utilize high windswept and south-facing slopes up to 2,700 m (8,800 ft), especially during low

snow periods. During more severe winters, elk from the upper and middle portions of the range, travel to low elevation areas on the lower northern range (Farnes 1991).

Climate

The climate of the Yellowstone region has been described by Meagher (1971), Dirks and Martner (1982), and Despain (1987). The climate across the northern winter range varies with topographic influences. A continental montane climate, it is characterized by long, cold winters and short, cool summers. Precipitation generally averages between 61 and 1524 cm (25 to 50 inches) per year depending on the elevation, most of which is in the form of snow. Climatic patterns vary considerably across the northern range, although most of the area lies within the semi-arid zone. In general, elevations are lower and climatic conditions somewhat milder, with many areas receiving less precipitation than the higher plateaus of the Park's interior; hence the area's ability to support more wintering ungulates (Meagher 1973, Houston 1982, Singer 1990b).

The Gardiner weather station is characteristic of the lower elevation, dry shrub/steppe habitat of the rain shadow area along the Yellowstone River north and just inside the Park. This is the driest portion of the winter range, receiving 36% less precipitation (26 cm [10-12 inches]) annually than Mammoth (40 cm [16 in]) only 6 km away, and 60% less than the Northeast Entrance (65 cm [25 in]) at the upper end of the range. In between these extremes, the Tower and Lamar Ranger Stations receive 43 cm

(17 in) and 37 cm (15 in) of annual precipitation, respectively (Soil Conservation Service (SCS), pers. commun.). From 1948 to 1993, average daily temperatures in January were: -5.5°C (22°F) at Gardiner, -7.2°C (19°F) at Mammoth, -10.5°C (13°F) at Tower and NE Entrance, and -11.1°C (12°F) at Lamar (SCS, pers. commun.).

Snow depth and characteristics appear to be the main factors limiting elk movements and use of the range. Overall, the winter range has an average annual snowfall of 500 cm (197 in) or less (Houston 1982). Wintering areas occupied by the northern elk herd generally include locations receiving 75 cm or less precipitation annually (Farnes 1991), typically lower elevation areas and high windswept ridges with less snow accumulation.

Vegetation

Winter range areas consist primarily of steppe and shrub steppe habitat with scattered small conifer stands at lower elevations and more continuous forests, sagebrush grasslands, and wet meadows occurring at higher elevations (Houston 1982, Merrill and Boyce 1991). Roughly 41% of the northern winter range is forested, primarily Douglas-fir stands with grass understory (20%). Douglas-fir occurs as small, open canopy forest stands at lower elevations generally between 1,500 and 2,100 m (4,900-6,900 ft), with larger contiguous stands occurring around the periphery of the winter range. Other forest types include lodgepole pine (13%) primarily on north slopes at 2,100 to 2,500 m (6,900-8,200 ft), Engelmann spruce/subalpine fir (8%)

along streams and on north slopes above 2,300 m (7,500 ft), whitebark pine (*Pinus albicaulis*) (<1%) on north slopes above 2,700 m (8,800 ft), and small groves of aspen (*Populus tremuloides*) (2%) occurring in flood plains, along streams, and in grassland ecotones. Upland and shrub steppe habitat types make up 55% of the area, primarily Idaho fescue (*Festuca idahoensis*) and big sagebrush (*Artemisia tridentata*) as well as bluebunch wheatgrass (*Agropyron spicatum*) and exotic grasses (in old fields). Willow (*Salix* spp.) and alder (*Alnus* spp.) are found in small stands on mesic sites and along streams, rivers, and springs (<1%) (Houston 1982).

The vegetation in the BLA and outside the Park is dominated by shrub steppe and upland grasslands with greasewood (*Sarcobatus vermiculatus*) and saltbrush (*Atriplex* spp.) common and small amounts of Douglas-fir and lodgepole pine on upper slopes. On the more xeric sites around and north of Gardiner, limber pine (*Pinus flexilis*) and Rocky Mountain juniper (*Juniperus scopulorum*) are also more common (Vore 1990). Most lower elevation, arable land is used for agriculture with bottomlands consisting of irrigated hay fields. Livestock grazing occurs on portions of the upland areas.

Fauna

During winter, the northern range supports roughly 11,600-19,000+ elk, 233-500+ bison, 1,000-2,000 mule deer, and smaller numbers of moose (<200), bighorn sheep (300-600), white-tailed deer (<100), and pronghorn (100-400)(Houston 1982,

Singer 1990). During most years, the majority of mule deer winter outside of the Park along the lower Gardiner and Yellowstone rivers, migrating back into Yellowstone and other areas each summer. Wintering pronghorn occupy a small, narrow portion of the range along the Yellowstone River near Gardiner, migrating to higher elevation areas in the Park in summer.

Predators and secondary consumers on the northern range include the grizzly bear (*Ursus arctos horribilis*), mountain lion (*Felis concolor*), coyote (*Canis latrans*), black bear (*Ursus americanus*), and wolverine (*Gulo luscus*). Scavenger species include the raven (*Corvus corax*), black-billed magpie (*Pica pica*), golden eagle (*Aquila chrysaetos*), and bald eagle (*Haliaeetus leucocephalus*).

CHAPTER 3

HISTORY OF THE NORTHERN YELLOWSTONE ELK HERD

Throughout the history of Yellowstone National Park, management of the elk population and habitat within its boundaries have been the subject of controversy. Interpretations of historical accounts of population explosions and crashes were used as rationale to support a wide range of programs within the Park including: winter feeding, extensive elk population reductions, and predator control (Houston 1979). Houston (1982) provides a detailed account of elk population dynamics and management through 1979. Kay (1990) further analyzes the principles and philosophies including the contradictions behind elk management in Yellowstone over the years. Several accounts have summarized the recent history of the herd (Lemke and Singer 1989, Singer 1991, Lemke et al. 1996).

Prior to establishment of Yellowstone National Park, wildlife in the Yellowstone area were the subject of market hunting. After the Park's establishment in 1872, hunting was allowed and encouraged within Yellowstone's boundaries, until officially banned in 1883 (Haines 1977, Lemke and Singer 1989, Boyce 1991). However, market hunting and poaching continued in the area. It was not until roughly 1890 that illegal hunting was stopped by the U.S. Army, which had taken over responsibility for

running Yellowstone in 1886 (Houston 1982). Estimates of the elk population in the Park at that time ranged from 15,000 to 40,000.

The NPS took over administration of Yellowstone in 1918. Since then, the management philosophy of the NPS within the Park has fluctuated from one of intensive manipulation to a protective "hands-off" strategy. Early on, predator control programs were carried out, resulting in the near eradication of mountain lions and the elimination of wolves from the Yellowstone area by 1925 (Weaver 1978, Lemke and Singer 1989, Fritts et al. 1997).

By the early 1900's, the northern elk herd had, by some accounts, erupted to some 30,000 animals though the accuracy of this estimate has been challenged (Houston 1982). At the same time, increased livestock grazing, fencing, and hunting outside Park boundaries also served to reduce available winter range and cut elk migration to winter ranges north of the Park (Lemke and Singer 1989). Artificial feeding was initiated in 1904, continuing until 1937. Over the next 33 years (1935-1968), the Park's official policy was that removal of elk from the northern range was necessary to maintain the population in balance with the carrying capacity of the vegetation (estimated at 4,000-5,000 elk); and large-scale elk reductions were carried out by NPS personnel from 1935 through 1968 (Boyce 1991). From 1950-1968, an average of 1,200 elk were removed annually from the northern herd, with a total of 19,976 elk removed between 1955-1968 (MTFWP 1993).

During this time, hunting also continued outside Park boundaries, and by the late 1960's the northern herd was reduced to approximately 4,000 animals. In 1968,

Congress placed a moratorium on all NPS reduction efforts, which remains in effect today. Following the moratorium on elk reductions and adoption of a "natural regulation" philosophy by the NPS (Cole 1971), the elk population increased. From 1970 through 1988, the northern elk herd was characterized by steady population growth, increased migrations north of the park, and increased hunter harvests. Houston (1982) postulated that the northern Yellowstone elk herd was regulated primarily by juvenile mortality in a density dependent fashion as affected by winter severity and population density. He predicted that the northern herd would stabilize at 12,000 to 14,000 animals.

By the late 1970's, elk counts had reached about 12,000 animals (Houston 1982). Minimum fall elk population estimates ranged from 11,149-12,941 animals in the late 1970's. From 1981 to 1988, the herd averaged 16,488 animals, reaching an estimated high of 18,913 animals counted in 1988. Ratios for the northern herd averaged 30 bulls:100 cows and 20 calves:100 cows from 1986-1988 (Singer 1990). Minimum fall populations averaged $17,409 \pm 1,377$ (SD) animals based on annual counts conducted between 1981-82 and 1994-95, excluding unreliable counts in 1988-89 and 1990-91 (Lemke et al. 1996).

Winter 1988-89

Variation in winter severity can cause substantial population fluctuations in ungulate populations in the Yellowstone area, and such fluctuations are documented

(Meagher 1971, Houston 1982). Historical records indicate that roughly 10% of the elk population die in a "normal" winter in Yellowstone, and higher than normal levels of mortality probably occur on average once every 7 years (Houston 1982). During the winter of 1988-89 on Yellowstone's northern range, elk numbers decreased by an estimated 8,000-10,000 due to a combination of factors including: hunting, drought, fire, and slightly above average winter severity (Singer et al. 1989, Singer and Schullery 1989, Boyce and Merrill 1996). Seven of the first 8 winters of the 1980's were relatively mild, bringing less than average precipitation to the Yellowstone region, while summers were unusually wet. These circumstances combined to enhance winter survival. As a result, the northern herd increased from about 16,000 in 1983 to roughly 19,000 counted during the winter in 1987-88.

During the winter and summer of 1988 (January - August), the Yellowstone area experienced one of the most severe droughts in history. Precipitation during June and July of 1988 was the least in 45 years (Farnes 1993), resulting in early plant senescence and a sharp reduction in available plant biomass. The 1988 fires burned approximately 39% of the northern winter range. Although only approximately 9% of the primary grazing areas in the northern range were affected by fire, this coupled with the major impact of the drought served to reduce available forage and thermal cover for all ungulate species. Summer grassland production was reduced more than 50% of normal due to the drought (Singer et al. 1989). As a result of this and other factors, elk began to leave summer ranges 4-6 weeks earlier than normal. Over the course of the winter, roughly 54% of the northern herd migrated outside of Park boundaries to areas to the

north, marking only the third time since 1916 that more than half of the herd moved to winter range outside the Yellowstone (Houston 1982, Singer et al. 1989).

The drought was followed by what was historically a slightly more severe winter than normal for Yellowstone in terms of snow depths and temperature extremes. Winter storms only exacerbated the severity of conditions. A record number of elk migrated out of the Park during the winter of 1988-89. Aerial surveys counted 4,835 elk outside Yellowstone, compared to 3,845 inside, the highest single elk count ever recorded north of the Park up to that time. Based on this count, a record 8-9,000 elk (estimated) migrated out of YNP in 1988-89 (Singer and Lemke 1989, MTFWP 1993). They also migrated 4-8 weeks earlier than usual (in the 1980's). Large groups of animals also remained in relatively small areas, especially along the Park boundary, intensively using and depleting available forage (Lemke and Singer 1989).

Studies of condition based on analysis of urine samples showed many elk entered the winter in poorer condition than usual as a result of the reduced forage availability caused by drought and high elk numbers (Farnes 1993; Lemke and Singer 1989; Frank 1990; DelGuidice et al. 1991a, b; Frank and McNaughton 1992). Heavy snows contributed to nutritional deprivation reducing available grasses and increasing energy expenditures/demands for locomotion and foraging (Parker et al. 1984, DelGuidice et al. 1991), resulting in substantial ungulate mortality.

Late season hunt quotas were increased during the 1988-89 season in an attempt to reduce pressure on the winter range. Hunters took an estimated 14-16% of the herd. Another 24-27% of the elk herd died from malnutrition and related causes during the

winter of 1988-89 (Singer 1990). All factors combined resulted in an estimated decline in the northern Yellowstone elk population of roughly 40%, with counts down to 10,908 animals by late winter (Singer 1990). Estimates based on computer modeling of count data show that roughly 18,506 to 20,358 elk were present in the northern herd during early winter 1988-89. By mid-April, the same model estimated the population at between 11,801 and 13,137 elk (Lemke and Singer 1989).

Since the large die-off during the winter of 1988-89, elk numbers have gradually increased with some fluctuations, reaching a high in 1994 of some 19,045 animals counted (Lemke et al. 1996).

Sex and Age Composition of the Herd

Distinct segments have been identified and are generally recognized within the northern Yellowstone elk herd (Craighead et al. 1972; Houston 1979, 1982; Vore 1990). These include "migratory" animals, that occupy home ranges east of the Yellowstone River, summering mostly within Yellowstone National Park and wintering outside Park boundaries, "resident" elk, which occupy home ranges east of the Yellowstone River (either within or outside the Park) remaining within this general area throughout the year, and "West River" elk, which summer in the Gardner's Hole area south of the Yellowstone River, wintering in the BLA on the Park's northern border:

Studies have revealed differences in the sex and age composition of the various herd segments, making any statements about overall herd composition difficult.

Houston (1982) noted that the composition of age and sex samples sometimes differed within the winter range, with the proportion of young (calves) being lower on the upper winter range (Lamar Valley area). His interpretation of these differences was that, "given the fidelity to home ranges of some females, ... the dynamics of herd segments on the upper range (i.e. production and survival of young, age distribution of females, etc.) differs from those segments wintering farther down the Yellowstone River. These latter groups may be hunted more frequently at higher population levels and some also winter at lower elevations and contend with less severe snow conditions" (Houston 1982).

Vore (1990) also documented lower calf:cow ratios on the upper range and noted calf:cow ratios found in groups of resident elk differed from those for groups of primarily migratory animals. Singer and Harting (1988) attributed the differences seen in calf:cow ratios between the upper and lower range to predation.

Data from Houston (1982) show that prior to the intensive Park removals begun in 1956, the composition of the overall winter populations fluctuated around $57 \pm 3.3\%$ cows (1 year old or greater), $16 \pm 3.2\%$ calves, and $27 \pm 2.3\%$ bulls (Table 1). During 1964-70, a period of much lower winter populations, cows averaged $53 \pm 3.8\%$, calves $22 \pm 2.6\%$, and bulls $25 \pm 4\%$ of the population. In the 1970's, the overall population composition changed steadily as elk numbers increased, with the proportion of adult males, yearling males, and calves decreasing while adult females increased. From 1973-1979, when winter populations rebounded to over 10,000 animals, cows averaged $64 \pm 6.7\%$, calves $16 \pm 2\%$, and bulls $20 \pm 5.5\%$ of the

population (Table 1). Complete data are not available on herd age and sex composition between 1980 and 1985 due to poor census conditions and questionable accuracy or missing data for some age groups.

Table 1. Summary/comparison of sex and age composition of elk classified during early winter surveys on the northern winter range (Houston 1982, F.J. Singer 1990, unpubl. data, Mack and Singer 1992).

Winter Period	Number Classified	Percent		
		Cows	Calves	Bulls
Prior to 1956 ^a		57	16	27
1964-70 ^a		53	22	25
1973-79 ^a		64	16	20
1979-80 to 84-85 ^b				
1985-86	5363	56	27	17
1986-87	5574	64	21	15
1987-88	4697	61	24	15
1988-89	2613	70	17	13
1989-90	5479	69	13	17

^a Numbers are from Houston 1982.

^b Complete data for all classes not available for these years.

Early winter classification data on the northern Yellowstone elk herd (F.J. Singer 1990, unpubl. data; Mack and Singer 1992, Lemke et al. 1996) indicate that during the winter of 1988-89, the population consisted of approximately 70% cows, 17% calves, and 13% bulls. In 1989-90, after a decrease in the population due to drought, winter kill, and increased harvest, the composition of the northern

Yellowstone herd was 69% cows, 13% calves, and 17% bulls (Table 1).

From 1986 until 1988, data from early winter classifications on the northern herd revealed that calf ratios ranged from 33 to 48 calves:100 cows and bull ratios ranged from 23 to 30 bulls:100 cows (Mack and Singer 1992). As stated, calf:cow ratios have typically been higher for elk that move outside of the Park in winter. Bull ratios for the northern herd are affected by the number of bulls harvested outside of YNP boundaries. Since 1987, the number of either-sex permits has been reduced resulting in the higher bull:cow ratios listed above (Lemke and Singer 1989). Early winter classification surveys in 1987-88 showed 24 bulls:100 cows and 40 calves:100 cows and late winter counts were 30 bulls:100 cows and 25 calves:100 cows (Mack and Singer 1992).

By early winter 1988-89, aerial counts of the northern herd revealed 19 bulls:100 cows and 24 calves:100 cows. As the winter progressed, deep crusted snow caused elk to split into smaller groups with a greater tendency to seek cover. This also served to decrease observability and the reliability of any count/classification data. By late winter, bull ratios were down to 18:100 cows and calf ratios reached 7 calves:100 cows (Singer et al. 1989).

By early winter 1989-90, counts revealed that calf ratios were again low with 19 calves:100 cows, while bull ratios appeared to increased to 25 bulls:100 cows. This apparent increase may be a function of greater observability of bulls at the time of the 1989-90 classification surveys. Late winter classifications during 1989-90 revealed approximately 17 bulls:100 cows and 20 calves:100 cows.

CHAPTER 4

THE GARDINER LATE ELK HUNT

History of the Gardiner Late Hunt

In addition to the general elk hunt in Montana, a special late season, known as the "Gardiner late hunt," was initiated with the specific purpose of harvesting elk moving north out of Yellowstone National Park. It has been one of the most popular and successful elk hunts in the State of Montana with more than 5,000 individuals applying for a tag and a harvest success rate over the last 10 years of between 80 and 90% (compared to an average success rate of 15 or 20% statewide) (Lemke and Singer 1989). This hunt generally runs between early December and mid-February depending upon elk dynamics, weather, and forage conditions, all of which influence the number of animals migrating to wintering areas outside the Park boundary. Since 1990, the opening date for the late hunt has been delayed until early January, allowing more animals to move through the boundary line area and better dispersal over wintering areas north of Yellowstone. Erickson (1981) and Houston (1982) have summarized the history of the Gardiner late hunt. Lemke et. al. (1996) provides an update through 1995 including revised data on population counts, harvests, and winter distribution.

Elk were hunted on the winter range around Gardiner prior to establishment of Yellowstone National Park in 1872. Since this time, annual hunter harvests in the area have ranged from less than 25 elk in 1929 to 6,539 in 1943. The goal of the hunt was to control the size of the Yellowstone elk population by killing as many animals as possible once they left the Park (Lemke et al. 1996). Prior to 1968, the Gardiner late hunt was open to any resident or nonresident with a valid Montana elk tag. No limits were placed on participation, no harvest quotas were established, which resulted in elimination of much of the migratory segment of the herd (Lemke and Singer 1989).

By 1968, only 3,172 elk were counted during aerial surveys of the northern Yellowstone herd (MTFWP 1993). These herd reductions prompted the close of the late hunt between 1969 and 1975. Under the moratorium on control efforts within YNP, elk numbers increased and, by 1976, larger numbers of elk were migrating outside Yellowstone. The percent of the northern elk herd migrating from the Park averaged 7% between 1970 to 1974 (Houston 1982) and 17% from 1975 to 1988.

The Gardiner late hunt was reinstated in 1976. Since then, it has been conducted as a limited access hunt using a drawing system for issuance of special late season antlerless and either-sex permits to more strictly control the type and number of elk harvested (MTFWP 1993). The goal of MTFWP is to influence elk movements outside the Park and thus better distribute animals and harvest over the winter range. Consequently, the late hunt has evolved from an unregulated population-control effort into a regulated hunt aimed at: protecting and maintaining a productive winter range; regulating the harvest of elk to maintain a significantly large migration of elk out of

Yellowstone; and providing a late season hunting opportunity (Lemke and Singer 1989).

Several new restrictions, including mandatory check-in and check-out, have been added in recent years to assure limited access and account for all elk harvested. The hunt area has been subdivided into smaller hunting units that may or may not be open to hunting. In addition, hunting has been limited to specific 2- and 4-day periods with non-hunting periods in between to facilitate movement of elk across the Park boundary and promote dispersal across the winter range (Lemke and Singer 1989).

Annual harvest during the late season has been varied over the years, with an average of $1,192 \pm 661$ elk taken from 1981-82 through 1994-95 (Lemke et al. 1996). Late season harvests represented less than 1% of the prehunt population from 1970-1974 (Houston 1982:17), 8% from 1975 to 1980, and 9% from 1981 to 1988. Between 1988-89 and 1994-95, late hunt harvests averaged $1,323 \pm 833$ elk compared to $1,061 \pm 461$ animals removed from 1981-82 through 1987-88, an increase of approximately 25% (Lemke et al. 1996).

Known illegal kill and wounding loss during the late hunt has averaged 42 elk per year or 2-7% of the legal harvest (Lemke et al. 1996). Bulls represented the majority of the late season harvest until 1981-82 and the majority of the general season harvest until 1986-87. Between 1975-76 and 1981-82 an average of 1,350 either-sex tags were issued annually for the late hunt compared to only 250 antlerless tags (all of which were issued during 1980-81 and 1981-82). Therefore, harvest prior to 1981 had proportionally less effect (if any) upon population growth (Singer 1990). Since 1982,

the number of antlerless tags as a percent of total permits issued has increased. The lowest number of either-sex tags ever issued ($n = 44$) occurred in the 1989-90 season following the high mortalities of 1988-89 (MTFWP 1988).

1988-1989 Gardiner Late Hunt

Initially the 1988-89 Gardiner late hunt was set as a 36 day season running from December 9, 1988 through February 13, 1989, with 54 either-sex and 1,800 antlerless permits issued. Early in the season (December 9 -31), both antlerless and either-sex permits were valid for a specific 4-day period (Friday through Monday). Beginning in January 1989, antlerless permits were valid for a specific 2-day period (Friday-Saturday or Sunday-Monday) and either-sex permits were valid for the entire 4-day period (Friday through Monday). In response to the large numbers of elk migrating from Yellowstone and in an attempt to balance elk numbers with available forage on the winter range, MTFWP drew additional permits. Thus, 760 antlerless permits were added during established season dates starting January 23, 1989 (MTFWP 1993). In addition, the season was extended 1 week with an additional 510 permits added (170 permits per each 2-day period) between February 15-20, 1989. Ninety-eight antlerless permits were also issued to those applying as a party, bringing the total number of permits issued for the 44-day period from December 9, 1988 to February 20, 1989 to 54 either-sex and 3,168 antlerless (MTFWP 1993).

Hunter participation for the 1988-89 late hunt was estimated at 77% ($n =$

2,486), with an overall harvest season success rate of 95%, the highest ever recorded for the Gardiner late hunt.

Hunt areas 2, 3, 4, 5, and 6 were open to hunting (Figures 3 and 4) with Area 2 extending from Bear Creek to Cedar Creek, Area 3 from Cedar Creek to the Dome Mountain-Red Mountain divide, Area 4 covering Dome Mountain-Red Mountain divide to Sixmile Creek, Area 5 from the Yellowstone National Park boundary to Mol Heron Creek, including the Trestle Ranch, and Area 6 covering the west side of the Yellowstone River from Mol Heron to Wigwam Creek. Hunters were assigned to hunt in certain areas as indicated by a color coding system for permits. However, as additional permits were issued some hunters chose not to hunt in their assigned areas. Also, during the additional week extension, hunters were told to hunt wherever they wished within the Area 6 perimeter (which was incorrectly shown on the map provided as the entire area open to hunting in Hunt District 313.)

No data are available regarding when specific hunt areas were open. Apparently, Areas 2, 3, and 5 were open during the beginning of the hunt. Areas 4 and 6 were not opened until after the arrival of migratory elk, approximately January 20 and January 27, 1989, respectively.

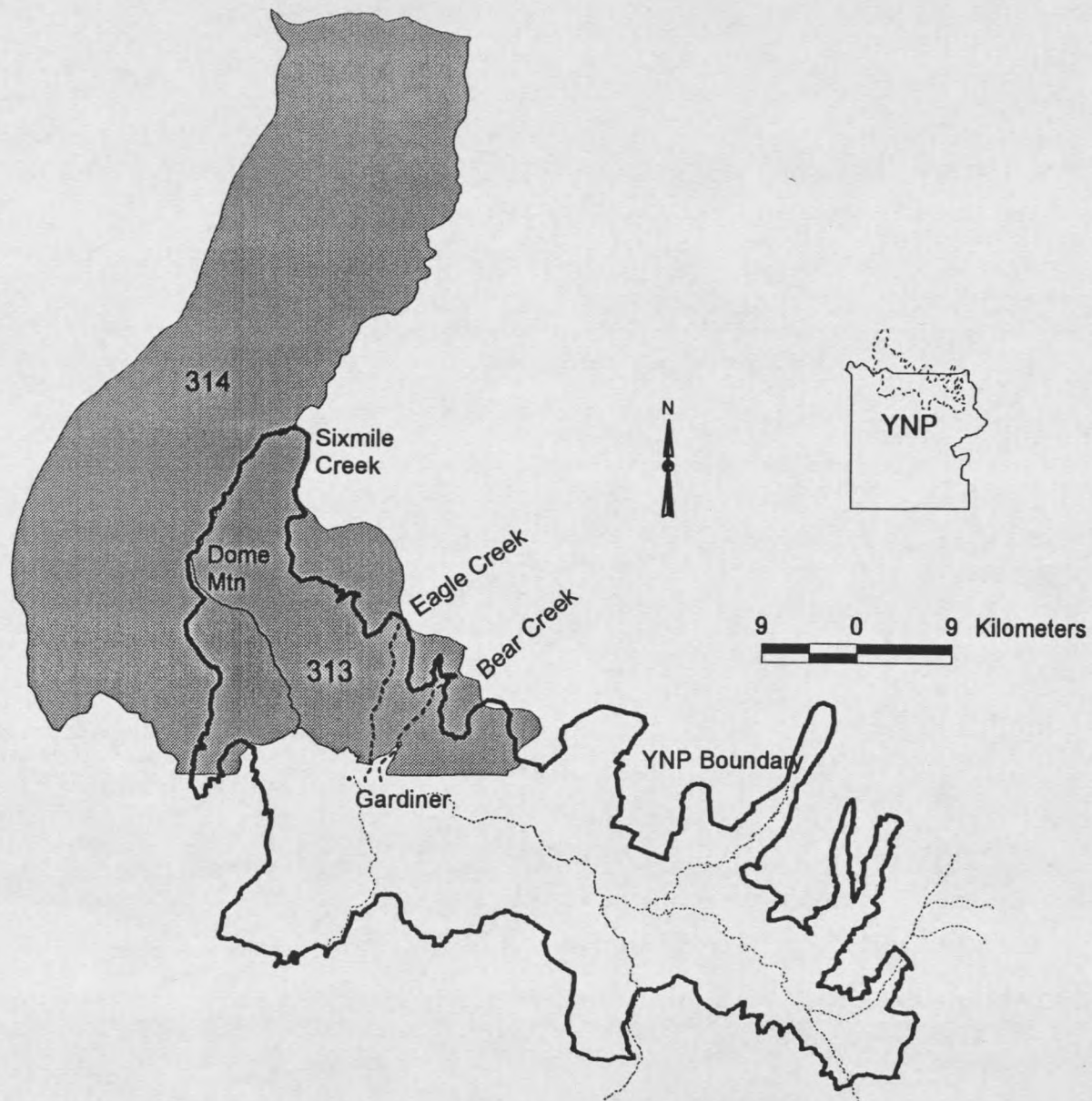


Figure 3. Montana hunting district boundaries north of Yellowstone National Park.

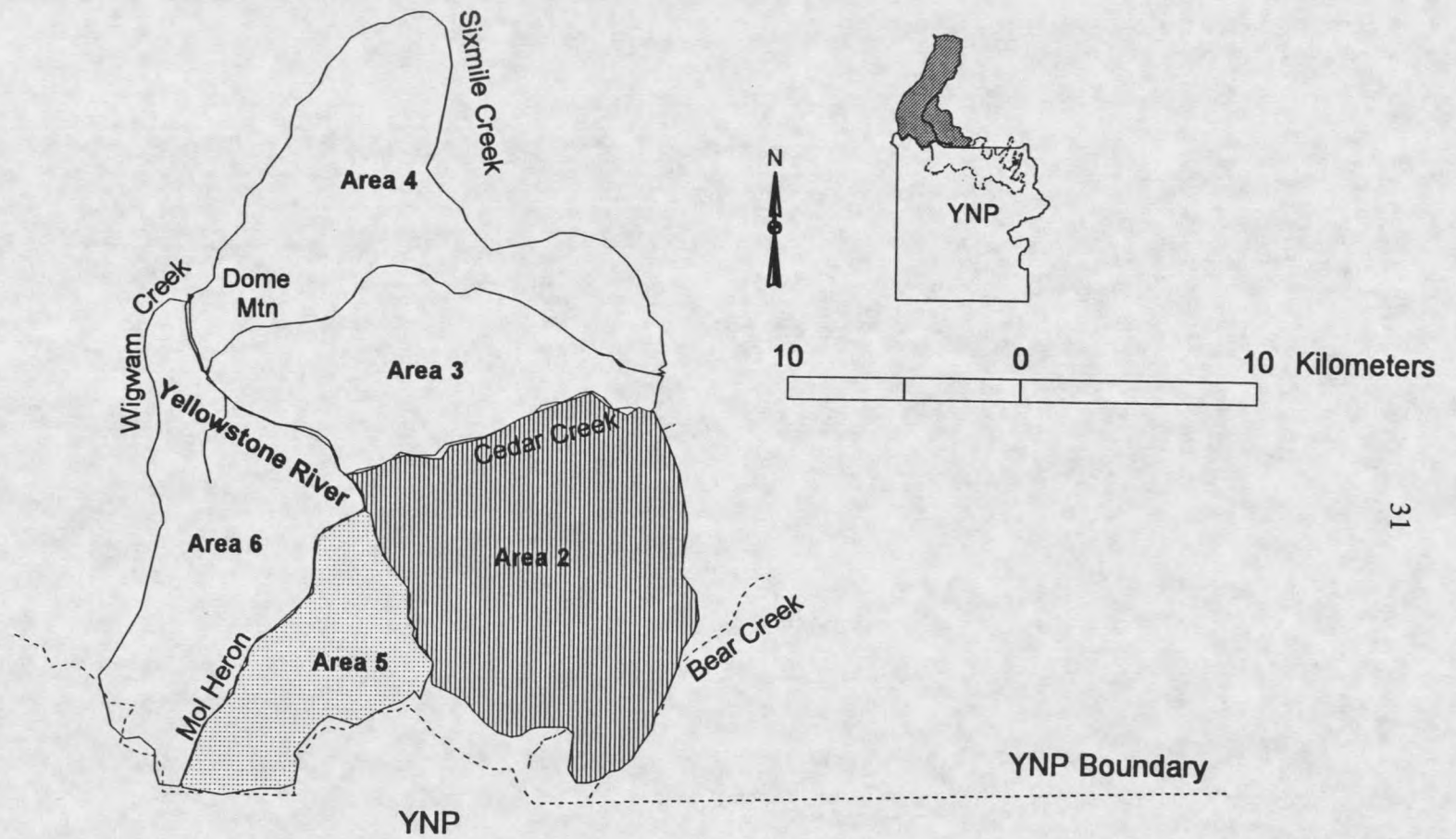


Figure 4. Late hunt administrative hunting areas for the 1988-89 season.

1989-90 Gardiner Late Hunt

The 1989-90 Gardiner late hunt was conducted during 8 separate periods between December 8, 1989 and February 12, 1990. Both antlerless and either-sex permits were valid for a specific 4-day period (Friday through Monday). A 3-day no hunting period was established between hunts to allow for migration of elk to winter ranges farther north and to promote even distribution of elk over the winter range. Permit numbers were reduced from 1988-89 levels to 44 either-sex and 830 antlerless.

Hunter participation for the 1989-90 late hunt was 79% (n = 690). The overall harvest success rate for those actually hunting during the late season was 61%; 87% for hunters with either-sex tags and 60% for those with antlerless permits (MTFWP 1993). During 1989-90, Hunt Areas 2, 3, 4, 5 were open to hunting. Area 2, 3, and 4 boundaries remained constant between the 1988-89 and 1989-90 hunts. Area 5 was revised to extend from Beattie Gulch to Cinnabar Mountain, while Area 6 was eliminated in the 1989-90 season. Hunters were assigned to hunt in certain areas as indicated by a color coding system for permits.

Methods

Elk harvest information for the late elk hunt was collected by MTFWP personnel at the check station north of Gardiner, Montana. Hunters were required to check in and out of the area for each hunt. Data were recorded on individual kill cards

for all harvested animals including: date checked, check station operator, hunter name, tag type, date of kill, hunt area, location of the kill (accurate to the drainage), sex, age (based on tooth eruption/wear), diastema length, antler length and number of points (left and right), whether lactating or pregnant, and sex and weight of fetus, if present. Diastema length, general condition, and fetus information were collected and weights of animals taken intermittently starting in the early 1980's. Age and diastema information were collected primarily from cows and calves.

All recorded harvest information for the 1988-89 and 1989-90 Gardiner late hunts, a total of 2,848 individual records, were entered into a computer database for analysis. Elk harvest and hunting statistics were also taken from the MTFWP's Gardiner late hunt annual reports (MTFWP 1991, 1992, 1993). The reports generally classified elk by sex as cows, spikes or mature bulls and by age as calves, yearlings, prime-age (2-8 year-olds), and 9 years-old or greater. More specific age classifications utilized 8 age categories (0.5, 1.5, 2.5, 3-5, 6-8, 9-11, 12-14, and 15+).

A Chi-square test for homogeneity (χ^2 statistic) was used to determine differences in relative frequency distributions of different kill locations within each harvest. In addition, the Chi-square test for homogeneity was employed to determine differences in the number of cows, calves, and bulls harvested and the number of antlerless and either-sex tags issued between the 1988-89 and 1989-90 seasons.

To compare the age structures or differences in relative frequency distributions of various age classes for 1988-89 and 1989-90 harvests, a Chi-square test for homogeneity was used. The Chi-square test for homogeneity assesses whether the age

structures of the 1988-89 and 1989-90 harvests could have arisen from the same underlying age distribution. For the purpose of analysis, elk were initially grouped into cow, calf, and bull categories and then placed into 8 age classes coinciding with MTFWP age groupings to facilitate comparisons and to avoid problems where significance tests were suspect due to expected frequencies of less than 2.

Data on the age structure of previous (1982-83 to 1987-88) and more recent harvests (1990-91 through 1992-93) were obtained from MTFWP. All data reflect eruption/wear age estimates. Chi-square tests for homogeneity were used to assess differences in the relative frequency distributions of various age classes between harvests, based on eruption/wear age estimates. Age structure data from the 1988-89 Gardiner late elk harvest were compared to previous years' harvest data, and similarly, the age structure of the 1989-90 harvest was compared to subsequent harvests.

The Chi-square test for homogeneity was also employed to assess differences in the number of cows, calves, and adult bulls harvested in the Gardiner late hunt compared to that in the wild population as estimated by early winter classification counts (Mack and Singer 1992). Elk were categorized into three groups: adult cows, adult bulls, and calves (animals < 1 year-old), as more specific age information is not available for the wild population. I also attempted to correct the relative proportion of cows, calves, and bulls in the live population to account for any bias from differential mortality or sightability, etc., using the total population estimate derived from the Pop-II model (Mack and Singer 1992). This model uses available harvest, mortality, and classification data to develop population estimates.

Fall/early winter population estimates and classifications were obtained from aerial counts conducted using fixed-wing aircraft (Mack and Singer 1992, Lemke et al 1996). While total aerial counts were attempted, it is recognized that these are underestimates. Based on several years of aerial surveys, the highest counts have been obtained during December-January when elk concentrate on open, snow-covered grasslands and steppes and use of forested habitats is low (Lemke et al. 1996). Maximum counts were obtained after the general fall hunting season (November) and prior to the late hunts (mid-December to January).

Survey procedures changed after the 1970's, with multiple aircraft being used to complete the count in 1 day. Since 1985, elk numbers have been estimated annually from 2 or 3 aerial surveys of the entire northern range. Surveys are conducted over 68 count units delineated across the winter range inside Yellowstone, north of and along the Park boundary, and north of Dome Mountain.

Results

1988-1989 Gardiner Late Hunt

A total of 2,412 elk were harvested during the 1988-89 late hunt, including 61 known illegal kills. Of the illegal kills for which age and/or sex information were available, 15 were calves (11 females, 2 males, 2 sex unknown), 11 yearlings (2 females, 9 males), and 19 were age 2.5 or older (17 females, 2 males). Ages were estimated for 2,409 harvested elk using eruption/wear; age was known for 3 animals.

Seventy-seven percent of harvested elk were cows ($n = 1865$), 20% were calves ($n = 476$), and 3% were bulls ($n = 67$) (Table 2). Females accounted for 90% of the harvest overall ($n = 2,161$) with the largest portion of the cow harvest consisting of animals in the 3.5-5.5 year-old age group (27%, $n = 575$), followed by 6.5-8.5 year-olds (15%, $n = 318$). By far the largest portion of the male harvest was calves (73%, $n = 177$), with 3.5-5.5 year-olds constituting 5% ($n = 13$) and 6.5-8.5 year-olds 6% ($n = 14$) of the harvest. Combining both sexes, the 3.5-8.5 year-old group and calves constituted the largest portion of the harvest, 24% and 20%, respectively.

Thirty-two percent of cows ($n = 689$) were 6.5 years of age or greater, while only 8% of bulls ($n = 19$) fell into this age group. Seventeen percent of cows ($n = 371$) were 9.5 years or greater while only 2% of bulls ($n = 5$) were, and 10% of cows ($n = 211$) were 12.5 years of age or greater while less than 1% of bulls were in this age category.

Table 2. Age distribution of 2,409 elk harvested in the 1988-89 Gardiner late hunt based on eruption/wear age estimation (includes illegally harvested animals). Percentages are based on the 2409 elk.

	Estimated Age								
	0.5	1.5	2.5	3.5-5.5	6.5-8.5	9.5-11.5	12.5-14.5	15+	Unk
Females	296	291	197	575	318	160	87	124	113
Males	177	15	2	13	14	4	1	0	18
Total	476	306	199	588	332	164	88	124	132
Percent	19.7	12	8.2	24.4	13.8	6.8	3.6	5.1	5.5

Maximum ages recorded for elk during the 1988-89 season, as determined by eruption/wear aging, were 21.5 years for cows, and 13.5 years for bulls.

The majority of elk, 81% (n = 1,908) were harvested in Area 2. A breakdown of the remainder of the harvest by area included: 6% (n = 147) taken in Area 3, 1% (n = 28) in Area 4, 8% (n = 197) in Area 5, and 3% (n = 79) in Area 6 (Table 3, Appendix A).

Table 3. Location, distribution, and percent of total harvest for 1988-89 Gardiner late elk hunt. Percentages are based on 2,359 elk for which location of kill was known.

Hunt Area	Location	Number of Elk	Percent (of 2,359)
Area 2		1911	81.0
	Airport	115	4.9
	Bassett Creek	36	1.5
	Bear Creek	48	2.0
	Eagle Creek	665	28.2
	Hitching Post	45	1.9
	Little Trail Creek	245	10.4
	LaDuke	119	5.0
	Phelps Creek	89	3.8
	Rex Coulee	97	3.6
	Trail Creek	230	9.8
	Travertine Flats	65	2.8
Area 3		147	6.2
	Slip & Slide	117	4.9
Area 4		28	1.2
	Daily Lake	18	0.76
Area 5		197	8.4
	Beattie Gulch	33	1.4
	Cinnabar Mtn.	146	6.2
Area 6		75	3.2
	Cutler Lake	12	0.5

1989-90 Gardiner Late Hunt

A total of 432 elk were harvested during the 1989-1990 late season including 9 known illegal kills (Table 4). Of the 423 elk legally taken, 77% were cows (n = 325), 14% were calves (n = 58), and 9% were bulls (n = 40). Illegal kills included 1 male of unknown age, 1 female calf, 4 yearling bulls, and 3 females age 2.5 or older, bringing the composition of elk taken to 76% cows (328), 14% calves (59), and 10% bulls (44). Females accounted for 85% of the harvest (n = 369) with the largest portion consisting of animals in the 3.5-5.5 year-old age group (30%, n = 117), followed by 6.5-8.5 year-olds (18%, n = 67). The largest portion of the male harvest was made up of calves (29%, n = 18) with yearlings, 3.5-5.5, and 6.5-8.5 year-olds each constituting 10% of the harvest (n = 6 ea). Age was not available for 21 harvested males). Combining both sexes, the 3.5-5.5 year-old age group made up the largest portion of the harvest (29%) followed by the 6.5-8.5 year-old group.

Thirty-four percent of cows (n = 126) were ≥ 6.5 years of age while only 14% of bulls (n = 9) fell into this age group. In addition, 16% of cows (n = 59) were ≥ 9.5 years old while only 5% of bulls (n = 3) were, and 9% of cows (n = 35) were ≥ 12.5 years of age while no bulls were in this age category.

Table 4. Age distribution of 432 elk harvested in the 1989-90 Gardiner late hunt based on eruption/wear age estimation (includes illegally harvested animals). Percentages are based on the 432 elk.

	Estimated Age								Unk
	0.5	1.5	2.5	3.5-5.5	6.5-8.5	9.5-11.5	12.5-14.5	15+	
Female	41	26	38	117	67	24	16	19	21
Male	18	6	3	6	6	3	0	0	21
Number	59	32	41	123	73	27	16	19	42
Percent	13.7	7.4	9.5	28.5	16.9	6.3	3.7	4.3	9.7

Maximum ages recorded for elk during the 1989-90 late season as determined by eruption/wear aging were 20.5 years for cows and 10.5 years for bulls. The majority of elk, 61% (n = 256), were harvested in Area 2 while 11% (n = 45) were taken in Area 3, 19% (n = 78) in Area 4, and 10% (n = 42) in Area 5 (Table 5). A further breakdown of location of the harvest is provided in Appendix B.

Table 5. Location, distribution, and percent of total harvest for 1989-90 Gardiner late elk hunt. Percentages are based on 421 elk for which location of kill was known.

Hunt Area	Location	Number of Elk	Percent (of 421)
Area 2		256	60.8
	Airport	3	0.7
	Bear Creek	15	3.6
	Eagle Creek	92	21.9
	Hitching Post	17	4.0
	Little Trail Creek	23	5.5
	LaDuke	11	2.6
	Phelps Creek	9	2.1
	Rex Coulee	12	2.9
	Trail Creek	20	4.8
Area 3		45	10.7
	Slip & Slide	31	7.4
Area 4		78	18.5
	Daily Lake	64	15.2
Area 5		42	9.8
	Beattie Gulch	16	3.8
	Cinnabar Mtn.	24	5.7

Location of kill differed significantly in the 1988-89 and 1989-90 late hunts ($\chi^2 = 325$, 4 d.f., $P < 0.0005$), despite the fact that the majority of elk were killed in Area 2 during both years. In 1988-89, over 80% of harvested elk were taken in Area 2, while the harvest was spread out over all open hunt areas the following year. There was no significant difference in the location of kill for male versus female elk during 1988-89 ($\chi^2 = 6.12$, 4 d.f., $P = 0.19$) or 1989-90 ($\chi^2 = 3.43$, 3 d.f., $P = 0.33$).

The hypothesis that the age distribution of the harvest was the same for both 1988-89 and 1989-90 was rejected. Percentage of bulls, cows, and calves in the harvest (Table 6) differed significantly between the 2 years ($\chi^2 = 58.82$, 2 d.f., $P < 0.0005$), even when bulls were eliminated from the comparison because of the potential bias due to limited availability of either-sex permits ($\chi^2 = 5.45$, 1 d.f., $P = 0.02$). When elk were grouped into 8 different age categories, age structure of the harvest (based on eruption/wear ages) also differed significantly between the 2 years ($\chi^2 = 22.02$, 7 d.f., $P = 0.003$), again even when adult bulls (≤ 1.5 years-of-age) were eliminated from the analysis ($\chi^2 = 22.7$, 7 d.f., $P = 0.002$).

Table 6. Cows, calves, and bulls harvested during the 1988-89 and 1989-90 Gardiner late hunts including known illegal kills [number (percent of total animals harvested)].

Winter Period	Number Harvested ^a	Number (Percent)		
		Cows	Calves	Bulls
1988-89	2412	1865 (77)	476 (20)	67 (3)
1989-90	432	328 (76)	59 (14)	44 (10)

Age and sex were unknown for 4 animals in 1988-89 and 1 animal in 1989-90.

Comparing the 2 years, females accounted for the majority of the harvest during 1988-89 and 1989-90, with the largest number of animals being 3.5-5.5 and 6.5-8.5 year-olds (Table 7). Calves accounted for the largest portion of the male harvest during both years (73% in 1988-89, 29% in 1989-90) with 3.5-5.5 and 6.5-8.5 year-olds making up most of the remainder of the harvest. Combining the sexes, most of the 1988-89 harvest consisted of 3.5-5.5 year-olds (24%) and calves (20%) compared to 1989-90 when harvested animals consisted primarily of 3.5-5.5 (29%) and 6.5-8.5 year-olds (17%). Only 14% of the 1989-90 harvest consisted of calves.

Comparison of Age Structure of Harvest with Live Population

The gross age/sex distribution (cows, calves, and bulls) of the harvest and that of the live population, as determined by early winter classification surveys on the northern winter range, were significantly different during 1988-89 ($\chi^2 = 183.2$, 2 d.f. $P < 0.0005$) and 1989-90 ($\chi^2 = 14.7$, 2 d.f. $P = 0.001$) (Table 8). However, when bulls were eliminated from consideration, due to limited antlered permit availability, no statistical difference was apparent between elk classified (percentage of cows or calves) in the live population versus the harvest for either the 1988-89 or 1989-90 late hunt ($\chi^2 = 0.666$, 1 d.f. $P = 0.414$ and $\chi^2 = 0.139$, 1 d.f. $P = 0.709$, respectively).

Table 7. Comparison of percentage of male and female elk in each age group for the 1988-89 and 1989-90 Gardiner late hunt based on eruption/wear age estimation. Percent is of total females or males harvested that year.

Year	Sex	Estimated Age Categories									Total ^a
		0.5	1.5	2.5	3.5-5.5	6.5-8.5	9.5-11.5	12.5-14.5	15+	Unk	
88-89	Female	14	13	9	27	15	7	4	6	6	2161
	Male	73	6	4	5	6	2	>1	0	33	244
89-90	Female	11	7	10	32	19	7	5	5	5	369
	Male	29	10	5	10	10	5	0	0	7	63

^a Total number of females or males harvested that year.

Table 8. Comparison of number (and percentage) of cows, calves, and bulls in the Gardiner late hunt harvest and estimated in the wild population in 1988-89.

Source	Population Distribution		
	Cows	Calves	Bulls
88-89 Hunt Harvest	1865 (77)	476 (20)	67 (3)
Population Estimate ^a	14419(70)	3460 (17)	2740 (13)
89-90 Hunt Harvest	328(76)	59(14)	44(10)
Population Estimate ^a	12391(69)	2354(13)	3098(17)

^a Based on early winter classification counts corrected using Pop-II population estimate.

Comparison of Age Structure of the Late Hunt Harvests from 1982-1993

I also compared the age structures of Gardiner late elk hunt harvests from 1982-83 through 1992-93 (Table 9). The hypothesis that age distribution of the 1988-89 late harvest was the same as that for previous years was rejected for all but the 1987-88 season ($\chi^2 = 9.4$, 7 d.f. $P = 0.2$) (Table 10). There was no significant difference between the age structures of the 1987-88 and 1988-89 late harvests despite the fact that 1,850 permits were issued with only 214 elk taken in 1987-88 compared to 3,222 tags issued in 1988-89 and 2,355 elk harvested. Similarly, there was a significant difference in the age distribution of the 1989-90 harvest and that of all subsequent years except 1990-91 ($\chi^2 = 10.9$, 7 d.f. $P = 0.143$) (Table 11).

Table 9. Age classification of elk harvested and aged in Gardiner Late elk hunts 1982-83 through 1992-1993 [number (percent of total)] and minimum prehunt population estimates based on census counts.

Age Class	Year										
	1982-83	1983-84	1984-85	1985-86	1986-87	1987-88	1988-89 ^a	1989-90 ^a	1990-91	1991-92	1992-93
0.5	239 (17)	398 (25)	288 (24)	204 (20)	270 (24)	58 (26)	476 (20)	59 (14)	144 (21)	401(22)	407 (26)
1.5	175 (12)	219 (14)	131 (11)	92 (9)	77 (9)	31 (14)	306 (13)	32 (7)	51 (7)	179 (10)	202 (13)
2.5	179 (13)	73 (5)	87 (7)	97 (9)	58 (7)	17 (8)	199 (8)	41 (9)	66 (9)	120 (7)	144 (9)
3.5-5.5	304 (22)	317 (20)	275 (23)	269 (26)	216 (26)	44 (20)	588 (24)	123 (28)	208 (30)	394 (22)	322 (21)
6.5-8.5	282 (20)	297 (18)	167 (14)	163 (16)	108 (13)	23 (10)	332 (14)	73 (17)	89 (13)	310 (17)	204 (13)
9.5-11.5	96 (7)	172 (11)	126 (10)	97 (9)	72 (9)	18 (8)	164 (7)	27 (6)	50 (7)	192 (11)	125 (8)
12.5-15.5	29 (2)	33 (2)	44 (4)	49 (5)	29 (3)	11 (5)	88 (4)	16 (4)	21 (3)	66 (4)	36 (2)
15.5+	21 (1)	7 (<1)	11 (1)	24 (2)	35 (4)	10 (5)	124 (5)	19 (4)	31 (4)	71 (4)	64 (4)
Unknown	87 (6)	94 (6)	72 (6)	46 (4)	43 (5)	8 (4)	132 (5)	42 (10)	35 (5)	55 (3)	66 (4)
Total ^b	1,412	1,610	1,201	1,041	845	220	2,409	432	695	1,788	1,570
Kill ^c	1,434	1,657	1,211	1,042	845	220	2,409	484	697	1,787	1,574
Min. Popu. ^d	No Count	No Count	No Count	16,885	17,901	19,316	11,148	15,805	10,287	15,587	18,066

^a Age structure data from Tables 2 & 4.

^b Includes data from kill cards plus known illegal kills where age was known.

^c Figures include check station total plus known illegal kills and wounding losses. Data revised to correct discrepancies between earlier reports and kill card information (Lemke et al. 1996).

^d Includes survey count plus estimated fall harvest and late hunt removals occurring before survey (Lemke et al. 1996).

Table 10. Summary of the Gardiner late elk season, 1982-83 through 1988-89 (MTFWP, C. Simme. unpubl. data) and Chi-square values comparing 1988-89 age distribution with previous years.

Year	# Permits ¹	# Hunters	Elk Harvested ²	Success Rate	x ² Values ³
1982-83	1600 ES, 800 A	1737	1361	78 %	x ² = 84.8, 7 d.f., P < 0.0005
1983-84	800 ES, 1600 A	1799	1551	86 %	x ² = 145.7, 7 d.f., P < 0.0005
1984-85	300 ES, 2100 A	1835	1166	63 %	x ² = 62.7, 7 d.f., P < 0.0005
1985-86	200 ES, 2200 A	1676	1009	55 %	x ² = 34.3, 7 d.f., P < 0.0005
1986-87	200 ES, 2200 A	1448	830	57 %	x ² = 19.7, 7 d.f., P = 0.006
1987-88	50 ES, 1800 A	967	214	22 %	x ² = 9.4, 7 d.f., P = 0.224
1988-89	54 ES, 3168 A	2486	2355	95 %	

¹ (ES) Either-sex permits, (A) Antlerless permits

² Legal harvest only

³ Tables 2 & 4

Table 11. Summary of the Gardiner late elk season, 1989-90 through 1992-93 (MTFWP, C. Simme. unpubl. data) and Chi-square values comparing 1989-90 age distribution with subsequent years.

Year	# Permits ¹	# Hunters	Elk Harvested ²	Success Rate	x ² Values ³
1989-90	44 ES, 830 A	690	423	61 %	
1990-91	70 ES, 2310 A	1637	684	42 %	x ² = 10.9, 7 d.f., P = 0.143
1991-92	70 ES, 2310 A	1752	1719	95 %	x ² = 32.4, 7 d.f., P < 0.0005
1992-93	105 ES, 2310 A	1952	1510	77 %	x ² = 48.5, 7 d.f., P < 0.0005

¹ (ES) Either-sex permits, (A) Antlerless permits

² Legal harvest only

³ Tables 2 & 4

Discussion

During the winter of 1988-89, those factors mentioned above combined to increase the vulnerability and availability of elk and facilitate the 95% success rate seen during the late hunt. Many elk encountered during January through March 1989 were noticeably weakened and reluctant to move very far even when within sight of humans. Animals often remained bedded until carcass survey crews were within a few feet. Generally, during the 1988-89 hunt, elk remained in the small pockets of available forage and did not disperse as far or as quickly upon encountering hunters. This coupled with the high accessibility (to hunters) of many of the areas immediately north of the park boundary (where most animals were killed) resulted in the high harvest rate.

The substantial decrease in the population during the winter of 1988-89 and the nutritional status of pregnant animals served to limit recruitment the following spring. Relatively mild conditions during the 1989-90 winter and the smaller population size resulted in fewer elk migrating north of the Park and thus, a lower harvest success rate in 1989-90.

Comparison of Females Versus Males in Harvest

Harvest data for both 1988-89 and 1989-90 indicate that more female calves (than male) were taken by hunters. The observed calf harvest sex ratios are contrary to past studies indicating males show greater vulnerability to hunters than females of

similar age (Maguire and Severinghaus 1954, Quick 1958, Picton 1961).

Recent studies also indicate that the sex ratio at birth may be differentially biased depending on winter severity and overwinter nutrition and thus the condition of cows. Houston (1982) and Vore (1990) reported the sex ratio of newborn calves on the northern range to be 50:50. Other studies have documented in-utero sex ratios for elk not statistically different from 50:50; however, these were generally rates from mid-pregnancy. It now appears under some conditions post-conception sex ratios favoring males may be the general rule for cervids (Flook 1970; Verme 1983, Smith et al. 1996), and intrauterine mortality may be heavier in male fetuses than female (Flook 1970).

Trivers and Willard (1973) hypothesized that among polygamous mammals where males exhibit a greater variance in reproductive success than females, maternal investment should be greater in sons (than daughters) and that mothers should produce more sons (than daughters) when their body condition is superior during pregnancy. Studies by Smith et al. (1996) on elk in northwestern Wyoming support this theory. According to their results, sex ratios of neonates were male biased on calving areas having lower densities of elk with the proportion of males born increasing with earlier initiation of supplemental feeding and higher digestibility of feeds. Smith et al. (1996) state that, "survival of male fetuses, which are more energetically costly to produce, is favored by nutritional supplementation early in gestation, when prenatal mortality becomes male-biased under the stress of winter malnutrition." Thus, if poor winter nutrition is associated with fetal loss and such loss is heavier in male fetuses, the sex

ratio at birth should be correlated with nutrition and the proportion of males positively associated with the quality of winter diet and condition of cows (Thomas and Toweill 1982). In view of the relatively good condition of cows in the spring of 1988, prior to the drought, more male than female calves may have been produced. The differential sex ratio of the 1988-89 calf harvest may be an indication that mortality postpartum, but prior to late winter, occurs more commonly among male than female calves. Greater vulnerability and removal of male calves may also occur during the regular season hunt, depending on season regulations. This may result in removal of more male calves prior to the late season in those years when early migration occurs and portions of the herd are available to regular season hunters. Based on the above information regarding correlating winter severity and poor winter nutrition with heavier male fetal loss, the sex ratio at birth during the spring of 1989 likely favored females.

During both the 1988-89 and 1989-90 seasons, most of the male harvest consisted of calves, due (in part) to the limited availability of either-sex tags. Differential habitat use between the sexes might have been a contributing factor. Numerous studies have documented sexual differences in habitat use resulting in sexual segregation (Clutton-Brock et al. 1982, Geist 1982, Clutton-Brock et al. 1987, Marcum and Edge 1991). Adult bulls generally occupy more remote habitats (away from cow/calf groups and thus humans). Cow/calf groups occupy more accessible lower elevation habitats away from predators and close to humans, resulting in greater availability and vulnerability of calves.

The extreme variation in percent calves in the male harvest during my study can

be attributed to the severe conditions and circumstances that occurred during 1988-89. Large numbers of calves were present and more vulnerable to mortality and hunting during 1988-89 and fewer calves were produced and survived the following spring. Cow elk surviving the winter of 1988-89 were in poor condition and calves born that spring were 17% lighter (in weight). As a result, the calf mortality rate was double that of previous years (Singer et. al. 1989, Singer and Harting 1989). This is consistent with research suggesting that progeny are lighter following periods of severe winter and food shortage and documenting higher survival for heavier calves. Several studies have documented the relationship between overwinter nutrition, winter severity, and reproductive success (Thomas and Toweill 1982). McNeil (1972) reported that cow elk on poor range reabsorb, abort, or produce smaller, weaker calves than normal, resulting in unusually high mortality. Studies by Thorne et al. (1976) also correlate high winter weight loss in cows with higher prenatal calf losses, lower calf birth weights, and lower calf survival rates. Lower birth weights appear to result in higher mortality from all causes (Singer et al. 1993). Greer (pers. commun. *in* Thomas and Toweill 1982) also observed the inverse relationship between winter severity and calf weights at birth. In addition, recent studies (Smith et al. 1996) have documented the effects of nutrition and condition on sex ratio indicating that prenatal mortality becomes male-biased under the stress of winter malnutrition.

Based on the age structure and maximum ages of elk recorded during the 1988-89 and 1989-90 harvests (Tables 2, 4, and 6), cows live longer than bulls. While past studies have documented elk living longer than 20 years (Quimby and Gaab 1957),

mean life expectancies are far lower and significantly different for males and females (Flook 1970a, Peek et al. 1967, Kimball and Wolfe 1974). Studies show progressive decreases in life expectancies of bulls compared to cows as winter range forage conditions deteriorate (Peek et al. 1967). This agrees with the results of Flook (1970b) who reported that populations of predominantly older animals where exploitation was low showed a greater disparity in sex ratios because winter mortality due to debilitation was apparently greater in adult bulls than cows. This higher mortality rate among bulls may be attributed to several factors including: differences in growth rate and years required to reach maximum development, required food intake and tooth wear; greater aggressiveness and range of movement (of bulls), and the energy depletion and injuries associated with rutting activity (McCullough 1969, Flook 1970b). Bulls expend great amounts of energy during the rut, predisposing them to malnutrition and death especially in those winters when energy intake is inadequate.

Another factor contributing to the sex differential may be differential migration and thus availability to hunters. Proportionately fewer mature bulls than cows left the mostly or partially burned wintering areas in the Park or unburned higher elevation areas to moved north during the 1988-89 winter (Singer et al. 1989). It is probably also reflective of the significantly higher number of either-sex tags issued during the several previous seasons which served to remove high numbers of adult bulls from the population.

Location of Kill

The largest percentage of the late hunt harvest has historically occurred in Area 2 due to the large number of elk moving through the area, the accessible terrain, and location of local outfitters (MTFWP 1993). This tendency was also observed in both the 1988-89 and 1989-90 late season. It was exacerbated in 1988-89 with a combination of factors leading to more animals being available to a greater number of hunters within Area 2. The massive migration of elk out of the Park, poor condition of animals, and limited forage availability resulted in elk bunching into small groups and remaining for extended periods in areas where forage was available. Elk carcass surveys conducted as part of our study as well as by MTFWP (Vore 1992) indicated a concentration of elk and elk carcasses at the boundary area and southern portion of Hunt Area 2 during the 1988-89 season. This concentration was the result of the above factors as well as hunting pressure to the north. Movement and distribution data presented by Vore (1990) have shown that hunting concentrates elk at the no-hunting/hunting boundary and in areas of limited public access. Concentration of elk along the boundary area may also be the result of further deterioration in the condition of animals as a result of the required river crossing; for although portions of the Yellowstone River were frozen, several sections of open water existed with treacherous ice fields surrounding the river on both sides.

During the relatively mild winter of 1989-90, far fewer elk moved north out of YNP. Elk movement out of the Park was sporadic and spread out over the hunting

season. Hunting pressure was also reduced with roughly one quarter the number of hunters of the previous season.

Differences in Age Structure of the Harvest

Percentages of bulls, cows, and calves harvested as well as the number of animals in each age class/grouping differed significantly between the 1988-89 and 1989-90 late elk seasons. Some of this variation may be attributed to differences in the number of either-sex and antlerless tags issued during the two seasons. Chi-square tests for homogeneity reveal a significant difference in the number of either-sex and antlerless tags issued for the two seasons ($\chi^2 = 33$, 1 d.f., $P > 0.0005$). Of 3,222 tags issued during the 1988-89, roughly 2% ($n = 54$) were either-sex and 98% ($n = 3,168$) were antlerless. In 1989-90, of 874 total tags issued, 5% ($n = 44$) were either-sex and 95% ($n = 830$) were antlerless.

The difference in age structure of the two harvests can be attributed to a significant reduction in the elk population due to the drought and winter-kill; differences in harvest rate between the 2 years; and differential survival of various sex and age classes. Bulls and calves died at a higher rate than cows during the severe winter. Early winter 1988-89 aerial counts of the northern herd revealed 19 bulls:100 cows and 24 calves:100 cows. By late winter, bull ratios were down to 18 bulls:100 cows and calf ratios reached 7 calves:100 cows (Singer et al. 1989). While these ratios must be viewed with caution as the accuracy of counts during 1988-89 are questionable

in view of the poor survey conditions, they are significantly lower than typical late winter ratios of previous years (23 - 30 bulls:100 cows and 33 - 48 calves:100 cows (Mack and Singer 1992).

Higher bull and calf mortality are expected during severe conditions due to the limited ability of calves to store energy and put on fat reserves while growing and the poor condition of bulls going into the winter due to energy expenditures, loss of body condition, and injuries obtained during the rut. Survival of calves through the winter is influenced by several major factors, the calf's physical condition (size and vigor) as influenced by date of and size at birth, quality and quantity of nutrition, and presence of disease or parasites, climate (which dictates available forage and the severity of the winter), and elk densities (Thomas and Toweill 1982, Sauer and Boyce 1983). Houston (1982) identified significant inversely density-dependent relationships between survival and total population size for elk calves and males 1 year of age and older. With lower energy reserves, calves are more sensitive to density-dependent overgrazing. In addition, more dominant individuals often exclude calves from food resources (Espmark 1974). Climate acts to ameliorate these density dependant factors in mild winters or intensify them in severe winters (Sauer and Boyce 1983).

Early winter 1989-90 counts of 19 calves:100 cows, and 25 bulls:100 cows are still somewhat lower at least for calves than typically seen in previous years. This is due in part to the poor condition of cows and associated low birth rate and survival of calves coming out of the 1988-89 winter. While bull ratios appear to have increased, this may be a function of better weather conditions and thus, greater observability of

bulls at the time of the 1989-90 classification surveys, or it may be the result of loss of cows from the population due to hunting, debilitation, predation or emigration.

Comparison of Age Structure of Harvest with Live Population

The fact no statistical difference was apparent between elk classified in the live population versus the harvest for either the 1988-89 or 1989-90 (once bulls were eliminated from consideration), may indicate that cows and calves were harvested in direct proportion to their availability. However, if finer age classifications were available for the live population, comparisons might reveal differences due to differential mortality (prior to the late hunt) and thus availability as well as differential vulnerability among different age and sex classes.

Also, several variables affect census data including weather conditions, elk behavior, and observer ability. Errors in enumerating elk due to differences in personnel may or may not be compensatory. Census conditions were very poor during the winters of 1976-77, 1988-89, and 1990-91, due to minimal snow cover or extremely heavy snow in early winter. Elk either dispersed widely over the winter range or clumped in small groups, often in forested habitats, thereby reducing their visibility and resulting in unreliable counts (Lemke et al. 1996). While I attempted to correct count data for any bias by using the total population estimate derived from the Pop-II model, the relative proportion of cows, calves, and bulls obtained from the original flight data remained the same.

Comparison of Age Structure of the Late Hunt Harvests from 1982-1993

There was a significant difference in the age distribution of the late hunt harvest over time. This can be attributed to the stochastic nature of the many factors influencing harvest rates. Forage conditions, winter severity (snow cover and temperature), population densities, sex differential in habitat preference and range affinity, and timing of the season all influence how many and what age and sex classes of elk migrate north and are thus available to hunters. Number of permits issued and weather conditions as well as forecasts of migration (and thus the chance for success) serve to influence the numbers of hunters in the field each season. Variable migration behavior related to weather and snow conditions make different proportions of the population available for harvest each year (Lovaas 1964). In addition, sexual differences between adult bulls and cows have been observed in habitat use, vulnerability (Marcum and Edge 1991), and affinity to specific ranges.

All late hunt seasons between 1982-83 and 1988-89 were held during similar time periods (mid-December to mid-February). However, hunter success and thus the number of elk harvested during late hunts is dependent on the number and timing of elk migrating out of Yellowstone Park. This, in turn is dependant on the forage availability, winter severity, and population density.

The 1988-89 harvest age distribution differed significantly from that for all previous hunts except the 1987-88 season. The northern herd steadily increased

throughout the 1980's and thus, the age structure of the live herd in 1988-89 was more similar to that in 1987-88 than previous years, at least before substantial winter kill occurred. The 1987-88 winter was extremely mild and elk migration from the Park was both late and quite low, resulting in a hunter success rate of only 2% and 214 elk harvested. Probably one of the most significant factors influencing the 1987-88 and 1988-89 harvest sex/age distributions is the fact that the number of either-sex permits was substantially reduced (Table 10). Only 50 either-sex permits were issued compared to an average of 600+ during the previous 5 years. The 1988-89 season marked the lowest number of either-sex permits ever issued for the late season ($n = 44$). Thus, the number of either-sex permits and percentage of the harvest made up of adult bulls were similar for 1987-88 and 1988-89, compared to previous years.

Although the distribution of the 1989-90 harvest differed significantly from both the 1991-92 and 1992-93 harvests, no significant difference was found with the 1990-91 harvest age structure. During both 1989-90 and 1990-91, the northern herd was basically recovering from the massive reductions of 1988-89. Both years were relatively mild, with low numbers of elk migrating north of the Park and relatively few elk harvested. Thus, while the number of permits issued more than doubled over the two years, there was probably relatively little change in the live population except possibly for greater calf recruitment in 1990-91.

The 1991-92 late season brought another record number of elk moving north of the Park early in the season due to unusually severe weather conditions and deep snow cover. As a result 3-4 times as many elk were harvested as in the previous 2 years.

More elk migrated out of the Park in 1993 due to relatively mild weather conditions, yet slightly more either-sex permits were issued and 200 fewer elk were harvested than in 1991-92 (MTFWP 1992, 1993).

CHAPTER 5

COMPARISON OF AGING TECHNIQUES

Introduction

The age of harvested elk was determined at the Gardiner check station by the eruption/wear method. During the 1988-89 and 1989-90 Gardiner late hunts, teeth were also collected and submitted for cementum analysis to test the accuracy of the eruption/wear age estimation method and compare the age structure of the harvest resulting from these two techniques.

The tooth eruption/wear technique basically relies on the pattern and timing of tooth eruption and rate of tooth wear on the lower jaw to determine age. The eruption/wear method is considered a reliable indicator of age in elk (Quimby and Gaab 1957), and has long been used for determining age at big game check stations (Greer and Yeager 1967, Keiss 1969).

Cementum analysis, the technique of examining annular rings in the dental cementum of teeth, has also become widely used for age determination in mammals due to its apparent accuracy (Cook and Hart 1979, Dimmick and Pelton 1994, McCullough 1996). The annular rings or cementum annuli found in teeth result from differences in the animal growth rate over the seasons (McCullough 1996). Cementum is deposited

on teeth throughout the life of an animal, with the first layer laid down directly on top of the dentine. Subsequent layers are deposited on the previous layer(s) of cementum. Rate of deposition and thus density of cementum varies based on the season of year and growth rate of the animal (Keiss 1969, McCullough 1996). A wide band of more translucent cementum is laid down during periods of rapid growth (i.e. in spring and summer) and a narrow opaque band deposited during periods of slow growth (i.e. during dry periods or in the fall and winter). This pair of cementum bands (one wide/translucent and one narrow/opaque) makes up one annulus. Thus, the number of annuli can be associated with the age of the animal in years (Keiss 1969).

There is a general relationship between cementum aging accuracy and the clarity of cementum patterns. Certain tooth sections show distinct cementum patterns allowing age analysis to be nearly certain. Aging is less certain when teeth have indistinct or irregular patterns or when portions of the tooth or root are missing. Clarity of cementum annuli is correlated with the severity of the slow growth period. In those environments with little or no seasonal variation, annuli are less apparent and often unreliable for age determination (McCullough 1996).

Certainty codes and accuracy limits for cementum age analysis have been established by Matson's Laboratory. Determination of whether an age estimate could be in error is based on a set of criteria including: the distinctness of cementum band staining, regularity of cementum band pattern, relative amount and location of cementum and dentine, and histological characteristics of cementum (Matson 1991a). Using these criteria, age estimates are given a certainty code of: (A) for nearly certain;

(B) some error possible, or (C) error likely. Accuracy limits have also been established based on the certainty code and general age class of the animal (Table 12). For example, if the technician believes a 6 year-old animal could be a year older or younger because the cementum pattern is not clear, it is given a certainty code of "B". If the technician thinks a 9 year-old-animal may actually be 1 year older or younger due to an unclear cementum pattern, it is given a certainty code of "A".

Table 12. Established certainty codes and associated accuracy limits used as reliability indicators for cementum aging (Matson 1991b).

Determined Age (years)	Certainty Code		
	A	B	C
1-8	+/- 0 years	+/- 1 year	+/- 2 year
8-15	+/- 1 year	+/- 2 year	+/- 3 year
15+	+/- 2 year	+/- 3 year	+/- 4 year

The accuracy of the dental cementum technique has been evaluated for various species. In general, data from Matson (1991a) comparing known ages and cementum ages in several species reveal that exact agreement between actual and cementum aging will occur roughly 70% of the time. Averaging over all species, cementum age was correct or within 1 year of known age 90% of the time. Species such as elk possess more distinct cementum patterns, thus facilitating greater cementum aging accuracy (Matson 1991a). In addition, there are differences in clarity of cementum pattern and thus, cementum aging accuracy, even between different elk populations and subspecies.

In general, 75% of cementum ages for elk have an "A" accuracy rating (Matson 1991a). However, this figure combines data for several different elk populations. In our study on northern Rocky Mountain elk from the northern range, approximately 87% of the cementum ages had an "A" accuracy rating. It should also be noted that accuracy of the cementum analysis technique declines for older elk (Matson, pers. commun. 1991).

In studies with known age elk, Matson (1991a) reported an overall accuracy of 73% based on evaluation of 15 known-age animals. However, more recent work with 52 known-age Rocky Mountain elk shows 98% of cementum ages were correct (Matson, pers. commun. 1997). Keiss (1969) reported 100% accuracy for 18 Wyoming elk of known age. DeSimone and Vore (1992) noted 96% accuracy for 25 known-age elk in the Elkhorn Mountains, Montana.

Methods

Ages of elk harvested during the 1988-89 and 1989-90 Gardiner late hunts were estimated at the Gardiner (Slip & Slide) check station using the eruption/wear method (Quimby and Gaab 1957, Greer and Yeager 1967). A jaw board and eruption/wear chart were available inside the check station but were generally not taken outside when elk were examined. Incisors (I1) were also collected during these late elk hunts and submitted to Matson's Laboratory in Milltown, Montana, for cementum analysis. The first permanent incisor (or deciduous incisor in young animals) was extracted from the

lower jaw using a channeled scraping tool or hunting knife. Each tooth was cleaned superficially to remove excess tissue, taking care to avoid scraping or damaging the root surface, and was then sealed in a small envelope. Envelopes were sequentially numbered to correspond with the kill card number assigned to the carcass by the check station attendant. Lab procedures included cleaning of the tooth surface and sectioning the root. Specimens were then mounted on a slide, stained, and examined under a microscope to count the annuli.

Use of the eruption/wear aging technique is generally considered quite accurate for younger age class animals (calves, yearlings, and 2.5 year-olds) due to the specific tooth eruption/wear characteristics present at these stages of development. Quimby and Gaab (1957) state that calves, yearlings, and 2 year-olds are easily recognized on the basis of type (deciduous or permanent), number, and stage of eruption of teeth.

To assess whether their assumption was valid, teeth were initially collected and submitted for cementum analysis from all age classes, including calves, yearlings, and 2.5 year-olds. Unfortunately, ages for some of the samples (elk ≤ 2.5 years old) were verified by Matson's Lab based on examination, not cementum analysis (Matson 1991b).

During the 1988-89 late hunt, teeth were collected from a sample of 21 elk estimated to be ≤ 2.5 years of age. Incisors taken from these animals were submitted for cementum analysis in order to test the accuracy of the tooth replacement/wear technique for this age group (calves, yearlings, and 2.5 year-olds). After this initial collection, teeth were not collected from calves, yearlings or 2.5 year-olds and eruption

aging was considered accurate and adequate for these age classes. Thereafter, teeth were extracted for cementum analysis only from animals > 2.5 years old.

Though the intent was to collect teeth from all elk (> 2.5 years old) passing through the check station, due to time and personnel constraints, teeth were extracted from a sample of 1109 harvested elk. As no known-age elk were available, I was unable to assess the accuracy of cementum analysis through comparison with known ages for this study.

A paired t-test was utilized to evaluate differences in eruption/wear versus cementum analysis ages within each harvest. I also attempted to develop a model to predict true age using check station (eruption/wear age) estimates using simple linear regression. A Chi-square test (χ^2 statistic) was used to determine differences in relative frequency distributions of various age classes within each harvest based on the different aging techniques. The Chi-square goodness-of-fit test assumes the relative frequency or proportions in each age class given by cementum analysis represent the model or theoretical age distribution of the harvest. Goodness-of-fit tests were used to investigate whether the relative frequencies of the estimated ages determined by eruption/wear aging coincided with the assumed model (given by cementum aging). Chi-square tests for homogeneity were also conducted. This approach tests whether the age structure determined from eruption/wear and the cementum analysis based age structure could have arisen from the same age distribution. For the purpose of analysis, elk were categorized by individual age class and combined into 8 general age groups to facilitate comparisons and improve statistical reliability.

Results

Of teeth collected from the sample of 21 elk estimated to be ≤ 2.5 years old (calves, yearlings, and 2.5 year olds), 12 were cementum aged with an "A" accuracy. Excluding outliers that most likely resulted from handling error, comparison of eruption/wear age estimates with cementum aging or lab inspection revealed roughly 70% accuracy in age determination by check station personnel. A paired t-test revealed no significant difference between eruption/wear and cementum analysis based ages ($t = -0.801$, 9 d.f., $P = 0.44$).

During the 1988-89 Gardiner late hunt, teeth were collected from 873 elk for cementum analysis. Of these, 699 animals had been aged by eruption/wear and had a cementum age with "A" accuracy. Paired t-tests revealed a significant difference between eruption/wear and cementum analysis ages ($t = -10.5119$, 698 d.f., $P < 0.0005$). While the scatter plots of eruption/wear versus cementum ages for both years suggested a fairly strong positive linear relationship between the two techniques, the magnitude of deviation about the lines (Figures 5,6) suggested that any prediction of cementum (actual) age based on eruption/wear estimates would be unreliable. Simple linear regression also revealed a significant lack of fit between the model and my data ($y = 0.91x + 1.79$, $r = 0.829$) (Figure 5).

Percent error in age estimation for the 699 elk harvested and aged by the eruption/wear technique during the 1988-89 Gardiner late elk hunt ranged from

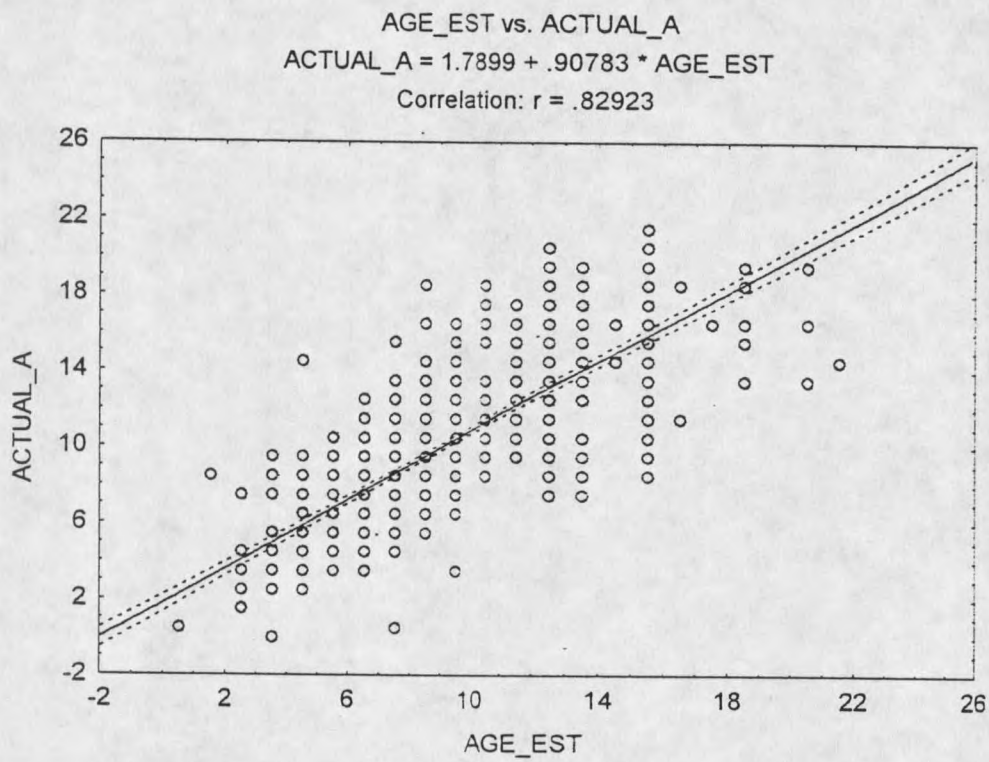


Figure 5. Scatterplot of eruption/wear (AGE_EST) versus cementum age (ACTUAL_A) for elk harvested in the 1988-89 Gardiner late elk hunt.

Table 13. Error in age estimates for 699 elk harvested in 1988/89 and aged using the eruption-wear technique as compared to actual age determined from cementum analysis [number (percent of total in age group)].

Age Class	No. in Each Age Class	No. Incorrectly Aged in Each Age Class	Overestimated Age [number (percent)]	Underestimated Age [number (percent)]	Average Discrepancy and (Range)
0.5	3	1 (33)	1 (33)		7
1.5	1	1 (100)	1 (100)		1 (1)
2.5	11	6 (55)	6 (55)		1.3 (1 to 2)
3.5	41	31 (76)	30 (73)	1 (2)	1.5 (-1 to 6)
4.5	51	27 (53)	16 (31)	11 (22)	1.3 (-2 to 3)
5.5	49	26 (53)	11 (22)	15 (31)	1.3 (-2 to 3)
6.5	63	48 (76)	19 (30)	29 (46)	1.4 (-2 to 3)
7.5	56	43 (77)	10 (18)	33 (59)	2.0 (-5 to 6)
8.5	63	56 (89)	12 (19)	44 (70)	2.4 (-7 to 7)
9.5	66	58 (88)	11 (17)	47 (71)	2.6 (-6 to 6)
10.5	57	50 (88)	10 (18)	40 (70)	2.6 (-5 to 5)
11.5	29	27 (93)	6 (21)	21 (72)	2.7 (-5 to 5)
12.5	43	38 (88)	9 (21)	29 (67)	2.9(-6 to 3)
13.5	32	29 (91)	7 (22)	22 (69)	2.96 (-6 to 7)
14.5	17	16 (94)	8 (47)	8 (47)	2.8 (-10 to 7)
15.5	36	23 (64)	4 (11)	19 (53)	4.2 (-8 to 3)
16.5	36	36 (100)	8 (22)	28 (78)	2.7 (-8 to 4)
17.5	15	15 (100)		15 (100)	3.7 (-7 to -2)
18.5	14	13 (93)		13 (93)	5.0 (-10 to -2)
19.5	13	13 (100)	1 (8)	12 (92)	3.2 (-7 to 1)
20.5	2	2 (100)		2 (100)	6.5 (-8 to -5)
21.5	1	1 (100)		1 (100)	-6 (-6)
Total	699	560	170	390	

33 to 100 (Table 13), assuming that cementum aging was accurate. For the purposes of this analysis, any deviation from the cementum age was considered an error.

Overall error in age estimation by eruption/wear for check station attendants during the 1988-89 late hunt was 80%. The degree of error for younger age classes (<6.5 years old) was approximately 60%, more than 86% for elk ≥ 6.5 years old, and 99% for elk ≥ 16.5 years old. Results also reveal that attendants overestimated age for younger age classes, while underestimating the age of animals ≥ 5.5 years of age.

For the 1989-90 Gardiner late hunt, teeth were collected from 258 elk for cementum analysis. A total of 215 elk were aged using eruption/wear and had a cementum age with "A" accuracy. A paired t-test revealed a significant difference between eruption/wear and cementum analysis ages ($t = -10.157$, 214 d.f., $P < 0.0005$). The scatter plot of eruption/wear versus cementum age suggested a positive linear relationship between the two techniques ($y = 1.02x + 1.32$) (Figure 6).

Of the 215 elk aged by cementum analysis and eruption/wear during the 1989-90 late hunt, attendants correctly aged 42, resulting in an overall error rate of 80% (Table 14). Younger age classes (<6.5 years old) were incorrectly aged approximately 58% of the time. Eruption/wear ages were incorrect 91% of the time for animals ≥ 6.5 years old and wrong 100% of the time for elk ≥ 16.5 years old. Although teeth from younger age classes (calves, yearlings, or 2.5 year-olds) were not collected for cementum analysis during this season, the data clearly show that, as in 1988/89, check station attendants overestimated age for 3.5 and 4.5 year-olds while underestimating age for all older age classes (≥ 5.5 years old).

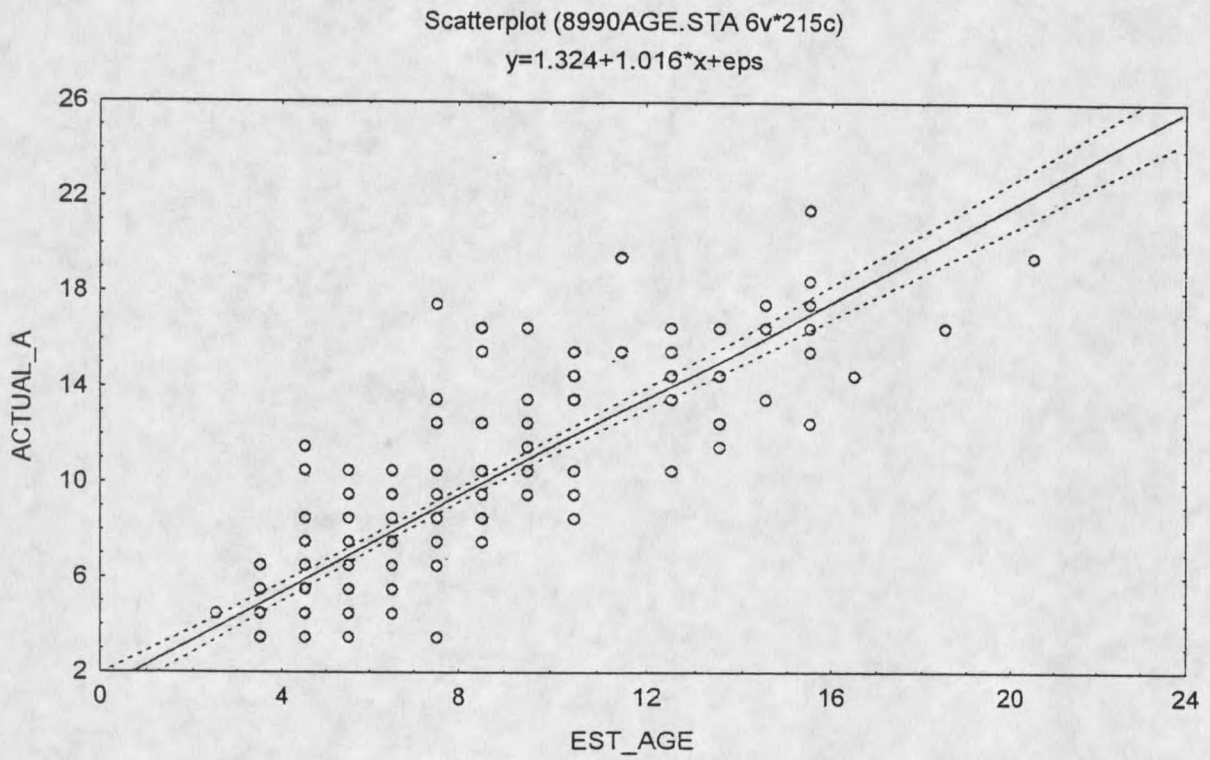


Figure 6. Scatterplot of eruption/wear (EST_AGE) versus cementum age (ACTUAL_A) for elk harvested in the 1989-90 Gardiner late elk hunt.

Table 14. Error in age estimates for 215 elk harvested in 1989/90 and aged using the eruption-wear technique as compared to actual age determined by cementum analysis [number (percent of total in each age class)].

Age Class	Number in Each Age Class	Number Incorrectly Aged in Each Age Class	Overestimated Age [number (percent)]	Underestimated Age [number (percent)]	Average Discrepancy and (Range)
3.5	26	9 (35)	9 (35)		1.7 (0 to 4)
4.5	21	15 (71)	5 (24)	10 (48)	1.1 (-2 to 2)
5.5	19	14 (74)	1 (5)	13 (68)	1.3 (-2 to 1)
6.5	17	15 (88)	1 (6)	14 (82)	1.5 (-3 to 1)
7.5	19	16 (84)	2 (11)	14 (74)	1.9 (-3 to 1)
8.5	24	22 (92)	2 (8)	20 (83)	2.1 (-4 to 2)
9.5	14	12 (86)	1 (7)	11 (79)	2.3 (-4 to 1)
10.5	21	19 (90)	1 (5)	18 (86)	2.7 (-6 to 2)
11.5	4	4 (100)	1 (25)	3 (75)	3.3 (-7 to 2)
12.5	8	8 (100)	2 (25)	6 (75)	3.5 (-5 to 3)
13.5	9	9 (100)	1 (11)	8 (89)	2.3 (-6 to 1)
14.5	5	5 (100)	1 (20)	4 (80)	2.6 (-4 to 2)
15.5	8	5 (63)		5 (63)	4.4 (-7 to -3)
16.5	11	11 (100)	1 (9)	10 (91)	3.4 (-8 to 2)
17.5	4	4 (100)		4 (100)	4.3 (-10 to -2)
18.5	2	2 (100)		2 (100)	3.0 (-3)
19.5	2	2 (100)	1 (50)	1 (50)	4.5 (-8 to 1)
20.5	0	0			
21.5	1	1 (100)		1 (100)	6 (-6)
Total	215	173	29	144	

The observed differences in ages using the two techniques also resulted in significant differences in age structure of the harvest (Table 15, Figures 7a, 7b). Of 699 elk harvested and aged during the 1988-89 late hunt, 52% (n = 361) were ≥ 9.5 years of age based on cementum analysis compared to only 39% (n = 272) using the eruption/wear aging method. Of 215 elk killed in the 1989-90 late harvest, 69% (n = 149) were ≥ 6.5 years of age as determined by cementum analysis, while only 54% (n = 116) fell into this category using the eruption/wear aging technique.

Table 15. Comparison of age distribution of elk harvested in the 1988-89 and 1989-90 Gardiner late hunts based on eruption/wear age estimation (ErW) and cementum (Cem) analysis [number (percent of total carcasses aged)].

Year	Aging Tech	Estimated Age Categories							
		0.5	1.5	2.5	3.5-5.5	6.5-8.5	9.5-11.5	12.5-14.5	15+
88-89	ErW	471	305	186	198 (28.3)	218 (31.1)	110 (15.7)	68 (9.7)	94 (13.4)
	Cem	471	305	186	141 (20.1)	182 (26.0)	152 (21.7)	92 (13.1)	117(16.7)
89-90	ErW	59	32	40	98 (45.6)	60 (27.9)	24 (11.2)	16 (7.4)	16 (7.4)
	Cem	59	32	39	66 (30.7)	60 (27.9)	39 (18.1)	22 (10.2)	28 (13.0)

Chi-square goodness-of-fit tests revealed a significant difference in the proportion of animals in each age class using the different aging techniques for both 1988-89 ($\chi^2 = 48.1$, 4 d.f., $P < 0.0005$) and 1989-90 hunt data ($\chi^2 = 29.80$, 4 d.f., $P < 0.0005$). Chi-square tests for homogeneity also revealed that the age distribution of the harvest differed significantly for eruption/wear compared to

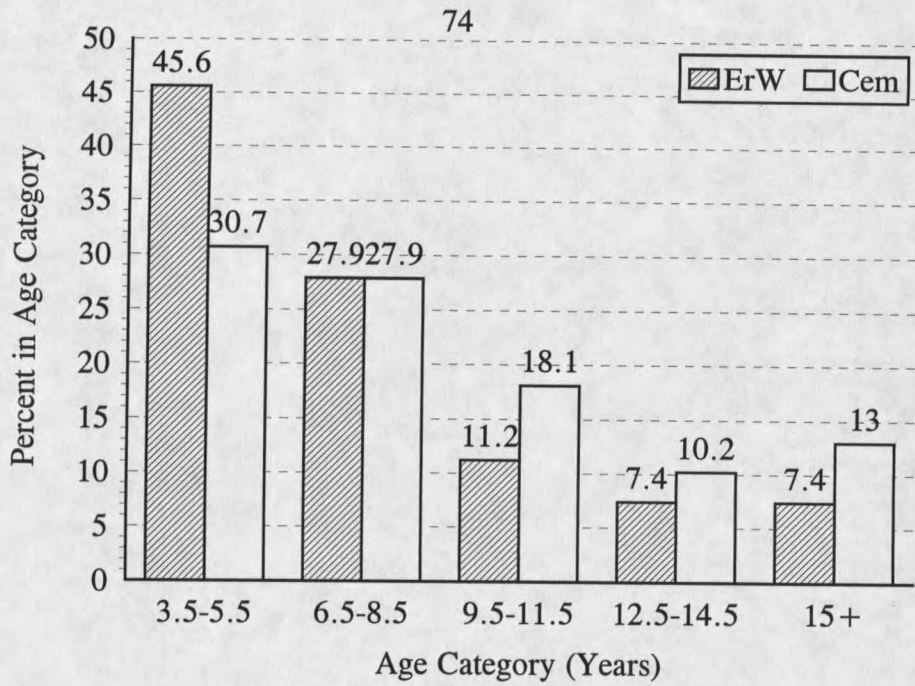


Figure 7a. Eruption/wear versus cementum age structure for 1988-89 late hunt harvest.

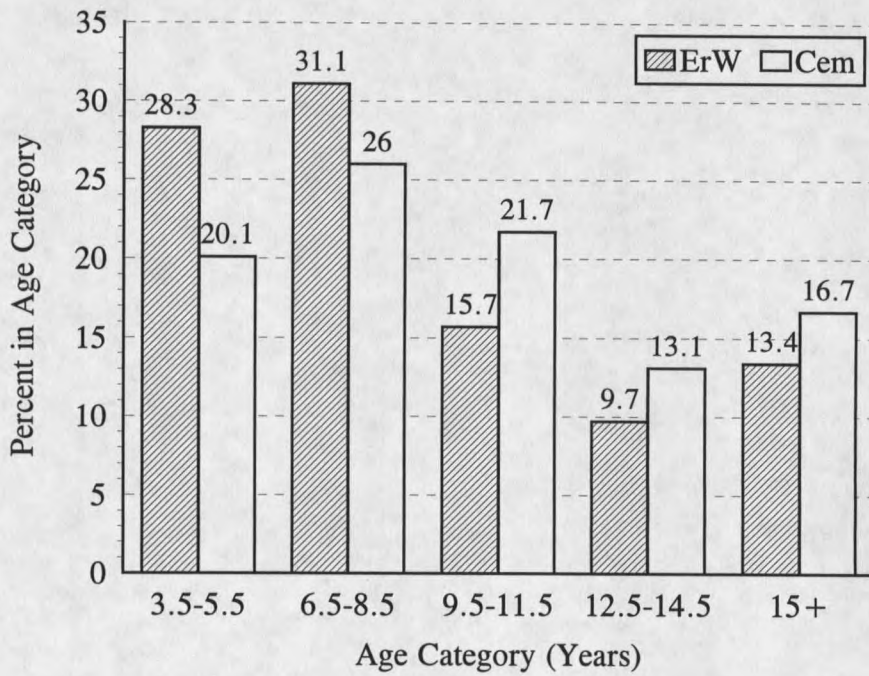


Figure 7b. Eruption/wear versus cementum age structure for 1989-90 late hunt harvest.

cementum analysis for the 1988-90 hunt regardless of whether elk were divided into 14 age classes or grouped into 5 age categories for comparison ($\chi^2 = 25.65$, 4 d.f., $P < 0.0005$; $\chi^2 = 86.53$, 13 d.f., $P < 0.0005$). Calf, yearling, and 2.5 year-old age classes were excluded from all comparisons as these age groups were aged primarily by eruption/wear techniques. Tests for homogeneity on the 1989-90 harvest data also revealed that age distribution as determined by the two techniques differed significantly when elk were grouped into 5 age categories ($\chi^2 = 14.03$, 4 d.f. $P = 0.007$) as well as for 14 age classes ($\chi^2 = 30.13$, 13 d.f., $P = 0.005$). Again, tests excluded calf, yearling, and 2.5 year-old age classes.

The null hypothesis that age distribution of the 1988-89 and 1989-90 harvests were the same was also rejected when based on cementum analysis ages. Chi-square tests revealed a significant difference in the relative frequency distribution within 8 age categories for the 1988-89 and 1989-90 harvests ($\chi^2 = 70.65$, 7 d.f., $P < 0.0005$). Maximum cementum ages recorded for elk were 21.5 years for cows and 13.5 years for bulls in 1988-89 and 21.5 years (for cows) and 10.5 years (for bulls) in 1989-90.

Discussion

The variability inherent in the age estimates obtained by the eruption/wear technique has long been recognized (Quimby and Gaab 1952,1957; Keiss 1969). Such discrepancies are due, in large part, to differences in the ability/experience levels of personnel, use or non-use of jaw boards or other reference material, as well as to

variations in tooth wear between individual animals as a result of sexual, genetic, diet, and habitat/environmental differences. Quimby and Gaab (1957) describe inaccuracies between actual age and that estimated by their eruption/wear technique. They recommend several ways of reducing error, but indicate that inaccuracies can still be expected. They subsequently dismiss these inherent discrepancies, suggesting that such errors will average out overall, yielding a fairly reliable determination of percentage composition by age class.

Many wildlife management agencies rely on eruption/wear aging data, often combining age class data into broad age groups or categories for analysis, in part, to compensate for potential errors in age estimation. Such data are then used to compare trends in age structure of harvested animals over time.

My results reveal a significant difference in ages of elk >2.5 years old as determined by the two aging techniques. In 27 to 31% of the cases (1989-90 and 1988-89 hunts, respectively), check station estimates were 3 or more years off. Many eruption/wear estimates (7 to 11%) were 5 or more years off; and, in extreme cases, there was as much as a 10 year difference between the 2 techniques. In general, ages estimated by eruption/wear were younger than those determined by cementum analysis for the same elk, with the discrepancy between the techniques increasing as age (of the animal) increased. Studies comparing eruption/wear and cementum aging on elk populations in Canada (Flook 1970a), the Elkhorn Mountains of Montana (DeSimone and Vore 1992) and Jackson Hole, Wyoming (Cain, pers. comm. 1997) have revealed similar results. During my study, it was also noted that fewer discrepancies between

eruption/wear and cementum analysis occurred for elk in the 15.5 year-old age group than any other age class ≥ 6.5 years of age. This may be attributable to more consistency in or more identifiable wear characteristics on the permanent teeth than in other age classes, though this was not substantiated.

Aging discrepancies resulted not only in placement of elk into the wrong year class but often into the incorrect age group based on the 3-year age grouping commonly used by MTFWP. Thus, even with combining animals into age groups, differences in estimated ages between the 2 aging techniques resulted in significant differences in the age distribution. Age classification based on eruption/wear placed more animals in the 3.5-5.5 year age group than cementum aging, reflecting the tendency to overestimate age of younger animals and underestimate age on those 5.5 years of age or greater. For example, during the 1988-89 hunt, attendants overestimated the age on 6 animals shown to be 2.5 years of age through cementum aging, while underestimating age on 29 animals cementum aged at 6.5 years and 33 elk cementum aged at 7.5 years (18 of which were off by 2 or more years). Thus, more than 50 animals were erroneously placed in the 3.5-5.5 year-old age group.

The number of elk in older age categories was also falsely represented by use of eruption/wear aging. As seen in 1988-89 hunt data, the majority of animals (58%, $n = 106$) in the 6.5-8.5 year-old age group were underaged by eruption/wear aging, resulting in 60 animals being placed in the wrong age group. More than 71% of animals in the 9.5-11.5 age group ($n = 108$) were underaged, resulting in 99 animals being erroneously placed in the younger (6.5-8.5) age category. Similar discrepancies

existed within the 1989-90 harvest age distributions based on cementum versus eruption/wear aging.

The sex differential in survival was even more dramatic when looking at cementum ages since, as shown by our study, use of the eruption/wear method resulted in underestimating age for older age classes. However, comparison of age structures for the different harvests based on cementum ages was biased by the fact that teeth were not collected from all elk or from a stratified random sample of elk during either harvest. Cementum ages with "A" accuracy were available for approximately 29% (699 of 2,412) of elk harvested during the 1988-89 late hunt and 50% (215 of 432) of elk killed in the 1989-90 late hunt.

Eruption/wear age information has long been used at check stations to determine age-class composition of elk harvests and as an indication of trend in age distribution, despite the inherent errors. This is based on the belief that errors either average out or are present each year allowing for valid comparisons and determination of trends. However, in my study, the percent error for each age group differed between years. In addition, age was underestimated for 56% of the animals in 1988-89, while 67% were underaged in 1989-90.

These deficiencies are probably due, in part, to changes in check station staff over the season or years and the presence of less experienced attendants during some periods. It should be noted that Keiss (1969) found the range in percent error between the most and the least experienced biologist to be only 10%, suggesting that experience level is not as great a factor in erroneous age classification as the method of

eruption/wear aging itself. However, his results and interpretations have since been questioned. Discrepancies in aging may also be attributed to exceptionally busy times at check stations when aging may have been rushed or to periods when conditions were otherwise unfavorable for accurate age estimation (i.e. due to condition of the elk jaw/teeth or weather). Although I did not look at differences in tooth wear between individual elk of the same age nor attempt to account for variation in tooth wear due to changing environmental conditions (i.e. changes in vegetation characteristics on the northern range over time), these differences also influence aging error.

Whatever the contributing reasons/influences, my data suggest that erroneous age classification frequently occurs with the eruption/wear technique. Further analysis may be warranted to look at several years of data and determine if the variation in percent error for each age group is statistically significant. Based on my harvest data, age estimations determined by eruption/wear, resulting age distributions, and any trends or comparisons of age structures over the years are suspect.

While cementum analysis appears the most accurate, and thus recommended, aging technique for ungulates in seasonal environments, the costs associated with the technique (in terms of personnel, lab analysis and, time required to extract and prepare teeth) is often viewed as prohibitive. However, for those populations where accurate age distribution information is critical, the benefits of more reliable information ultimately outweigh the cost of cementum analysis.

While I was unable to develop a reliable predictive model based on my data, accurate identification of individuals responsible for each eruption/wear age estimate on

kill cards may allow for better estimation of the error and variability in eruption/wear ages. If eruption/wear techniques continue to be used at the majority of check stations, further analysis should be conducted to determine if variations in percent error are consistent within age categories over subsequent years. This information may then allow for development of a more accurate correction factor or predictive model to estimate true age based on eruption/wear estimates and provide more accuracy and consistency in harvest age data.

Several techniques have been recommended for eruption/wear aging (Quimby and Gaab 1957) and are listed in the order of their apparent accuracy: 1) direct comparison with known-age jaws, 2) comparison with assigned-age jaws, and 3) comparison with good drawings or photos. Aging jaws through comparison with assigned-age jaws on a jaw board will generally give more accurate results than aging by specific characteristics.

Maintaining the same well trained, experienced attendants at check stations over the years appears essential to increase consistency in age estimates and enhance the comparability of age distributions over time. However, this is not often feasible. Other possible suggestions include: requiring a photograph of all jaws for later review by one individual, having a specific check list outlining eruption/wear characteristics or several jaw boards of known-age animals that attendants could take with them when examining elk.

Another possible method for double-checking eruption/wear age estimates is examination of canine teeth. Although this technique only allows placement into broad

age categories, it could provide a method for double checking age estimates when/if lower jaws are absent or eruption/wear characteristics are confusing. As outlined by Greer and Yeager (1967), upper canine teeth differ morphologically according to sex of the animal, while the eruption, development, and attrition of canine teeth reflect age of the animal. Canine teeth are often removed by hunters before they arrive at the check station. However, of those successful hunters questioned at Montana check stations (Greer and Yeager 1967), 60 to 75% had upper canines in their possession even though many of the carcasses they brought in were missing the head or jaws. In addition, since all hunters are required to check into the hunt area, attendants could request hunters leave all jaws intact or save any canines until checkout is complete.

CHAPTER 6

HUNTER SURVEY

Harvest rates for different sex and age groups are inherently and intentionally biased, due to changing hunting regulations/quotas as well as factors relating to differential elk vulnerability. Thus, harvest data can not be interpreted as a random sample of the live population, nor can trends in the harvest across years necessarily be interpreted as indicative of population trends. Check station data provide information only on the animals harvested and direct inferences generally should not be made from such data to the live population. Differential vulnerability or susceptibility in sex and age classes is a result of various factors: hunter preference and behavior, length and timing of the season, weather conditions, access (open road density), habitat conditions (security cover and patch size), and elk behavior (Lyon and Christensen 1990, Lyon and Canfield 1991, Picton 1991, Vales et al. 1991, Youmans 1991).

Interpretation of harvest data to determine the impacts of harvest on the population requires an understanding of the differential vulnerability of various segments of the population. With this information one can potentially adjust any harvest data to achieve a more accurate description of the live population. While many aspects of vulnerability of different sex and age classes have been discussed, little

information is available on hunter selection and preference, especially relative to the Gardiner late hunt. In order to better understand and quantify hunter selection and thereby interpret harvest data, I developed and administered a survey to a random sample of participants in the Gardiner late hunt.

Gardiner Late Hunt 1990-91

The 1990-91 Gardiner late hunt was conducted between January 4, 1991 and February 18, 1991. The 28-day hunt consisted of 14, 2-day hunts (Friday/Saturday or Sunday/Monday) and 7, 4-day either-sex hunts, with either-sex permits valid from Friday through Monday. Approximately 165 tags were issued for each of 14 antlerless hunts. Between 8-11 either-sex permits were issued for each 4-day hunt. This was the first year the late hunt was postponed until January to assure an adequate number of elk had migrated into the hunt area and to protect native, resident elk from early harvest (MTFWP 1991). The boundaries of the hunt area were adjusted due to the purchase of the OTO Ranch. As a result, the boundary between Area 2 and 3 changed allowing the entire OTO to be opened or closed as a single unit.

During the 1990-91 late hunt, 2,310 antlerless and 70 either-sex permits were issued. This represented a substantial increase over the 830 antlerless and 44 either-sex permits issued in 1989-90. The 1991 level was set with the objective, based on past participation and success rates, of harvesting 1,000-1,200 elk.

Seventy two percent of permitted hunters participated. Harvest success was

41% overall, 39% for antlerless permits and 76% for either-sex permits, with 494 cows, 144 calves, and 59 bulls harvested, including illegal kills (MTFWP 1991).

Methods

A telephone survey was developed and administered to a stratified random sample of permitted Gardiner late hunt participants from 2 of the 7 either-sex hunts and 7 of the 14 antlerless hunts. Respondents were selected from the MTFWP list of antlerless and either-sex permittees for the 1990-91 hunt. The list was constructed by randomly selecting individuals from the group of all applicants and assigning them to specific hunts according to their tag type (T. Lemke, MTFWP, pers. commun.).

A 3-page questionnaire consisting of 23 survey questions was developed and used in the telephone interviews (Appendix C). At the beginning of each interview, a concise statement was read clarifying interviewer identity, explaining the purpose of the survey, and emphasizing the importance of respondent cooperation and input. The questionnaire contained primarily closed-end questions aimed at determining: (1) what type of animal (in terms of age, condition, size, and/or rack size) individuals were hunting for; (2) if the animal they took met these preset specifications; (3) if not, how it differed from these specifications; (4) why they took an animal that did not meet their specifications; and (5) whether their hunting practices were actually selective? We attempted to assess whether hunters had the experience and knowledge to distinguish between different types of elk (age, sex, and condition) in the field and whether hunting

conditions and number of elk present allowed them to be selective. Questions focused on past hunting experience, including the number of years spent elk hunting and years spent participating in the Gardiner late hunt. Hunter opportunity to make a choice was assessed based on the number of elk available, whether participants took an animal from the first group of elk encountered, whether the animals were in the open or in cover and thus, less visible, and the time available to shoot.

I also looked at how consistently participants answered questions regarding their original specifications and the animal they ultimately harvested. The type of animal desired and harvested was assessed by 9 multiple choice questions dealing with hunter perceptions before the hunt, while shooting, and after taking an animal. Degree of selectivity was further investigated with questions regarding the circumstances of the hunt (i.e. Was it in the first group of elk encountered or the first elk stalked or shot at?), and whether conditions and location of the animal allowed for selectivity (i.e. "time to get shot off", "number of elk present", "in timber or open" and "number in hunting party"). Familiarity with the area and hunting experience were assessed with 4 open-questions (i.e. years participated, number elk taken"). The remainder of the questionnaire looked at additional hunter preferences/characteristics: (1) principal reason for hunting; (2) hiring of a guide or outfitter; and (3) type and location of hunt.

The survey was initially pre-tested by conducting personal interviews with hunters at the Gardiner check station during the late hunting season. The telephone survey was initiated in April, following the 1990-91 Gardiner late elk hunt. Major inconsistencies were detected in some respondent's answers after conducting a portion

of the telephone interviews. Though the original intent was to interview hunters from the 1990-91 hunt, and then survey hunters who participated in the 1989-90 and 1988-89 late hunts. However, the survey was terminated after conducting only a portion of the sample interviews when the validity of responses to key questions on hunter selectivity appeared questionable and it became clear I could not use the information to interpret harvest data as originally intended. In particular, I could not determine whether hunters accurately remembered selecting or settling for a particular animal or if they were honest in admitting so. Telephone interviews were conducted with 77 individuals receiving permits for the 1990-91 Gardiner Late Hunt.

Although survey results could not be used for the intended purpose of assessing hunter preference, only the validity of certain responses dealing specifically with hunter selectivity were questioned. Although this limits the statistical analysis and inferences that can be made regarding hunter selection, responses to remaining segments of the survey are considered accurate and provide invaluable information on hunter demographics and hunting characteristics.

The Chi-square test for homogeneity was employed to test the significance of differences in permit type between male and female hunters. Information on sex of hunters was not available from MTFWP. Thus, for the purposes of analysis, sex of permittees was determined by name when possible or recorded as unknown.

Chi-square tests for homogeneity were used to determine whether significant differences existed between male and female hunters, either-sex versus antlerless permittees, and in-state versus out-of-state hunters with regard to: reason for hunting,

hunting method, hunting areas, and whether participants hired a guide to locate elk. Because of small sample size, state of residence data were analyzed by 2 categories: Montana and out-of-state. Based on hunter responses, principal reason for hunting in the Gardiner late hunt was analyzed based on 6 categories including: meat, trophy, experience/sport, meat & trophy, meat & experience/sport, and trophy & experience/sport.

Results

Of the 2,380 hunters permitted in the 1990-91 late hunt, approximately 83% (n = 1977) were men, 15% (n = 367) were women, and sex was unknown for 2%.

While the late hunt drew participants from 14 different states, most hunters, approximately 97% (n = 2,295), were Montana residents with only 3% (n = 78) residing out-of-state. Ninety percent of the 70 either-sex tag holders and 97% of the 2,310 antlerless tag holders resided in Montana. The largest number of out-of-state hunters traveled from Minnesota (n = 15), North Dakota (n = 13), Washington (n = 13), and California (n = 11).

Seventy-seven individuals or approximately 3% of the 2,380 permitted hunters were interviewed. Although a stratified random sample of permitted hunters was selected for interview, by coincidence all those interviewed were successful in harvesting elk. The 77 individuals surveyed represent 11% of the 697 successful hunters. Eighty-two percent of survey participants were men (n = 63) and 18% (n = 14) were women. Thus, pooling over all tag types, approximately 4% of all female

hunters and 3% of all male hunters permitted in the late hunt were represented in our survey. With regard to specific tag type, 14% of the 70 either-sex tag holders and 3% of the 2,310 antlerless permittees were surveyed. Ninety-four percent of those surveyed ($n = 72$) were Montana residents, 6% ($n = 5$) non-residents. Therefore, our survey sample, although not representative of unsuccessful hunters, was representative of the total population of successful hunters permitted in the 1990-91 late hunt with regard to hunter sex, tag type, and place of residence.

Sex of the hunter was not a significant determinant of whether an individual held an either-sex or antlerless tag. The percentages of men and women holding either-sex permits were not significantly different from those hunters with antlerless tags ($\chi^2 = 2.48$, 1 d.f., $P = 0.116$) (Table 16.). The majority of either-sex tag holders were men (89%), while 83% of the 2,310 antlerless permittees were male. Women comprised 9% of the 70 either-sex hunters and 16% of antlerless hunters.

Table 16. Contingency table analysis of tag type by sex of hunter.

Tag Type ^a	Sex of Hunter		Total	
	Men	Women		
Antls	62	6	68	$\chi^2=2.48$, 1 d.f., $P = 0.116$
ES	1915	361	2276	
Total	1977	367	2344	

^a Antls = Antlerless Permit, ES = Either-Sex Permit

The following highlights major results of the hunter survey. The complete survey questionnaire is contained in Appendix C.

"What Was Your Principal Reason for Hunting in the Gardiner Late Hunt?"

Each hunter was asked to select their principal reason for hunting in the Gardiner late hunt from a choice of meat, trophy, experience/sport, or any combination of these. In total, 68% of respondents (n = 52) stated that "obtaining meat" was their primary reason for hunting in the 1990-91 late hunt (Figure 8); all 52 respondents held antlerless tags. Thirteen percent of respondents (n = 10) hunted primarily for "experience/sport", 9% (n = 7) for "meat & experience/sport", 5% (n = 4) for "trophy", 4% (n = 3) for "meat & trophy", and 1% (n = 1) for "trophy & experience/sport".

Sex of the hunter was not a significant determinant in why individuals participated in the late hunt. Of the 77 individuals surveyed, 63% of men and 86% of women hunted primarily for "meat." Another 13% of men and 14% of women stated that "experience/sport" were their principal reasons for participating. While 100% of female hunters chose "meat" or "experience/sport", only 76% of male participants selected either of these options. The other 24% (of men) stated that they hunted either for "trophy" or a combination of reasons (Figure 9, Table 17).

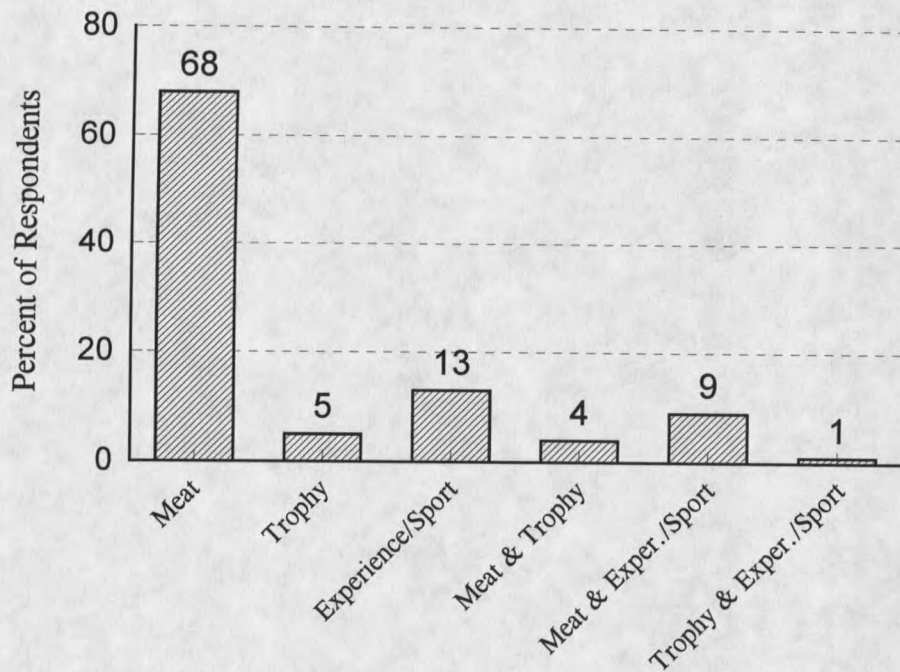


Figure 8. Respondents' reasons for hunting in Gardiner late hunt (n = 77).

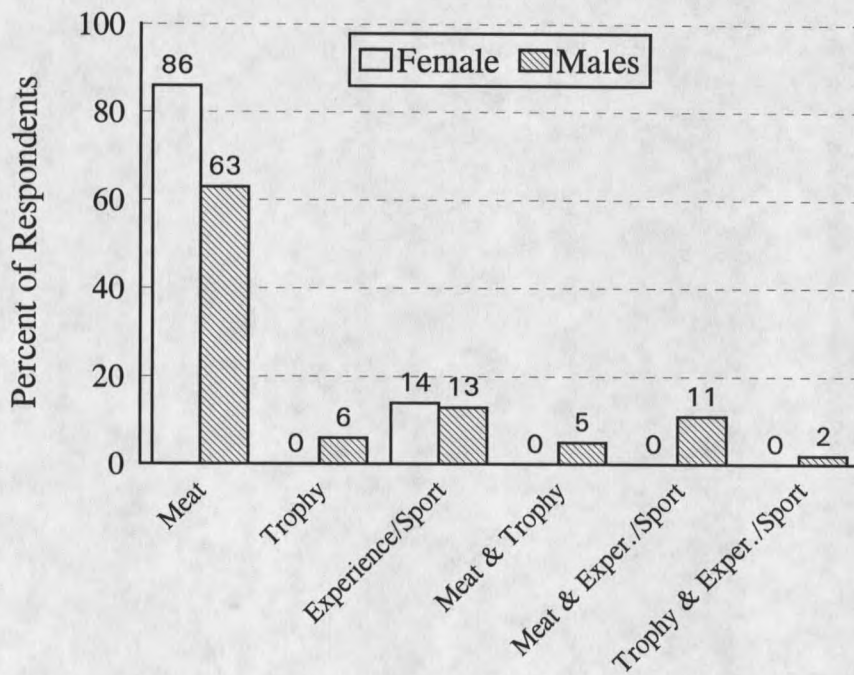


Figure 9. Respondents' reasons for hunting in the Gardiner late hunt by sex of hunter (n = 77).

Table 17. Contingency table analysis on reason for participating in the hunt by sex of hunter. ($\chi^2 = 4.39$, 5 d.f., $P = 0.495$)

Sex of Hunter	Reason for Participating						Total
	Meat	Trophy	Exp/sport	Meat & Trophy	Meat & Exp/Sp	Trophy & Exp/Sp	
Women	12	0	2	0	0	0	14
Men	38	4	8	3	7	1	61
Total	50	4	10	3	7	1	75

Table 18. Contingency table analysis on reason for participating in the hunt by tag type ($\chi^2 = 62.84$, 5 d.f., $P < 0.0005$)

Tag Type	Reason for Participating						Total
	Meat	Trophy	Exp/sport	Meat & Trophy	Meat & Exp/Sp	Trophy & Exp/Sp	
Antless	52	0	8	0	7	0	67
ES	0	4	2	3	0	1	10
Total	52	4	10	3	7	1	77

Table 19. Contingency table analysis on reason for participating in the hunt by state of residence ($\chi^2 = 24.18$, 5 d.f., $P < 0.0005$)

State	Reason for Participating						Total
	Meat	Trophy	Exp/sport	Meat & Trophy	Meat & Exp/Sp	Trophy & Exp/Sp	
In-State	52	3	8	3	6	0	72
Out	0	1	2	0	1	1	5
Total	52	4	10	3	7	1	77

My data reveal a significant difference in reason for participating in the late hunt between antlerless and either-sex tag holders (Table 18). Approximately 78% of antlerless tag holders surveyed (52 of 67) named "meat" as their primary reason for participating in the hunt. None of the 10 either-sex tag holders surveyed selected this option. Forty percent (of either-sex hunters) stated their principal reason for hunting was for "trophy", while 30% selected "meat & trophy", 20% chose "experience/sport", and 10% selected "meat & experience/sport" (Figure 10).

Reason for participating in the Gardiner Late hunt also differed significantly between Montana residents and out-of-state hunters surveyed (Table 19). While 72% of Montana residents hunted primarily for "meat", the 5 out-of-state hunters surveyed participated for a variety of reasons. Of the 5 non-resident hunters interviewed, 3 held either-sex tags, yet 40% stated they hunted primarily for "experience and sport."

"The Majority of Hunting Was done By: Foot Horseback ?"

Forty-eight percent (n = 37) of respondents reported the majority of their hunting was done using horses, 44% hunted by foot, and 8% went on foot and used horses. My data reveal no significant difference in hunting method between men and women (Table 20). Fifty-seven percent of women (8 of 14) and 46% of men (29 of 63) used horses.

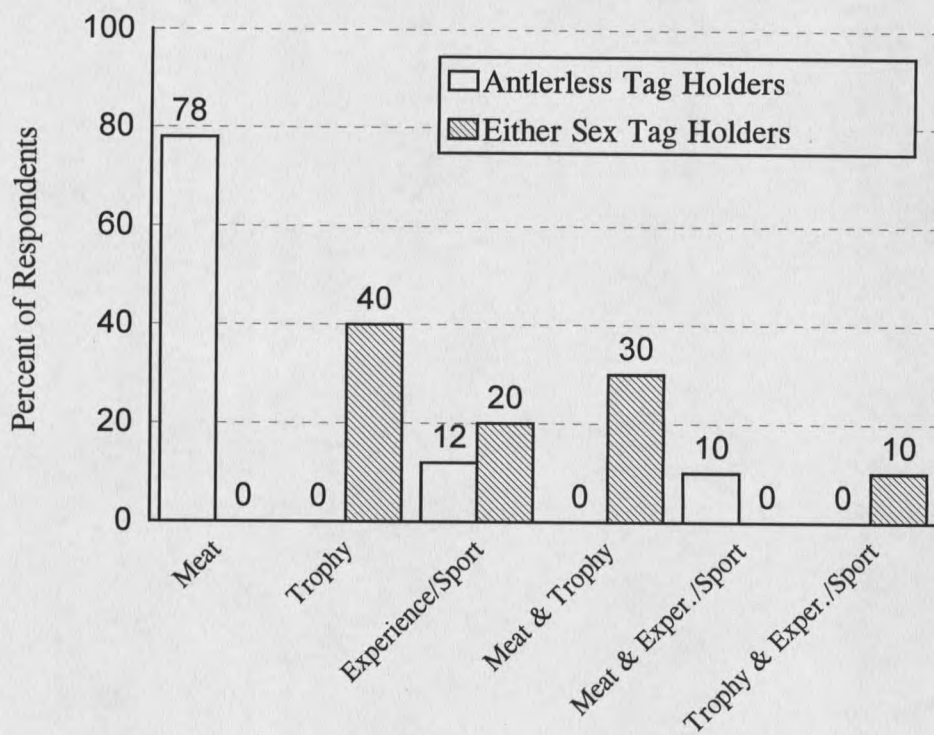


Figure 10. Respondents' reasons for hunting in the Gardiner late hunt by tag type (n = 77).

Table 20. Contingency table analysis of hunting method by sex of hunter.

Sex of Hunter	Hunting Method			Total	
	Foot	Horseback	Both		
Women	6	8	0	14	$\chi^2=1.63, 2 \text{ d.f.}, P = 0.44$
Men	28	29	6	63	
Total	34	37	6	77	

No significant difference was detected between the hunting methods of either-sex and antlerless tag holders ($\chi^2 = 2.73, 2 \text{ d.f.}, P = 0.256$) (Table 21). Fifty percent of either-sex tag holders hunted by horseback, 30% went on foot and 20% used a combination of foot and horseback. In comparison, approximately 46% of antlerless tag holders hunted on foot, 48% hunted by horseback and 10% used a combination of foot and horseback.

Table 21. Contingency table analysis of hunting method by tag type.

Tag Type	Hunting Method			Total	
	Foot	Horseback	Both		
Antless	31	32	4	67	$\chi^2=2.73, 2 \text{ d.f.}, P = 0.26$
ES	3	5	2	10	
Total	34	37	6	77	

"Did You Hunt Primarily in Areas:

Easily Accessible from Road Off Road/Backcountry Both

Most of the 77 respondents (79%) hunted primarily in offroad and backcountry areas. Sex of hunter did not appear to be a determining factor in area hunted (Table 22) with 93% of women and 78% of men hunting in backcountry areas. Either-sex and antlerless permit holders did hunt in different areas with 82% of antlerless tag holders hunting in backcountry areas compared to 60% of either-sex tag holders (Table 23).

Table 22. Contingency table analysis of hunting area by sex of hunter.

Sex of Hunter	Hunting Area			Total	
	Easily Access	Back Country	Both		
Women	1	13	0	14	$x^2=1.96, 2 \text{ d.f.}, P=0.375$
Men	8	49	6	63	
Total	9	62	6	77	

Table 23. Contingency table analysis of hunting area by tag type.

Tag Type	Hunting Area			Total	
	Easily Access	Back Country	Both		
Antless	9	55	3	67	$x^2=7.89, 2 \text{ d.f.}, P=0.019$
ES	1	6	3	10	
Total	10	61	6	77	

"How Many People Were in Your Hunting Party (with or without tags), Not Including Guide?"

Based on survey results, only 6% of participants hunted alone, while 80% hunted in groups of 2-4 individuals. Average group size was 3.4 individuals (not including guides).

"Did You Hire A Guide or Outfitter To Locate Animals?"

Outfitters can be hired for a variety of tasks including full camp services, guide, drop camp and packing out game animals, or use of horses only. Participants were asked if they hired a guide or outfitter specifically to locate animals. The majority of survey participants (51-57%) did not hire a guide or outfitter to locate elk (Figure 11). Neither sex of the hunter nor tag type proved a significant determinant of whether a respondent hired a guide (Tables 24, 25). However, 4 of 5 out-of-state hunters (80%) surveyed did hire a guide to locate elk compared to 46% of in-state participants.

Table 24. Contingency table analysis on whether participants hired a guide by sex of hunter.

Sex of Hunter	Did You Hire a Guide?		Total	
	Yes	No		
Women	6	8	14	$\chi^2=2.73, 2 \text{ d.f.}, P=0.26$
Men	30	32	62	
Total	36	40	76	

Table 25. Contingency table analysis on whether participants hired a guide by tag type.

Sex of Hunter	Did You Hire a Guide?		Total	
	Yes	No		
Antless	31	36	67	$\chi^2 = 0.27, 1 \text{ d.f.}, P = 0.60$
ES	5	4	9	
Total	36	40	76	

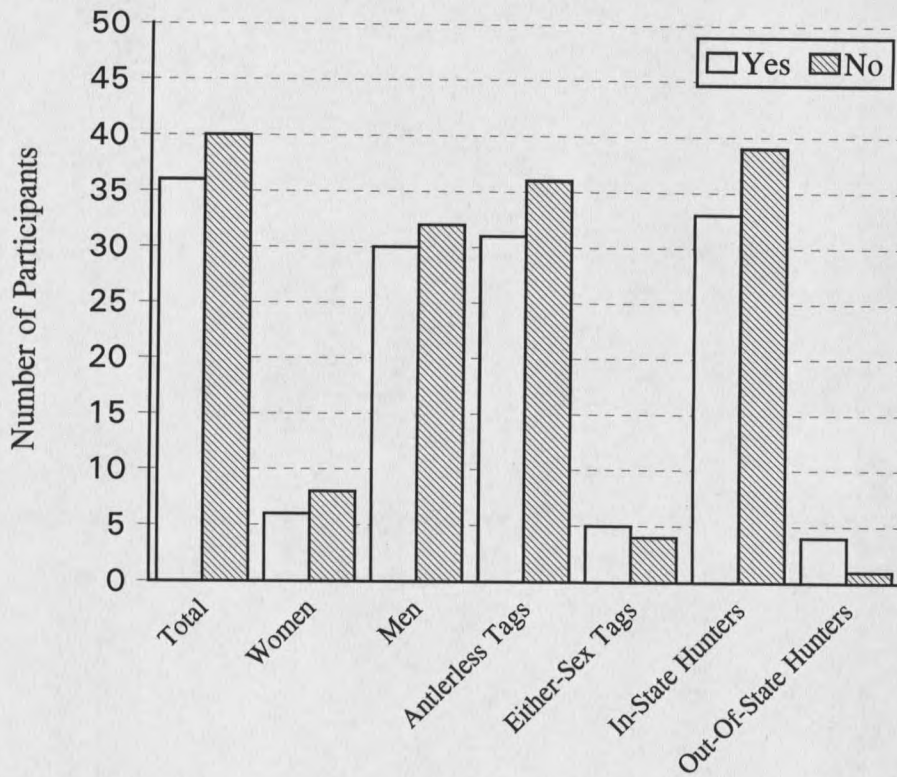


Figure 11. Respondents' indication of whether they hired a guide to locate elk (n = 76).

"How Many Years Have You Taken Part (with or without a tag) in the Gardiner Late Hunt?"

For 43% of participants (26 of 61), this was the first year they had taken part (with or without a tag) in the Gardiner late elk hunt. Respondents as a group averaged 3.5 ± 3.35 years participation in the Gardiner late hunt (Figure 12).

"How Many Years Have You Participated (with or without a tag) in an Elk Hunt?"

"How Many Days on Average, in Each Year, Did You Spend Actually Hunting?"

Respondents participated in elk hunting (either with or without a tag) an average of 11 ± 9.70 years, with 50 years being the maximum and spent on average, 7 ± 5.43 days each year actually hunting (Figure 13).

"How Long Did You Have to Get Your Shot Off (in Minutes)?" 1, 1-5, 6-10, >10

Forty-four percent of participating hunters ($n = 28$) reported that they had 1-5 minutes to get their shot off, 40% ($n = 25$) had less than 1 minute, and 11% ($n = 7$) said they had more than 10 minutes to shoot their animal.

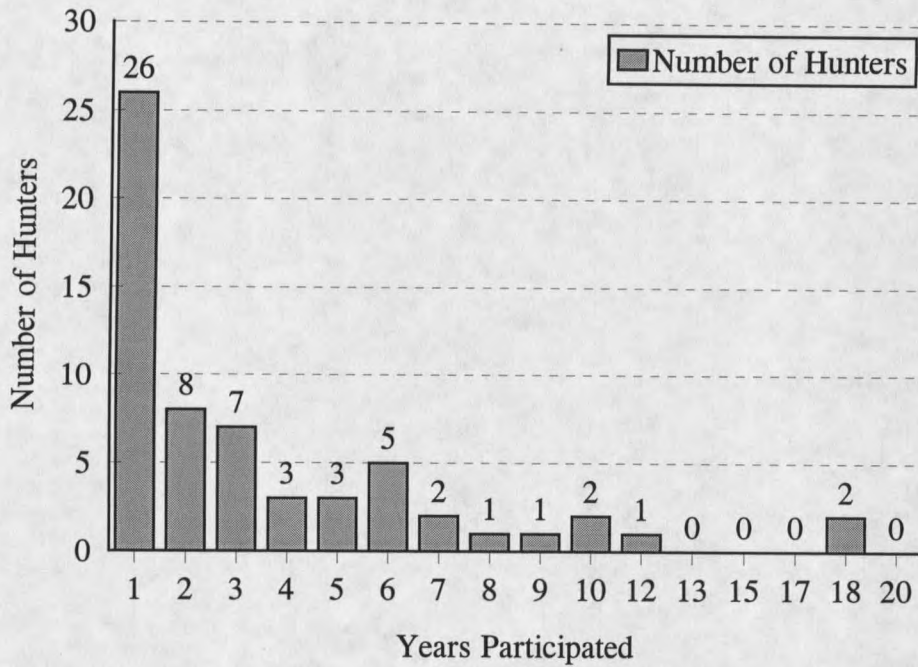


Figure 12. Number of years participated in Gardiner late elk hunt.

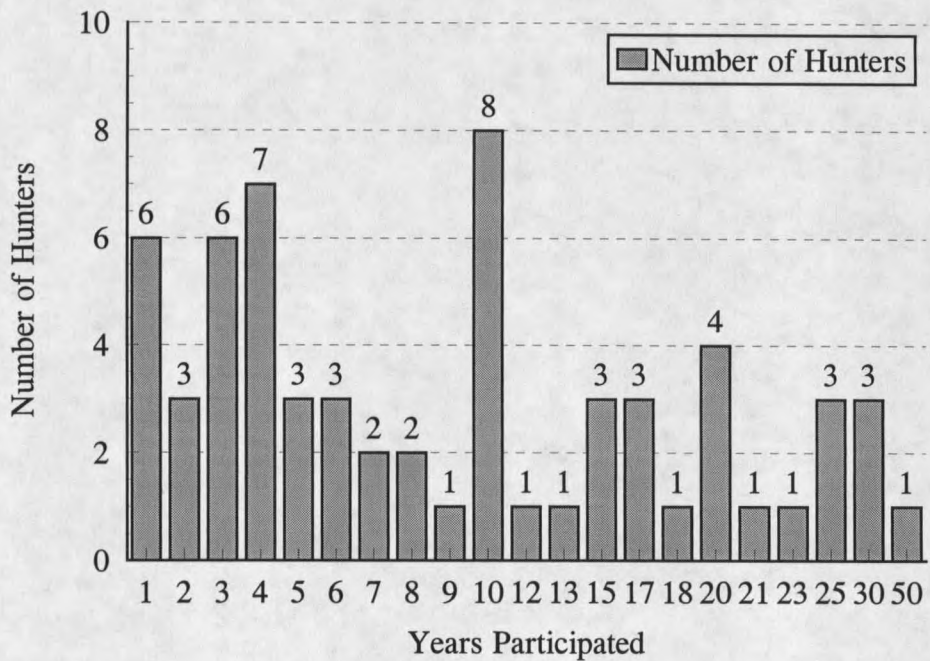


Figure 13. Number of years participated in an elk hunt.

"Why Did You Take an Elk That Did Not Meet Your Specifications?"

Availability Location Weather Conditions Time of Day Other

Of the 77 hunters interviewed, 36 believed they killed an elk that did not meet their specifications or their responses indicated disparity between what they thought while shooting versus after killing an elk. Only 19 hunters responded when asked why they took animals that did not meet their specifications. "Availability" was given as the primary reason for taking an elk that did not meet hunter specifications (n = 16)

(Figure 14).

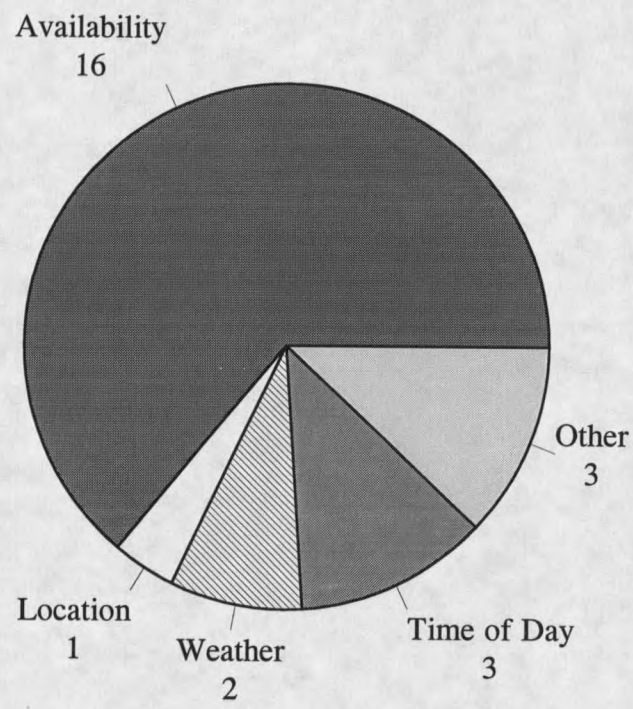


Figure 14. Why respondents took elk that did not meet their specifications (n = 19).

Discussion

Survey Coverage

Telephone interviews were conducted with 77 individuals receiving permits for the 1990-1991 Gardiner Late Hunt before the survey was terminated. Although the survey was terminated prior to conducting interviews with hunters from several hunts as intended, our survey sample is representative of the total population of successful hunters permitted in the 1990-91 late hunt with regard to hunter sex, tag type, and place of residence. Survey coverage of the target population is sufficient to allow generalizations regarding the total population of successful hunters participating in the Gardiner late elk hunt in 1990-91, as well as the total population of successful male and female hunters, either-sex and antlerless permittees and out-of-state and in-state hunters.

Validity of the Survey

Since survey efforts were terminated midstream, a smaller sample of hunters was interviewed than originally planned and though random, all survey participants interviewed were successful hunters. If hunt activity or preference, etc., of hunters interviewed differed from those we did not interview, any statements made regarding the entire harvest or all hunters would also be biased. Thus, it is important to note that all conclusions outlined here apply only to successful hunters and can not necessarily be extrapolated to apply to all hunters participating in the 1990-91 late elk hunt.

A problem common to all questionnaire surveys is that the response depends not only on how a question is worded, asked, and understood by the respondent, but on what the respondent is prepared and willing to report and what the respondent remembers (Dillman 1978, Barker et al. 1992). A number of possibilities for inaccurate reporting occur with this survey. Respondents may not remember specific details regarding the hunt. They may simply make up answers or they may be unwilling to admit the truth.

Dillman (1978) recommended against using survey questions that could be perceived as objectionable by the participants because they often elicit refusals or untruthful responses. Research has shown that questions about personal behavior can be threatening to respondents and may bias responses in a socially desirable direction (Dillman 1978, Gray and Kaminiski 1993.) Questions posed in this survey regarding hunter preference and selection relied on honest answers to direct questions concerning a hunter's initial preference, selection, and ultimate success. Due to the purpose of the questionnaire, inquiries regarding hunter selection and success could not be avoided.

Techniques have been developed to encourage survey participants to answer questions truthfully and some of these were implemented in conducting this survey. Special care was used in developing an introduction, as this is the point where most refusals occur in telephone surveys (Dillman 1978). The introduction was read prior to beginning the actual survey, requesting the participant's time and assistance, and outlining the interviewer's name, affiliation with Montana State University, the kind of information requested, and the purpose or use of survey information. Questions were

worded to convey no presumption of any societal consensus regarding the acceptability of not killing what you started out to kill. Respondents were first asked what they were hunting for rather than, "Did you get what you where hunting for?"

Many of the questions in the survey were designed to explore how selective hunters were based not only on their desire to kill a specific type of animal, but on all conditions influencing the hunt. Their ability to be selective was influenced by: hunting conditions, competition, time to shoot, location and visibility or availability of elk, as well as the hunting/experience level.

Despite careful survey/question design and testing, it became apparent during the survey that, in at least some cases, respondents either matched their stated prehunt preferences to what they actually ended up killing, were unwilling to admit that they did not kill the type animal they were initially hunting for, or there was not a clear understanding of choices/categories (i.e. what was meant by a prime age or young animal). During the survey, inconsistencies were detected in the answers of some respondents (n=7) with regard to what they were seeking and whether the elk they took met these specifications. When interviewed, some respondents stated they were hunting for a prime age or young animal and that the animal they killed met their specifications. However, in checking against hunt records, they actually took a 10 or 14 year old elk.

Such inconsistencies may have been due to memory failure, discrepancies regarding what constitutes a prime age animal, difficulty in identifying specific age groups under field conditions, or a combination of the above factors. Hunters also may have viewed certain survey questions (regarding what they were originally hunting for

and actually harvested) as intimidating or critical of their hunting ability. Whatever the cause, the inconsistencies made it impossible to use the hunter survey information for the intended purpose of weighting harvest data to account for hunter selection factors.

Problems with accuracy of response were not detected relative to any of the other questions used in the survey. Thus, it is important to note that all conclusions outlined herein are based on the assumption that responses were accurate.

Hunt Characteristics

Of hunters interviewed, all those hunting primarily for "meat" were Montana residents. There was a significant difference in reason for hunting between antlerless and either-sex permit holders and between resident and out-of-state hunters. However the small sample size does not allow inference regarding all out-of-state hunters. Presumably, hunters would not apply for an either-sex tag simply to hunt just for meat. Out-of-state hunters were more likely to hire a guide than local residents, most likely due to their probable unfamiliarity with the hunt area. The majority of respondents hunted in groups of 2-4 individuals, so there may have been some "peer" pressure to "bag an animal." While most hunters had participated in an elk hunt for several years, for many this was the first year they had hunted in the Gardiner late hunt.

Management Recommendations

Future attempts to determine hunter selection or preference should concentrate on increasing survey accuracy as well as sample size. An initial contact letter should be sent to hunters in the sample before the actual survey interview. Research has shown that sending a prior letter to respondents not only influences respondent cooperation, but affects the quality of the data obtained. According to Dillman (1978), a prior letter removes the element of surprise, jogs the respondent's memory and provides tangible evidence that the interviewer is legitimate and the call is not a practical joke. It may actually motivate the hunters to participate, especially if a real need for their help is expressed in the letter.

Pretesting of questionnaires should be conducted in the same manner as the survey will be conducted (i.e. personal interviews if the survey is to be conducted via personal interviews). I recommend that a pre-hunt personal interview be conducted with participants when they (hunters) are checking into the hunt area. This would allow establishment beforehand of what "type" of animals they are hunting for. In addition, some of the inconsistencies seen in our survey may have been due to misunderstanding of response choices especially regarding what type, size, or condition animal respondents were hunting. Thus, response categories (age classes, etc.) need to be more precisely and clearly defined and readily distinguishable by the average hunter under field conditions. Follow-up face-to-face interviews should be conducted at the

check station as hunters check out in order to verify if the elk harvested actually met their earlier specifications.

Despite the limitations of elk category definition and distinguishability in the field as well as the added cost of personal interviews, I believe such measures would greatly increase the accuracy of any hunter selection information. Prehunt goals could be established beforehand; and, with the details of the hunt fresh in their minds, hunters may be more likely and able to give accurate statements. In addition, to follow the suggestions of Dillman (1978) for increasing accurate responses, any questions that might be objectionable to participants should be placed later in the survey after other topical questions. However, while these procedures may reduce the number of inaccurate responses, because of the nature of the questions and issues, it is unlikely that false statements would be completely prevented or all bias in responses removed.

In addition, a larger sampling effort would be desirable in order to allow for generalizations regarding all hunters participating in the late hunt as well as comparison between years and in different hunting conditions.

CHAPTER 7

ELK CARCASS SURVEYS

During the severe winter of 1988-89, MTFWP and the NPS conducted aerial surveys and on-the-ground follow-up checks to detect carcasses along some major drainages in an attempt to estimate elk mortality. I conducted carcass surveys in key elk wintering areas to determine the age and sex structure of mortality and the spatial and temporal distribution of carcasses on the northern winter range. These surveys were not designed to determine the total number of carcasses or estimate total mortality on the northern range.

Methods

During the winter of 1988-1989, carcass surveys were conducted from January 3 through March 18. The study area was divided into 4 sections (Gardiner, Mammoth, Tower, and Abiathar Peak) and survey routes (Figure 15) delineated along observed and historic early and mid-winter elk use/concentration areas (Houston 1982). Survey routes were delineated and surveys conducted with the intent of maximizing the number of carcasses located. Routes generally followed major drainages and game trails through historic wintering areas and travel corridors. Aerial flights were also

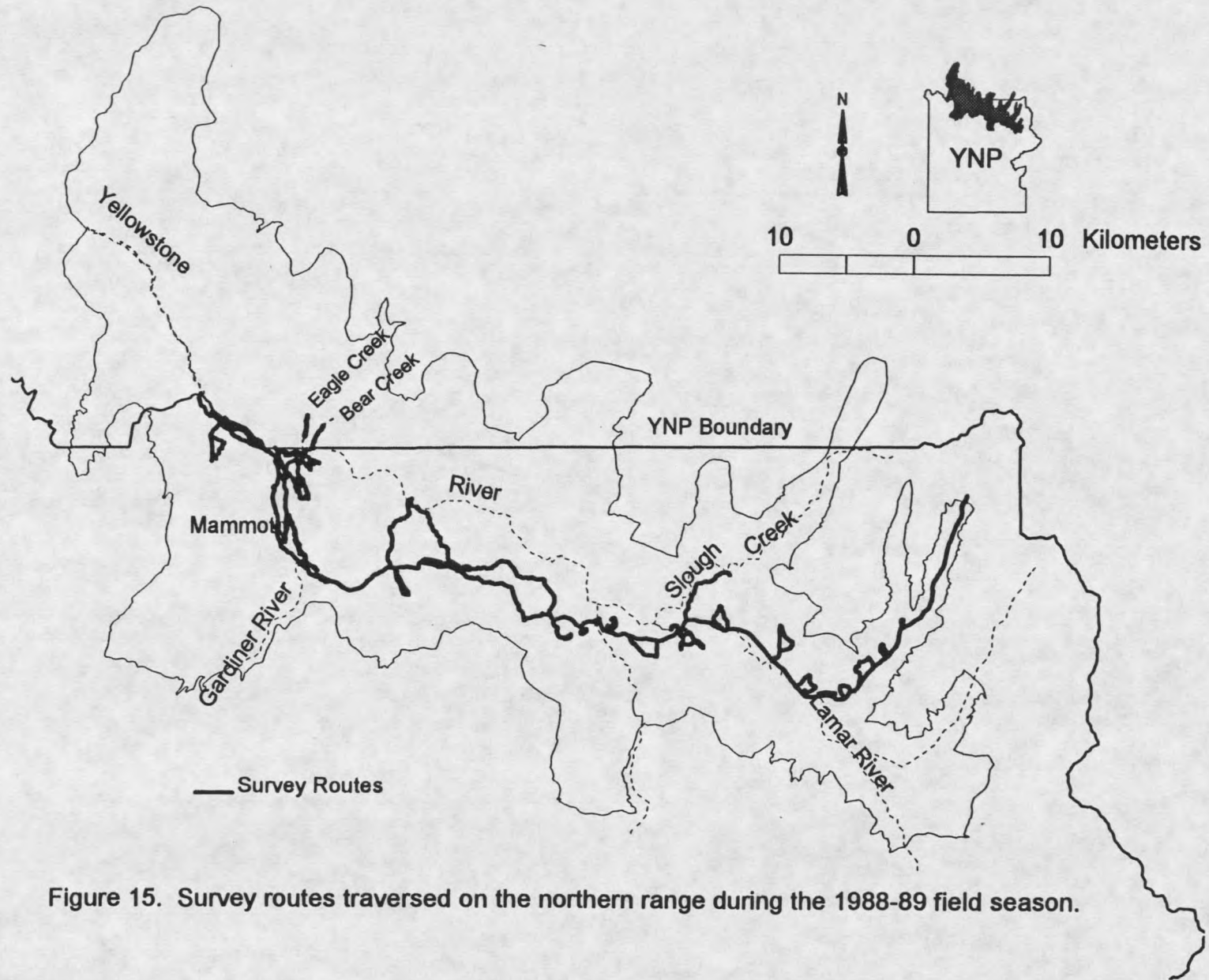


Figure 15. Survey routes traversed on the northern range during the 1988-89 field season.

conducted to locate elk and determine distribution patterns. Survey routes were modified, as necessary, due to changes in elk distribution (based on aerial and ground observations), the probability of locating carcasses, and the accessibility or logistics of traversing routes.

During the course of the winter, 39 different routes, totaling approximately 238 km including roadways (95 km) were surveyed at 10-12 day intervals within the Park and BLA (Figure 15, Appendix D). During surveys, all areas in the immediate vicinity of routes likely to harbor elk/carcasses were traversed and any signs of mortality or carcass presence (blood trails, ravens and other scavengers present) investigated. In addition, areas of reported carcasses within Yellowstone were searched. NPS personnel and other researchers reported carcasses and also provided carcass locations, data, and tooth and jaw samples for analysis. Two additional survey routes totaling 7.5 km were located north of the Park boundary. This area was searched in early March on a 1-day survey effort.

During the winter of 1989-90, carcass surveys were conducted between January 17 and March 18. Unlike the previous year, sampling employed a two-stage cluster design in order to effect a more random, repeatable, and statistically defensible sampling effort that still allowed us to focus on observed or historic elk use areas. The northern range was divided into 5 major areas, which were then broken into 24 subareas. One hundred and four semi-permanent transect lines totaling approximately 26.54 km were randomly located within the subareas using randomly selected points and compass bearings (Appendix E). Transects were marked with 6 foot orange

highway marker poles and orange flagging. Transect length and bearing were recorded. Once established, lines were surveyed by a crew of 2 individuals, 1 person following the flagging or compass bearing to ensure a position exactly on the transect line and the other person searching for carcasses along the route.

For each day of the 5-day sampling period, both the subarea and specific transect lines to be sampled were selected at random using a random number table. At least one different (major) area was surveyed during each day of the 5-day sampling period. When a carcass was located, sighting angle and perpendicular distance (from transect line to carcass) were recorded along with carcass and site information.

Carcasses seen from the road or reported were also examined and recorded including distance to and visibility from an established transect.

In both 1988-89 and 1989-90, survey routes were covered on foot, skis, snowshoes, and vehicle (for road routes). All ungulate remains, once located, were examined for species, sex, age at time of death, diastema length, marrow condition, estimated date of death (age of carcass), cause of mortality, condition of animal at time of death, and utilization by and type of scavengers. Age was determined by tooth eruption for animals ≤ 2.5 years-of-age and by cementum analysis for animals > 2.5 years-of-age when teeth were available ($n = 142$), or was otherwise recorded as unknown. On all surveys, a first permanent incisor (I1 incisor) was collected from each animal, when available, and sent to Matson's Lab in Milltown, Montana, for cementum analysis. Initially, a sample of 38 teeth from elk ≤ 2.5 years old was submitted for cementum analysis to test the accuracy of the tooth replacement and wear

technique for this age group (calves, yearlings, and 2.5 year-olds). Thereafter, teeth were extracted for cementum analysis only from animals >2.5 years-of-age. Lower mandibles were also collected when possible for comparison/analysis of wear. Date of death was estimated based on condition and degree of utilization of the carcass.

The location of each carcass was recorded using Universal Transverse Mercator (UTM) coordinates. Carcasses were numbered and locations mapped on 15 Minute 1:62,500 USGS topographic maps to avoid future duplicate counting. Group size (if more than one carcass present) and other environmental conditions were also noted. In addition, data were recorded on slope, aspect, elevation, cover type, percent crown cover, landform, distance to forest and road or ski trail, and whether the carcass was visible from the road.

Elk carcass data were evaluated and summarized by year. Data for 1988-89 were initially analyzed in 3 categories: carcasses discovered on established survey routes within Yellowstone, carcasses located on survey routes outside Park boundaries, and carcasses reported or discovered while traversing roads. The Chi-square test for homogeneity was used to determine differences in the frequency distribution of sex and age classes in the survey route and road/reported carcass databases. As no significant difference was detected between the 3 samples, the data bases were combined for the age structure analysis. Surveys outside the YNP were only conducted on a single day late in the survey period and in an area of higher human use and fewer predators than in the Park. This data was not used in other portions of the analysis (cause of death, date of death, location characteristics, etc.).

Cover type was categorized into one of 43 different types (Appendix F). Aspect data were analyzed based on 8 categories: North (337-22 degrees), Northeast (22-67 degrees), East (67-112 degrees), Southeast (112-157 degrees), South (157-202 degrees), Southwest (202-247 degrees), West (247-292 degrees), and Northwest (292-337 degrees). Categories for landform included: ridge, upslope, midslope, lowslope, bench, meadow, creek bottom, other, and unknown. The Chi-square test for homogeneity was used to determine differences in carcass location (in terms of slope, aspect, cover type, and landform) between years and/or between male and female elk. Data on estimated time of death were stratified into 15-day time periods, beginning on December 15 (Julian date 349) and ending on March 31 (Julian date 90) for analysis.

The Chi-square test for homogeneity was employed to determine differences in the frequency distribution of carcasses of calves, cows, and adult bulls in our carcass sample compared to that in the live population as determined by early winter classification counts (Mack and Singer 1992). I attempted to correct the relative proportion of cows, calves, and bulls in the live population to account for any bias from differential mortality or sightability, etc., using the total population estimate derived from the Pop-II model (Mack and Singer 1992). The Chi-square test for homogeneity (χ^2) was also used to determine differences the relative frequency distribution of calves, cows, and bulls in the carcass sample compared to the late hunt harvest. For the purposes of analysis, elk were grouped into gross sex and age classes (calf, cow, bull) and then categorized into 8 age classes for comparison with harvest data.

Cause of death was categorized as: accident, predation, disease, starvation/winter kill, or unknown. Cause of death was determined based on bone marrow characteristics (Greer 1968), physical condition of the animal, carcass condition, and physical evidence in the vicinity indicating accident or predation, if available. In many cases, the immediate cause of death could not be determined. Starvation/winter kill was used here to indicate the interaction of severe undernutrition, disease, and parasites if this was indicated by bone marrow and other physical characteristics. Predation was judged to be the cause of death if sufficient evidence of a chase and/or struggle were present including tracks, hair, a trail of blood stains on the ground or vegetation, and condition of the carcass. If sufficient evidence was not present to indicate accident or predation, age and condition of the animal (based on general appearance, obvious signs of illness, tooth condition and wear, and bone marrow characteristics) were noted and cause of death listed as starvation/winterkill, if appropriate, or simply as unknown. A Chi-square test for homogeneity was used to compare cause of death between 1988-89 and 1989-90 and for calves versus adult animals.

Utilization of carcasses by scavenger species was recorded including species and numbers present (as determined by tracks, scat, carcass condition, and direct observation) and percent of carcass utilization noted. Predator/scavenger categories included: coyote, raven, magpie, eagle, unidentified bird, unidentified canine, fox, lion, and unknown. Carcasses were revisited as routes were resurveyed and information was recorded on the date revisited, consumers present or evident, percent

of carcass consumed and any other changes. Observability of carcasses was recorded in terms of weather conditions and distance from route/observer to carcass when first observed (Appendix G). Distances traversed on survey routes were measured using a Geographic Information System (GIS) and by tracing the recorded route on a 15-minute map with a linear map measurer.

Index of Winter Severity

A method for scaling winter severity based on amount and condition of snow, temperature, and summer precipitation across years has been described by Farnes (1991). This scaled index of winter severity (IWS) enables researchers to determine how mild or severe a particular season or month might be relative to other or even historical conditions. In the case of elk, for this study, the accumulated sum of daily temperatures below -18°C for the Yellowstone National Park (Mammoth) weather station was used as a temperature index. This temperature represents the approximate lower critical temperature for elk (Picton, pers. commun). Snow/water equivalent data from the snow courses at Crevice Mountain and Lupine Creek were used for the snow variable. Precipitation amounts at Mammoth during the previous June and July were used as an index to the relative amount of summer forage growth on the northern range available to wintering elk (Farnes 1991).

The index is calculated for each variable (snow water equivalent, precipitation, and accumulated daily minimum temperature) and then weighted to determine the index

of winter severity. In this manner, the IWS was calculated for the winter season (October through March) for the northern range by weighting the snow course snow water equivalent as 40%, the accumulated sum of daily minimum temperatures below -18°C as 40%, and the previous June plus July precipitation as 20%. IWS values were computed for each 15-day period during January-March 1988-89 and 1989-90 in an attempt to estimate the influence of winter severity on natural elk mortality and harvest. The 15-day IWS values were computed by averaging between adjacent 30-day periods. In general, the following rating scale is suggested for describing IWS values (Farnes 1991).

Table 26. Rating scale for IWS values.

0 to +1.0	slightly mild	-1 to -2	severe
0	average (normal)	-2 to -3	moderately severe
0 to -1	slightly severe	-3 to -4	very severe

Results

Winter Carcass Surveys (1988-89)

Between January and mid-March (1/3/89 through 3/18/89), 349 elk carcasses were located and examined on survey routes, along roadways, or from reports (Figure 16). Forty-seven percent ($n = 165$) of elk carcasses were found along survey routes

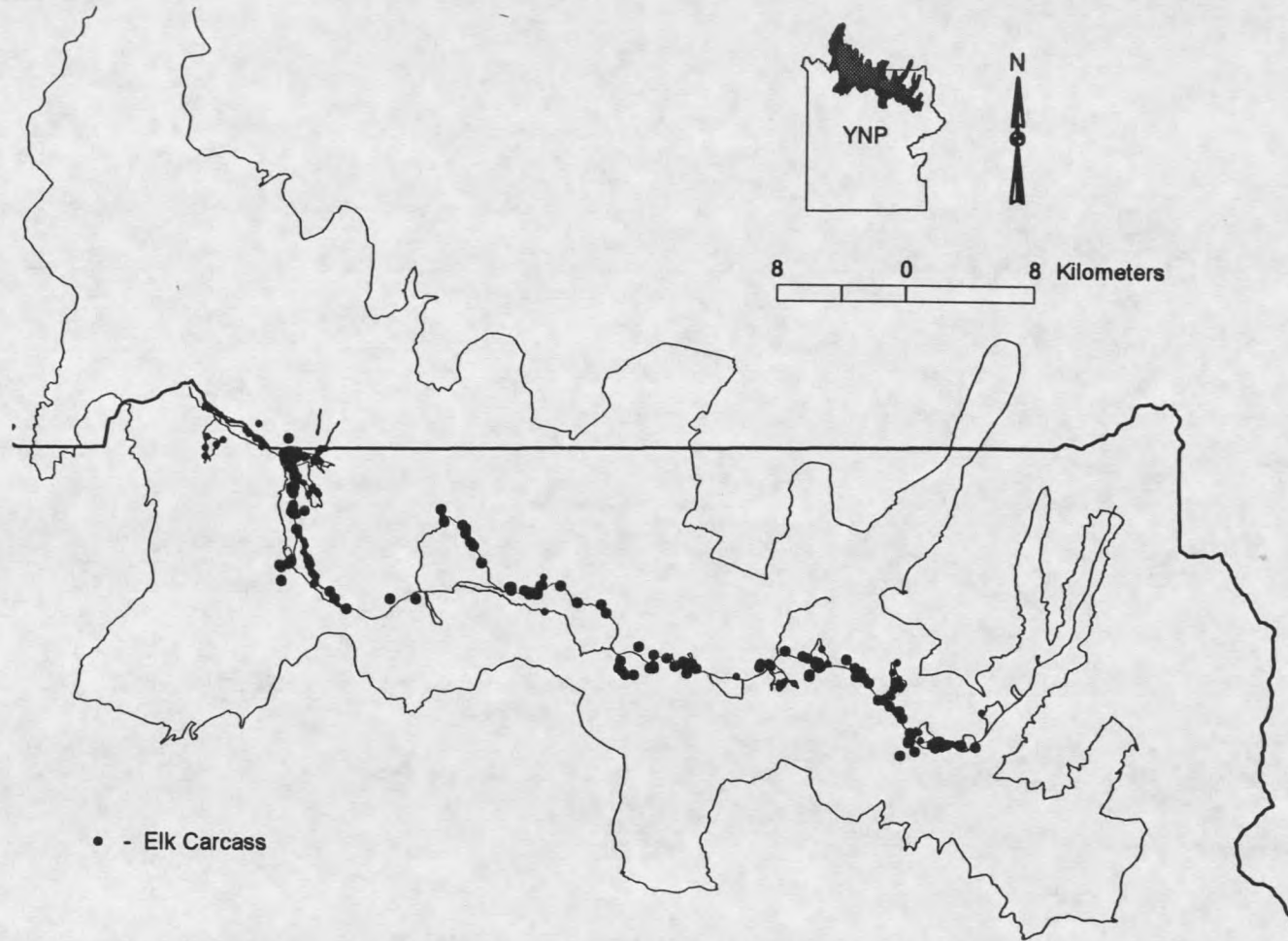


Figure 16. Approximate location of elk carcasses located on the northern winter range during 1988-89 carcass surveys.

within the Park, approximately 43% ($n = 149$) were located along roads or reported, and 10% ($n = 35$) were found on survey routes outside Yellowstone. In addition, 10 carcasses, located along roadways were classified as roadkills. These animals were considered a sample of live population and were not considered in further analysis.

Of the 349 elk carcasses examined, 55% ($n = 193$) were calves, 27% ($n = 94$) were females ≥ 1.5 years-of-age, 14% ($n = 50$) were males ≥ 1.5 years old, and age was unknown for 3% of the animals (7 females, 4 males). The test for homogeneity (χ^2) indicated proportions of elk in each age class did not differ significantly between the three surveys (carcass surveys inside YNP, road/reports, and surveys outside the Park) and the 3 data bases were combined for the age structure analyses. (Carcass survey versus road/report [$\chi^2 = 11.88$, 7 d.f., $P = 0.104$]; Combined survey/roads within Park versus surveys outside the Park [$\chi^2 = 10.9$, 7 d.f., $P = 0.142$]).

With regard to the age and sex distribution, approximately 48% ($n = 167$) of elk carcasses located in our study were female (Table 27, Figure 17). Calves made up the largest portion of females (40%, $n = 66$), followed by the 15+ year-old age group (28%, $n = 46$). Thirty-two percent of carcasses were male ($n = 112$). Approximately 52% ($n = 58$) of males were calves, with 6.5-8.5 year-olds constituting 29% ($n = 32$). Combining both sexes, calves and animals ≥ 15.5 years-of-age comprised the largest portion of carcasses located, 55% and 13%, respectively, followed by 6.5-8.5 year-olds (11%).

Maximum cementum ages recorded for elk during 1988-89 surveys were 22.5 years for cows and 14.5 years for bulls.

Table 27. Age distribution of 349 elk located/reported during carcass surveys in 1988-89. Percentages are based on 349 elk.

	Estimated Age Categories								
	0.5	1.5	2.5	3.5-5.5	6.5-8.5	9.5-11.5	12.5-	15+	Unk
Females	66	2	1	5	8	15	17	46	7
Males	58	1	0	4	32	9	4	0	4
Unkn	69	1	0	0	0	0	0	0	0
Total	193	4	1	9	40	24	21	46	11
Percent	55.30	1.14	0.28	2.57	11.46	6.88	6.01	13.18	3.15

Fifty-one percent of cows ($n = 86$) were ≥ 6.5 years-of-age, while 40% of bulls ($n = 45$) fell into this age group (Table 27). Approximately, 47% of cows ($n = 78$) were ≥ 9.5 years-of-age while only 11% of bulls ($n = 13$) were, 38% of cows ($n=63$) were ≥ 12.5 years-of-age while less than 45% of bulls were in this age category, and approximately 28% of cows were ≥ 15 years-of-age. No bulls (carcasses) greater than 14.5 years-of-age were located during our surveys.

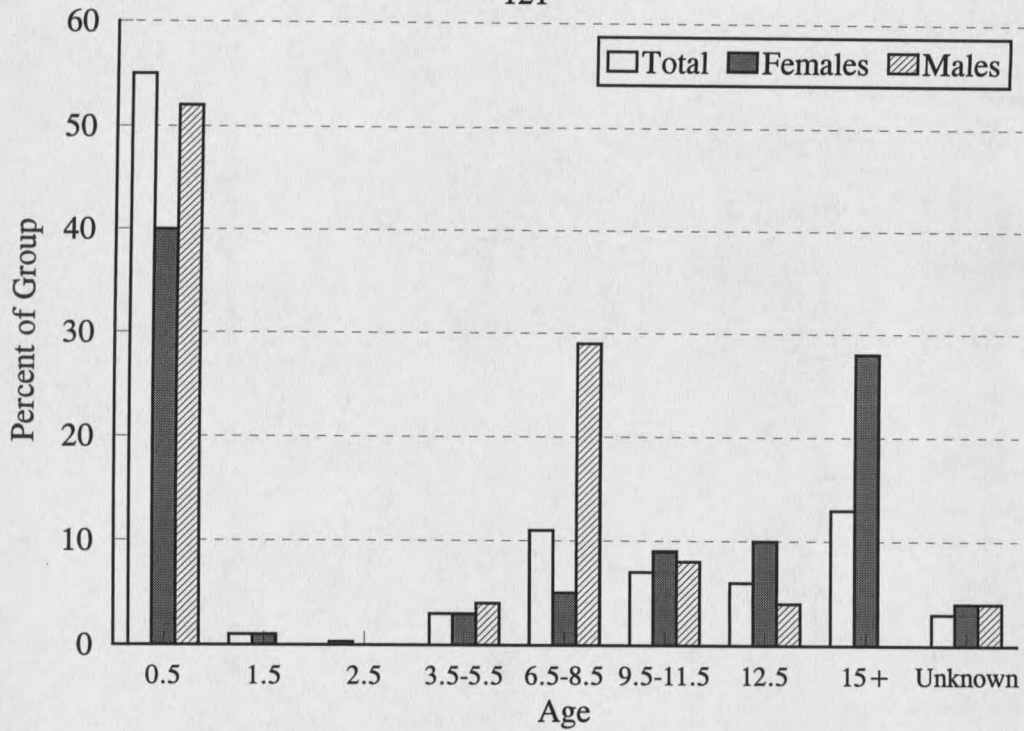


Figure 17. Age Distribution of 349 elk located/reported in 1988-89 carcass surveys.

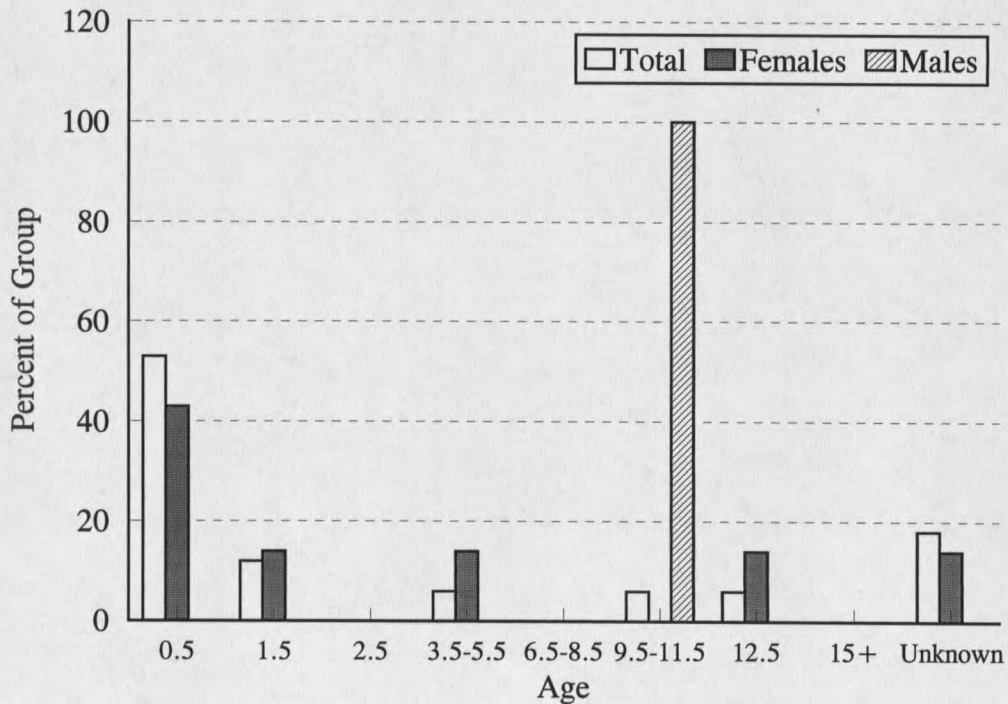


Figure 18. Age Distribution of 17 elk located/reported in 1989-90 carcass surveys.

Winter Carcass Surveys - (1989-90)

During the winter of 1989-90 carcass surveys were conducted between January 17 and March 18. Due to the relatively mild weather, forage availability, and condition of elk going into winter, only 17 elk carcasses were located and examined on transects, along roadways, or from reports in and outside the Park. Eighty-two percent of elk carcasses were found along roads ($n = 13$) or reported ($n = 1$), while only 18% ($n = 3$) were located along survey transects. Of total carcasses, 47% ($n = 8$) were located within 50 m of a roadway and 76% ($n = 13$) were found within 500 m of a road.

While I originally planned to extend the sampling period into April in order to get a sufficient sample size for comparison with 1988-89 data and sampling design, it appeared unlikely that a significant die-off would occur during the year and surveys were terminated in mid-March.

Due to the small sample size, age distribution of the carcasses located during 1989-90 was determined by tooth eruption/wear (when jaws were available) or was otherwise recorded as unknown (Table 28, Figure 18). Of the 17 elk carcasses examined, approximately 53% were calves ($n = 9$), 12% were yearlings ($n=2$), 18% were adult animals ≥ 3.5 years-of-age ($n = 3$), and age was unknown for 3 elk (carcasses). Only one male, an adult bull estimated at 10-12 years old, was found. The two adult cow carcasses located were aged at 3.5 and 12.5 years. Age and/or sex were undeterminable for 10 of the 17 carcasses located due to the degree of consumption and lack of evidence remaining by time of discovery.

Table 28. Age distribution of 17 elk located/reported during carcass transect surveys in 1989-90 as determined by eruption/wear. Percentages are based on 17 elk.

	Estimated Age Categories								
	0.5	1.5	2.5	3.5-5.5	6.5-8.5	9.5-11.5	12.5-14.5	15+	Unk
Females	3	1	0	1	0	0	1	0	1
Males	0	0	0	0	0	1	0	0	0
Unkn	6	1	0	0	0	0	0	0	2
Total	9	2	0	1	0	1	1	0	3
Percent	52.9	11.8	0	5.9	0	5.9	5.9	0	17.6

A Chi-square test of significance was not conducted to compare the age structure of carcasses between the 2 harvest years due to the small sample size in 1989-90. The number of cow, calf, and bull carcasses reported or otherwise located during 1988-89 differed significantly from that expected based on the relative number of animals in the wild population (Mack and Singer 1992) ($\chi^2 = 397$, 2 d.f., $P < 0.0005$) (Table 29, Figure 19). Calves comprised a much greater proportion of carcasses than was observed/estimated in the live population, while adult females comprised a much smaller portion.

Age distribution of natural mortality, as indicated by carcass surveys, also differed significantly from that of the late hunt harvest ($\chi^2 = 373$, 2 d.f., $P < 0.0005$), with calves and bulls making up the greater portion (55%) of natural mortality compared to adult cows, but a much smaller portion of the harvest. Adult females

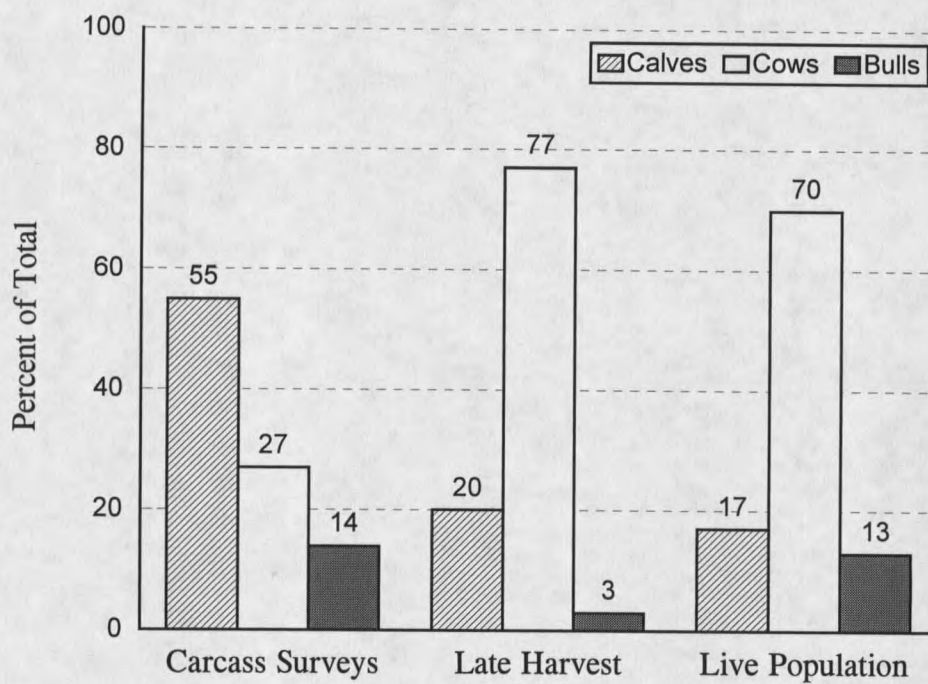


Figure 19. Distribution of calves, cows, and bulls among elk carcasses, harvested elk, and the estimated live population.

constituted 70% of the estimated live population, but were under-represented in the carcasses surveys and over-represented in the harvest.

Table 29. Comparison of number (and percentage) of cows, calves, and bulls observed in carcass surveys, the Gardiner late hunt harvest, and estimated in the wild population in 1988-89.

Source	Population Distribution		
	Cows	Calves	Bulls
Carcass Survey ^a	94 (27)	193 (55)	50 (14)
Late Hunt Harvest	1865 (77)	476 (20)	67 (3)
Population Estimate ^b	14419 (70)	3460 (17)	2740 (13)

^a Percentage is of 349 total carcasses, age/sex was unknown for 11 animals.

^b Based on early winter classification counts corrected using Pop II population estimate (Mack and Singer 1992).

Time of Death

Elk died at different rates during the winter of 1988-89. More calves and older animals (12+) died from December through January than animals in the 1-5 or 6-11 year-old age groups. However, the greatest number of animals (in all age groups) died during February, with most prime age (6-11 year-olds) and older animals (12+) dying between February 1-15 and the majority of calves and 1-5 year-olds dying between February 16-28 (Tables 30, 31, Figure 20). Despite the small sample size, 1989-90 field data show more calves (n = 5) died during March 1-15, while the majority of mature animals (n = 3) died from February 16-28 (Tables 32, 33, Figure 21).

Table 30. Age distribution of carcasses located in 1988-89 surveys by time period.

Age Class	Dec.	Jan.		Feb.		March	Total
	15-31	1-15	16-31	1-15	16-28	1-15	
Calves		4	24	57	65	18	168
1.5					1		1
2.5					1		1
3.5-5.5				2	3		5
6.5-8.5		1	1	14	11	6	33
9.5-11.5	1		1	8	3	8	21
12.5-14.5		2	1	6	7	4	20
15.5+	1	4	8	19	6	1	39
Unknown			3	5	4	1	13
Total	2	11	38	111	101	38	301

Table 31. Sex and age distribution of carcasses located in 1988-89 surveys by time period.

Age Class	Dec.	Jan.		Feb.		March	Total
	15-31	1-15	16-31	1-15	16-28	1-15	
<u>Calves</u>							
Female			3	15	26	6	50
Male			3	12	29	9	53
Unknown		4	18	30	10	3	65
Total Calves		4	24	57	65	18	168
Cows	2	6	12	33	21	10	84
Bulls		1	2	19	15	10	47
Unknown				2			2
Total	2	11	38	111	101	38	301

Table 32. Age distribution of carcasses located in 1989-90 transect surveys by time period.

Age Class	Dec.		Jan.		Feb.		March		Total
	15-31	1-15	16-31	1-15	16-28	1-15	16-31		
Calves				2	2	5		9	
1.5							2	2	
2.5								0	
3.5-5.5					1			1	
6.5-8.5								0	
9.5-11.5					1			1	
12.5-14.5					1			1	
15.5+								0	
Unknown			1		1		1	3	
Total	0	0	1	2	6	5	3	17	

Table 33. Sex and age distribution of carcasses located in 1989-90 transect surveys by time period.

Age Class	Dec.		Jan.		Feb.		March		Total
	15-31	1-15	16-31	1-15	16-28	1-15	16-31		
Calves									
Female				2	0	1		3	
Male					0	0		0	
Unknown					2	4		6	
Total				2	2	5		9	
Cows					2	0	1	3	
Bulls					1	0		1	
Unknown			1		1		2	4	
Total	0	0	1	2	6	5	3	17	

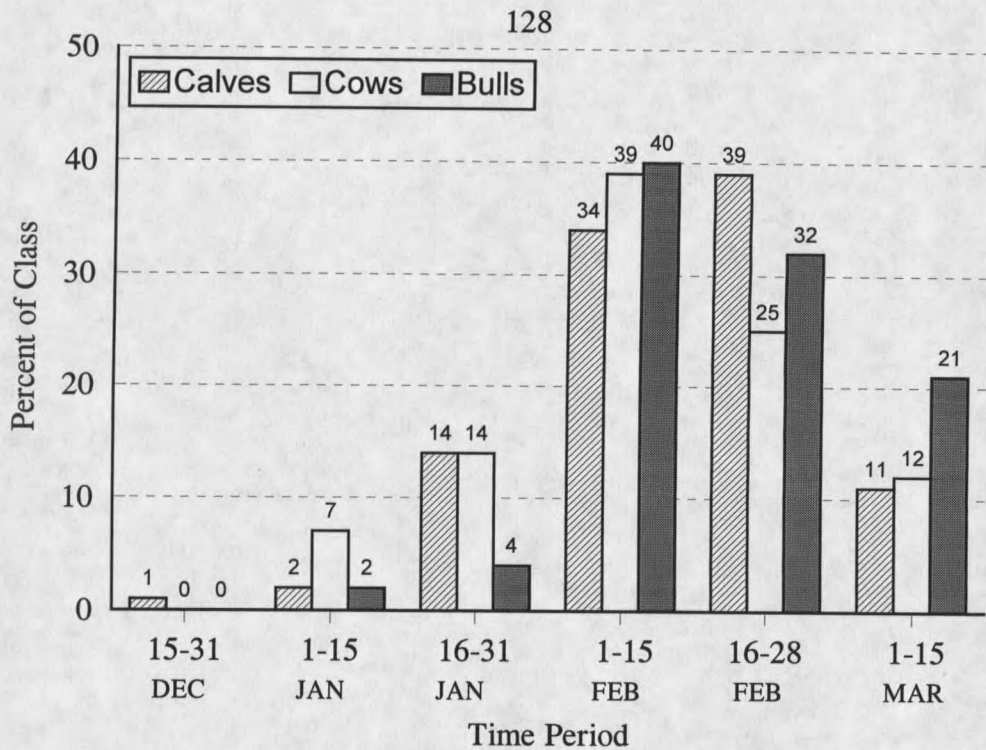


Figure 20. Percent distribution of elk by age/sex class that died in each 15-day time period based on date of death estimated during 1988-89 carcass surveys.

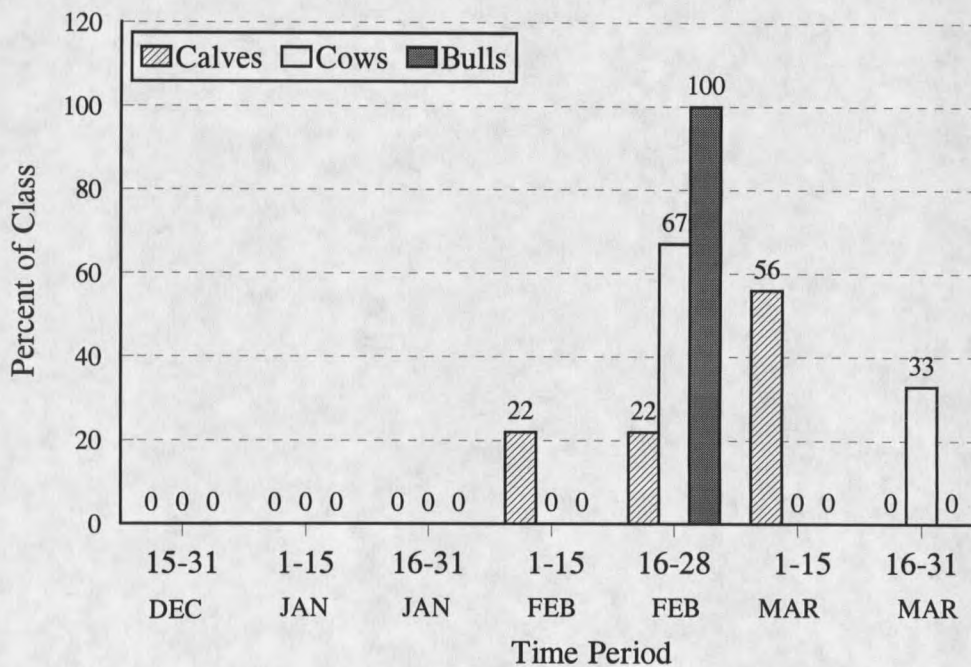


Figure 21. Percent distribution of elk by age/sex class that died in each 15-day time period based on date of death estimated during 1989-90 carcass surveys.

Correlation with Index of Winter Severity

Analysis shows that although there was higher mortality during all winter months in 1988-89 than seen in several previous winters, the greatest number of animals died during the period of February 1-28. While the severity index continued to decline from February through April, the large die-off seen during February coincided with a period of particularly harsh weather which presumably pushed many animals "over the edge." (Table 34, Figure 22).

Table 34. Index of winter severity for the northern range in 1988-90, as calculated for 15-day intervals.

Year	Time Period					
	Jan 1-14	Jan 15-31	Feb 1-14	Feb 15-28	Mar 1-14	Mar 15-31
1988-89	-0.2	-0.2	-0.2	-1.1	-2.0	-2.3
1989-90	-0.5	-0.3	-0.2	-0.3	-0.7	-0.6

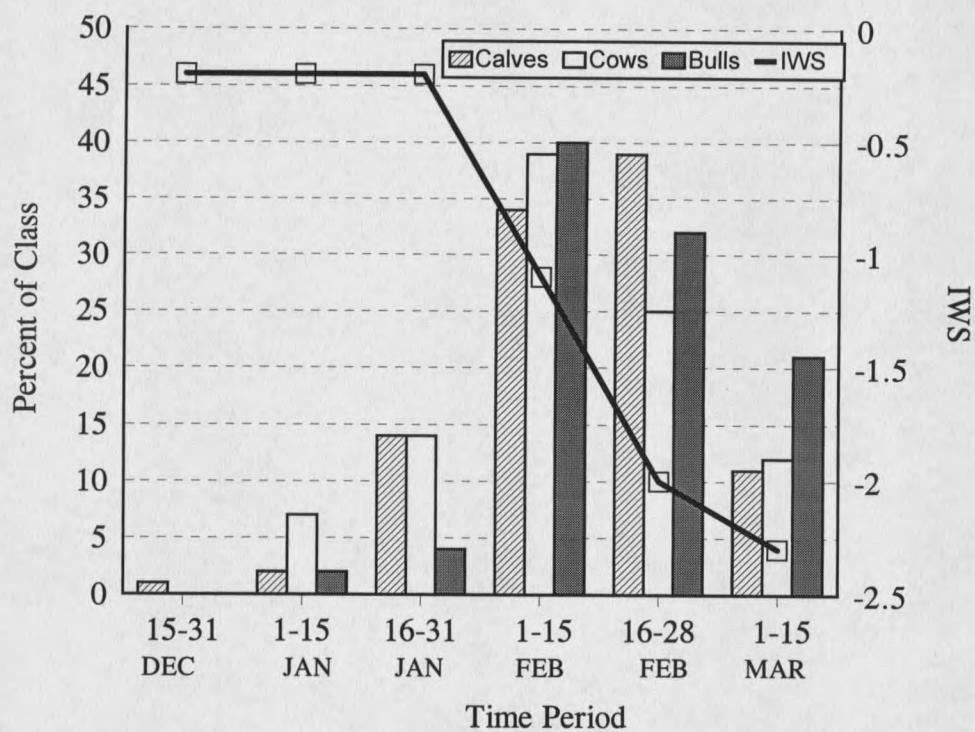


Figure 22. Percent distribution of elk that died in each 15-day time period as related to Index of Winter Severity (IWS) during 1988-89 carcass surveys.

Cause of Death

Cause of death differed significantly between 1988-89 and 1989-90 ($\chi^2 = 69$, 3 d.f., $P < 0.0005$). Starvation/winter kill claimed the majority of animals located in 1988-89 surveys (78%), while predation and unknown causes were the primary cause of mortality in 1989-90 (Table 35, Figure 23). During 1988-89, cause of death was unknown for 18% ($n = 55$) of carcasses, while 3% ($n = 8$) died as a result of predation, and 2% ($n = 5$) were the result of accident. One calf was killed by a mountain lion. Six calves and 1 adult bull died as a result of possible predation by coyotes. All suspected incidents of predation occurred fairly early in the survey period, prior to mid-February, with approximately 87% occurring on or before January 26th.

Table 35. Cause of death for elk located in 1988-89 and 1989-90 carcass surveys.

Year	Cause of Death			
	Accident	Predation	Starvation	Unknown
1988-89 ^a	5 (2)	8 (3)	246 (78)	55 (18)
1989-90 ^b	1 (6)	7 (41)	2 (12)	7 (41)

^a Percent is of 314 total carcasses. ^b Percent is of 17 total carcasses.

A significant difference in cause of death between calves and adult animals was not detected in 1988-89 ($\chi^2 = 6.8$, 3 d.f., $P = 0.078$) (Table 36, Figure 24). Starvation/winter kill was the major cause of death for both groups. However, a greater proportion of calves died as a result of predation, while more adults appeared to die from accidents. Accidents included falling in crevices, slamming into or locking

