

# Selection of Northern Yellowstone Elk by Gray Wolves and Hunters

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## Abstract

We compared selection of northern Yellowstone elk (*Cervus elaphus*) by hunters in the Gardiner Late Hunt and northern Yellowstone wolves (*Canis lupus*) with regard to sex, age, and impacts to recruitment. We compared harvest data from 1996–2001 with wolf-killed elk data from 1995–2001. We assessed the effects of hunting and wolf predation on reproductive female elk by constructing a life table and calculating reproductive values for females in the northern Yellowstone herd. We devised an index of total reproductive impact to measure impacts to calf production due to hunting and wolf predation. The age classes of female elk selected by wolves and hunters were significantly different. Hunters selected a large proportion of female elk with the greatest reproductive values, whereas wolves selected a large proportion of elk calves and older females with low reproductive values. The mean age of adult females killed by hunters throughout the study period was 6.5 years, whereas the mean age of adult females killed by wolves was 13.9 years. Hunting exerted a greater total reproductive impact on the herd than wolf predation. The combined effects of hunters killing prime-aged females (2–9 yr old), wolves killing calves, and predation by other predators has the potential to limit the elk population in the future. Yellowstone is unique in this regard because multiple predators that occur sympatrically, including hunters, wolves, grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), cougars (*Felis concolor*), and coyotes (*Canis latrans*), all prey on elk. Using an Adaptive Harvest Management process the known female elk harvest during the Gardiner Late Hunt has been reduced by 72% from 2,221 elk in 1997 to 620 elk in 2004. In the future, hunting harvest levels may be reduced further to partially offset elk losses to wolves, other predators, and environmental factors. (JOURNAL OF WILDLIFE MANAGEMENT 70(4):1070–1078; 2006)

## Key words

age structure, *Canis lupus*, *Cervus elaphus*, elk, Gardiner Late Hunt, gray wolf, predation, recruitment, reproductive value.

The growth rate of Yellowstone National Park's (YNP) northern elk (*Cervus elaphus*) herd has been shaped by many factors, which fall into 2 broad categories—wildlife management and natural ecological processes. Wildlife management activities include the extensive culling and removal of YNP elk that occurred from the 1930s until 1968, as well as the annual harvests of northern Yellowstone elk that occur outside the park during Montana's general (autumn) elk hunt and the Gardiner Late Hunt (Coughenour and Singer 1996, Lemke et al. 1998, Singer et al. 1998). Natural ecological processes that influence herd population dynamics include predation (Singer et al. 1997, Mech et al. 2001, Smith and Guernsey 2002), density-dependent mechanisms (Houston 1982, Singer et al. 1997, Taper and Gogan 2002), and weather effects. Historically, precipitation levels and winter severity have had the greatest impact on northern herd abundance through large reductions from winter-kill (Lemke et al. 1998, National Research Council [NRC] 2002).

Although a policy of natural regulation was instituted in YNP in 1969, harvest of northern Yellowstone elk during the 2 annual hunts continues to influence sex–age structure as well as elk abundance (Lemke et al. 1998). An average 1,590 elk, mostly females, were removed annually in the Gardiner Late Hunt from 1995–2001. During this same period, an average 333 elk, mostly males, were harvested annually in the autumn hunt (Montana Fish Wildlife and Parks, unpublished data).

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We examined and compared characteristics of female northern Yellowstone elk killed by gray wolves (*Canis lupus*) and harvested in the Gardiner Late Hunt. Key questions we examined included: 1) How does predation differ between humans and wolves with regard to elk sex and age?, 2) Is the reproductive segment of the female elk population differentially affected by wolf predation and human harvest?, and 3) Has the age structure of the female segment of the elk population changed from 1995–2001 since the reintroduction of wolves in 1995–1996?

## Background

Thirty-one gray wolves from Canada were reintroduced into YNP in 1995 and 1996. By the end of 2001, the YNP population was estimated at 132 wolves, including 77 wolves in the northern range of the park (Smith and Guernsey 2002). As the wolf population increases on YNP's northern range, it becomes increasingly important to understand differences in elk predation patterns between humans and wolves (Boyd et al. 1994). Local sport hunters and citizen's groups have expressed concern about wolf predation levels on ungulates, as well as impacts on elk-calf recruitment (Herring 2000, Zumbo 2000a,b).

Human attitudes toward wolves are one of the key factors influencing the success or failure of wolf restoration efforts (Paquet et al. 2001). This creates a critical demand for analysis of the effects of wolves and humans on the northern Yellowstone elk herd. This information is important for management decisions, policy making, public education, and other wolf restoration efforts. The United States Congress recently charged the NRC with the task of forming a committee on ungulate management to

review information on the population ecology and natural regulation of YNP's northern range ungulates. The NRC committee recommended an adaptive-management approach to northern range issues and continued monitoring of wolf-prey interactions based on the dynamic nature of ungulate population fluctuations and insufficient scientific knowledge to predict outcomes of different management approaches (NRC 2002). The committee acknowledged a need for additional research related to northern Yellowstone elk dynamics.

The effects of gray wolf predation on ungulate prey have been studied extensively. Biologists recognize the ability of wolves to influence sex and age composition, recruitment and death rates, and rates of population change in ungulate prey species (Pimlott et al. 1969, Mech 1970, Peterson 1977, Seip 1995, Mech and Peterson 2003). The selectivity of wolf predation and its role in predator-prey systems have illustrated that wolves generally cull the most vulnerable (e.g., young, old, weak, or diseased) individuals from a prey base (Peterson 1977, Fuller and Keith 1980, Carbyn 1983, Mech et al. 1995, Smith 1998, Mech et al. 2001). Selection of prey by wolves is likely governed by Temple's (1987) assertion that predator selectivity increases as the difficulty of capturing prey increases. In some instances, wolves are capable of regulating or limiting the population growth of a prey species (Fuller and Keith 1980, Gasaway et al. 1992, Bergerud and Elliot 1998).

Harvest of ungulates by humans can also strongly affect the population characteristics of hunted populations (McCullough 1979, Ginsberg and Milner-Gulland 1994, Bender et al. 1999, Bender 2002). In areas of North America where elk hunting occurs, it is the major source of elk mortality, and a stronger limiting factor than predation, habitat quality, disease, winter severity, or accidents (Ballard et al. 2000).

Montana's Gardiner Late Hunt has a rich and colorful history dating back to the early 1900s when most hunters arrived by train to harvest migrant Yellowstone elk (Lemke 1995a). Over time the Gardiner Late Hunt has evolved from a largely unrestricted elk hunting season to one of the most popular, closely regulated, and successful elk hunts in North America. The Late Hunt now begins the first week of January and runs until mid-February each year. In recent years 6,500 to 8,500 hunters have applied for Gardiner Late Hunt elk permits. The average annual hunter success rate since 1976 is 63%, compared to a 15–20% success rate during general autumn elk hunting seasons elsewhere in Montana.

Following an 8-year moratorium from 1968–1975, the Gardiner Hunt became a limited entry, permit-only hunting season with several management regulations. These changes included closing hunting on an important elk staging area immediately adjacent to YNP, designating specific numbers of antlerless or either-sex elk permits, assigning specific 2- or 4-day hunting periods for each hunter, dividing the hunting area into 5 units with the ability to open or close units depending on elk distribution, and requiring mandatory check-in and check-out for all hunters (Lemke 1995a,b).

The Gardiner Late Hunt has 2 primary objectives: 1) to ensure winter-range forage for migrant Yellowstone elk on a sustainable basis by using hunters to help manage the number of elk wintering

north of YNP, and 2) to harvest elk in ways that will minimize the effect of hunting on migratory behavior, allowing winter elk use to be distributed over the winter range in proportion to forage availability (Lemke 1995b). Because the Gardiner Late Hunt is a population management tool, the harvest is directed primarily toward females, with 90+% of all permits issued for antlerless elk.

The combination of human hunting and wolf predation, or predation from multiple large predators may offset or exceed recruitment, leading to a decline in the prey population (Bjorge and Gunson 1989, Dekker et al. 1995, Kunkel and Pletscher 1999). The potential of predation as a limiting factor on ungulate populations is greater in areas where multiple predators occur sympatrically (Kunkel et al. 1999, Kunkel and Pletscher 1999). Yellowstone's northern range is unique in this regard compared to most ecosystems in the contiguous United States because all of the large predators that occurred historically are present today. This includes humans (*Homo sapiens*), wolves, cougars (*Felis concolor*), coyotes (*Canis latrans*), black bears (*Ursus americanus*), and grizzly bears (*Ursus arctos*).

## Study Area

Yellowstone National Park is an 8,991-km<sup>2</sup> preserve of diverse habitats situated mostly in the northwestern corner of Wyoming, USA, but it extends into southwestern Montana and southeastern Idaho, USA. We focused on the northern Yellowstone winter range (1,531 km<sup>2</sup>) as described by Houston (1982) and Lemke et al. (1998). Sixty-five percent of the northern range was within YNP and 35% was located north of the park boundary on public and private lands. Our study area was the winter range of the northern Yellowstone elk herd. The northern range encompassed areas of lower elevations, 1,500–2,500 m, generally along the Yellowstone, Lamar, and Gardner river drainages. Most of the northern range was steppe or shrub-steppe (55%), dominated by Idaho fescue (*Festuca idahoensis*), bluebunch wheatgrass (*Pseudoroegneria spicata*), and big sagebrush (*Artemisia tridentata*). Conifer forest covered 41% of the northern range, with small amounts of aspen (*Populus tremuloides*) and willow (*Salix* spp.; Coughenour and Singer 1996). The climate was characterized by long, cold winters and short, cool summers, with average monthly temperatures ranging from –12°C–13°C. Annual precipitation within the range of the northern elk herd varied between 50–125 cm (Houston 1982). The climate, vegetation, and geology of the area were described in detail by Houston (1982) and Despain (1991).

## Methods

We collected wolf-kill and wolf abundance data during 2 field studies that occurred annually for 30-day periods from March 1995–May 2001 (Smith et al. 2004). These studies focused on wolf predation and other ecological relationships related to wolves on the northern range of YNP. The early study ran from 15 November–14 December annually, and the late study was 1 March–30 March annually. Outside of winter study periods, we recorded kills during weekly telemetry flights over the study area, and we collected them when possible.

We collected elk-harvest data at Montana Fish Wildlife and Parks (MFWP) hunter check stations from the 1995–2001

**Table 1.** Life table for female northern Yellowstone elk constructed using Gardiner Late Hunt harvest data from 1996–2001 in the s(x) column.

Elk age x	No. in population S(x)	Average pregnancy rate b(x)	Survivorship l(x)	Survival probability			Initial estimate $e^{-rx}$	Corrected estimate $e^{-rx} l(x)b(x)$
				g(x)	l(x)b(x)	l(x)b(x)x		
0	6528	0.0000	1.0000	0.8712	0.0000	0.0000	0.000	0.000
1	5687	0.0735	0.8712	0.8943	0.0640	0.0640	0.052	0.050
2	5086	0.5142	0.7791	0.9194	0.4006	0.8012	0.268	0.244
3	4676	0.7137	0.7163	0.8687	0.5112	1.5336	0.279	0.243
4	4062	0.6960	0.6222	0.8476	0.4331	1.7323	0.194	0.160
5	3443	0.7193	0.5274	0.8281	0.3794	1.8970	0.139	0.110
6	2851	0.7193	0.4367	0.8137	0.3142	1.8849	0.094	0.071
7	2320	0.7553	0.3554	0.8151	0.2684	1.8791	0.066	0.047
8	1891	0.7433	0.2897	0.8186	0.2153	1.7226	0.043	0.030
9	1548	0.7092	0.2371	0.8243	0.1682	1.5135	0.027	0.018
10	1276	0.6597	0.1955	0.8213	0.1289	1.2894	0.017	0.011
11	1048	0.7363	0.1605	0.7872	0.1182	1.3003	0.013	0.008
12	825	0.6853	0.1264	0.7952	0.0866	1.0393	0.008	0.004
13	656	0.6377	0.1005	0.7530	0.0641	0.8330	0.005	0.003
14	494	0.6262	0.0757	0.7065	0.0474	0.6634	0.003	0.001
15	349	0.5343	0.0535	0.6734	0.0286	0.4285	0.001	0.001
16	235	0.5240	0.0360	0.5787	0.0189	0.3018	0.001	0.000
17	136	0.5220	0.0208	0.5074	0.0109	0.1849	0.000	0.000
18	69	0.4462	0.0106	0.4928	0.0047	0.0849	0.000	0.000
19	34	0.2388	0.0052	0.4706	0.0012	0.0236	0.000	0.000
20	16	0.0000	0.0025	0.3125	0.0000	0.0000	0.000	0.000
21	5	0.0000	0.0008	0.8000	0.0000	0.0000	0.000	0.000
22	4	0.0000	0.0006	0.2500	0.0000	0.0000	0.000	0.000
23	1	0.0000	0.0002	0.0000	0.0000	0.0000	0.000	0.000
Net reproductive rate				Ro =	3.26	19.18	1.21	0.9998
Generation time				G =	5.876			
				r (est) =	0.201			
				r (Euler) =	0.2484			

Gardiner Late Hunts. The Late Hunt ran from the first week of January until mid-February during these years. All adult elk included in age class analysis (wolf- and hunter-killed) were aged by counting cementum annuli (Mattson's Lab, Milltown, Montana; Hamlin et al. 2000). Elk harvested during the autumn hunt could not be included in age-specific analysis because all information gathered for this hunt was based on a sample of hunter phone surveys (e.g., elk were not aged accurately). We describe data analysis methods below.

#### Age Comparison of Wolf- and Hunter-Killed Elk

We tested for a significant difference in the mean age of adult (yearlings and older) female elk killed by wolves and hunters using ANOVA. For this test, we compared pooled data on wolf-killed elk from 1995–2001 against pooled data on elk harvested in the Gardiner Late Hunt from 1996–2001.

We compared sex and age classes of female elk killed by wolves from 1995–2001 and in the Gardiner Late Hunt from 1996–2001 using Pearson's chi-square analysis. It was not possible to accurately compare male elk harvest with wolf predation of male elk because over 90% of the permits issued in the Late Hunt were for antlerless elk, and there were recognized biases for harvesting older, large-antlered bulls. Furthermore, females were much more important than males in a polygamous species in terms of species fecundity.

#### Life Table and Reproductive Values

We created a life table (Caughley 1966, Gotelli 2001) for northern Yellowstone female elk (Table 1) using pooled harvest data from 1996–2001 to represent frequencies of ages [s(x)] in the living

population (Caughley 1966). The life table allowed age-specific reproductive values,  $v(x)$ , to be calculated (Table 2). We defined reproductive value as the *relative* number of offspring yet to be born of a female at a given age, and we used reproductive values to determine which ages were most valuable to future population growth (Gotelli 2001). Reproductive value did not represent the total expected offspring to be produced because future production of offspring was discounted by the survival probability while in the current age class. A reproductive value of <1.0 means that the female will not contribute to any population growth while in her current age class.

We gathered pregnancy data from cooperating hunters during the Gardiner Late Hunts. Hunters are asked to check and report the presence or absence of a fetus after harvesting a female elk. We derived age-specific pregnancy rates from a sample of 5,367 reports by hunters (>50% of hunters) from 1996–2001. We used average pregnancy rates within each age class over the period 1996–2001 for life table and reproductive value calculations. We determined age classes by counting cementum annulations. We plotted age-specific reproductive values against the female age distributions of adult wolf-killed and hunter-killed elk to assess impacts to calf production.

#### Index of Total Reproductive Impact

We created an index of total reproductive impact to compare removal of potentially reproductive elk by wolves and hunters in 2001. We created this index only for 2001 because wolf abundance was greatest in that year. The index provided a single number that represented the relative impact on females with reproductive

**Table 2.** Calculation of reproductive values,  $v(x)$ , for female northern Yellowstone elk using Gardiner Late Hunt harvest data from 1996–2001.

Elk age $x$	Survivorship $l(x)$	Pregnancy rate $b(x)$	Stable age distribution			Reproductive value distribution		
			$l(x)e^{-rx}$	$c(x)$	$e^{rx}/l(x)$	$e^{-ry}/l(y)b(y)$	Sum $e^{-ry}/l(y)b(y)$	$v(x)$
0	1.000	0.0000	1.000	0.318	1.000	0.000	1.000	1.000
1	0.871	0.0735	0.680	0.216	1.472	0.050	1.000	1.471
2	0.779	0.5142	0.474	0.151	2.109	0.244	0.950	2.004
3	0.716	0.7137	0.340	0.108	2.941	0.243	0.706	2.077
4	0.622	0.6960	0.230	0.073	4.341	0.160	0.463	2.012
5	0.527	0.7193	0.152	0.048	6.565	0.110	0.303	1.990
6	0.437	0.7193	0.098	0.031	10.164	0.071	0.194	1.967
7	0.355	0.7553	0.062	0.020	16.012	0.047	0.123	1.966
8	0.290	0.7433	0.040	0.013	25.184	0.030	0.076	1.904
9	0.237	0.7092	0.025	0.008	39.438	0.018	0.046	1.818
10	0.195	0.6597	0.016	0.005	61.336	0.011	0.028	1.724
11	0.161	0.7363	0.010	0.003	95.738	0.008	0.017	1.661
12	0.126	0.6853	0.006	0.002	155.909	0.004	0.010	1.507
13	0.100	0.6377	0.004	0.001	251.362	0.003	0.005	1.324
14	0.076	0.6262	0.002	0.001	427.913	0.001	0.003	1.168
15	0.053	0.5343	0.001	0.000	776.490	0.001	0.001	0.984
16	0.036	0.5240	0.001	0.000	1478.333	0.000	0.001	0.856
17	0.021	0.5220	0.000	0.000	3274.764	0.000	0.000	0.735
18	0.011	0.4462	0.000	0.000	8274.629	0.000	0.000	0.538
19	0.005	0.2388	0.000	0.000	21527.692	0.000	0.000	0.239
20	0.002	0.0000	0.000	0.000	58645.562	0.000	0.000	0.000
21	0.001	0.0000	0.000	0.000	240582.413	0.000	0.000	0.000
22	0.001	0.0000	0.000	0.000	385525.083	0.000	0.000	0.000
23	0.000	0.0000	0.000	0.000	1976930.400	0.000	0.000	0.000
Sum $l(x)e^{-rx}$			3.144					

values  $>0.0$ . This index may be valuable for comparing long-term trends in the impacts of wolves and humans to herd recruitment. We calculated the index by multiplying the number of elk in age classes with reproductive values  $>0.0$  (calves through age 19) by the reproductive value for that age class. For hunters, we used Gardiner Late Hunt data. For wolves, our data were only a sample of the annual number of elk killed by wolves, so we first estimated annual off-take of elk due to wolves using Keith's (1983) method. We apportioned this off-take among sex and age classes based on the sex and age distribution of the wolf-killed elk sample. This is the least-conservative method of estimating annual wolf predation from winter kill rates, so the true total reproductive impact due to wolves is most likely lower than we reported in our analysis.

### Wolf-Killed Elk Extrapolation

We estimated per capita kill rates for northern Yellowstone wolves in winter at 1.83 kills/wolf/month (Smith et al. 2004). Because this kill rate was based only on winter study periods, there was a problem in extrapolating to a year-round rate of 22 kills/wolf/year. There are several approaches reported in wolf-moose literature to estimate summer predation rates from winter predation studies. Keith (1983) used the same rate year-round under the assumption that lower overall predation rates in summer are offset by a pulse of calf-kills by wolves in summer. Messier (1994) applied a correction factor of 0.71 to winter-kill rates to estimate year-round predation levels. In our study, Messier's approach would have resulted in an estimate of  $22 \text{ elk/wolf/year} \times 0.71 = 15.3 \text{ elk/wolf/year}$ .

We used Keith's approach to estimate annual wolf predation by multiplying the winter-kill rate of 22 elk/wolf/year by the northern Yellowstone wolf abundance estimate for 2001. We recognize that extrapolating kill rates from winter study periods to

annual kill rates is problematic (Smith et al. 2004) because it likely overestimates annual predation rates, but this was a necessary concession to calculate and compare total reproductive impact on female elk by hunters and wolves.

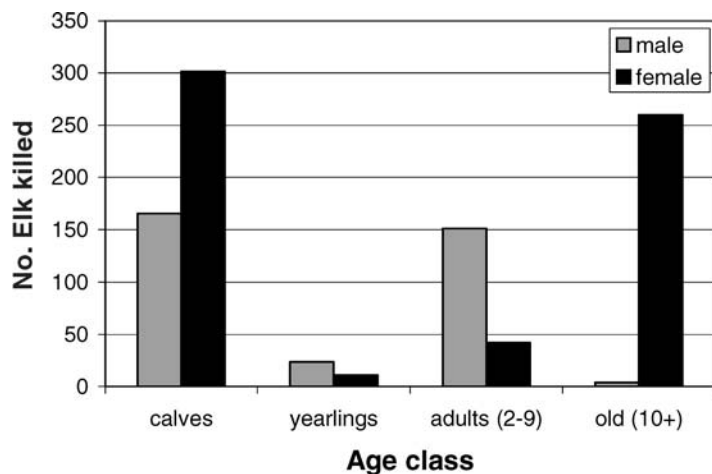
### Analysis of Elk Age Structure

To assess whether wolf predation has altered the age structure of northern Yellowstone elk since wolf reintroduction in 1995, we tested for differences in the proportions of female elk in each age class from 1996–2001 (calf, yearling, 2–9, and 10+), one age class at a time, using Pearson's chi-square analysis. Because Late Hunt age distributions for harvested females were representative of the female elk population (Lemke 2001), we used Late Hunt harvest data from 1996–2001. Although hunters may select against harvesting a calf or yearling due to the greater amount of meat provided by an adult female elk, this bias is carried through year to year. Therefore, any bias in hunter selection against calves or yearlings should not affect our analysis of wolf effects on elk age structure from year to year.

## Results

### Wolf Predation Overview

We examined 1,415 wolf-killed elk during March 1995–May 2001, including 526 females (37%), 294 males (21%), and 595 elk (42%) of unknown gender, which were mostly calves ( $n = 414$ ). We determined gender for only 53 of 467 wolf-killed calves because calf carcasses were usually fully consumed by wolves and scavengers. Therefore, we assigned gender to the 414 calves of unknown sex based on the sex ratio of calves harvested in the Gardiner Late Hunt from 1996–2001 (841 females and 518 males; 62% females). Because hunters cannot visually determine the sex



**Figure 1.** Sex and age class of 959 wolf-killed northern Yellowstone elk from Mar 1995–May 2001. Calf age class included 414 wolf-killed calves of unknown gender, which were assigned gender based on the sex ratio of calves harvested in the Gardiner Late Hunt from 1996–2001 (841 F and 518 M = 62% F).

of a calf before shooting it, we assume there were no other sex-related biases among hunter-killed calves, and that the harvest ratio reasonably reflects the calf sex-ratio in the population. We also assumed no sex-related biases when wolves kill calves, but this has not been studied in Yellowstone. After assigning the wolf-killed calf sex ratio for calves of unknown gender, the composition of wolf-killed elk was 783 females (55%), 451 males (32%), and 181 elk of unknown gender (13%).

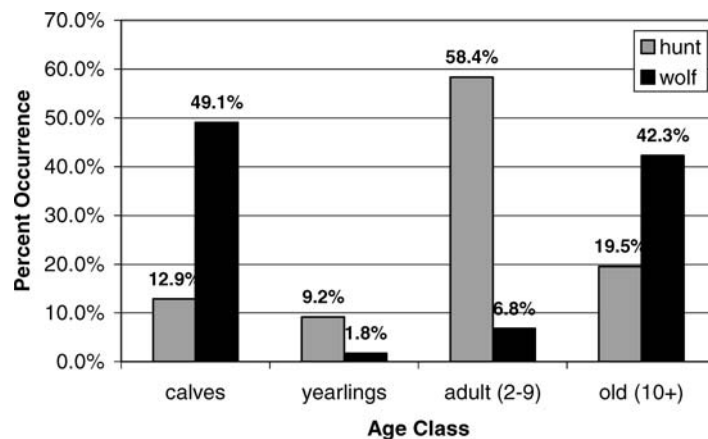
We excluded 456 wolf-killed elk from further analysis because of unknown gender ( $n = 181$ ), unknown age class ( $n = 145$ ), or age estimated only by tooth wear ( $n = 130$ ). The remaining 959 elk in the wolf-killed sample were aged accurately, either by tooth eruption for calves and yearlings, or by counting cementum annuli for adult elk (Hamlin et al. 2000). The wolf-killed sample contained 467 calves (49% of all kills), 35 yearlings (4%), 193 adults (2–9 yr old; 20%), and 264 old elk ( $\geq 10$  yr old; 27%; Fig. 1). Females comprised 64% of all known-sex elk killed, with 91% of females from the calf and old ( $\geq 10$  yr old) age classes. Overall, calves of both sexes and old female elk ( $\geq 10$  yr old) were most heavily utilized by wolves.

#### Age Comparison of Wolf- and Hunter-Killed Elk

The mean age of adult female elk killed by wolves (13.9 yr) was significantly older ( $F = 31.65$ ,  $P < 0.0001$ ) than the mean age of adult female elk killed by hunters (6.5 yr). The age classes of female elk selected by wolves ( $n = 615$ ) and hunters ( $n = 6,528$ ) in the Gardiner Late Hunt differed significantly ( $P < 0.0001$ ,  $\chi^2 = 908.8$ , 3 df; Fig. 2). Fifty-eight percent of female elk killed by hunters were adult females of prime breeding age (ages 2–9 yr), whereas wolves selected only 6.8% of elk from this age class. Wolves killed proportionally more calves (49.1%) than hunters (12.9%), and more old females (42.3%) than hunters (19.5%). Yearlings comprised a small proportion of both hunter and wolf-kills (9.2% and 1.8%, respectively).

#### Reproductive Values and Total Reproductive Impact

Reproductive values,  $v(x)$ , began at 1.0 for calves, peaked at values near or exceeding 2.0 for ages 2–9 years, and then gradually



**Figure 2.** Age distributions of female northern Yellowstone elk killed by hunters in the Gardiner Late Hunt (1996–2001) and by wolves (1995–2001).

declined, reaching values  $< 1.0$  beginning at age 15 (Table 2). The majority of adult hunter-killed females (ages 1–9 yr) had the greatest reproductive values (Fig. 3). In sharp contrast, the majority of wolf-killed females (calves and ages 14–20 yr) had reproductive values near or  $< 1.0$ .

For year 2001, the total reproductive impact of the Gardiner Late Hunt and northern range wolves was 1,394 and 1,055, respectively (Table 3). The wolf impact was probably overestimated due to using winter kill rates for an annual kill estimate (see Methods).

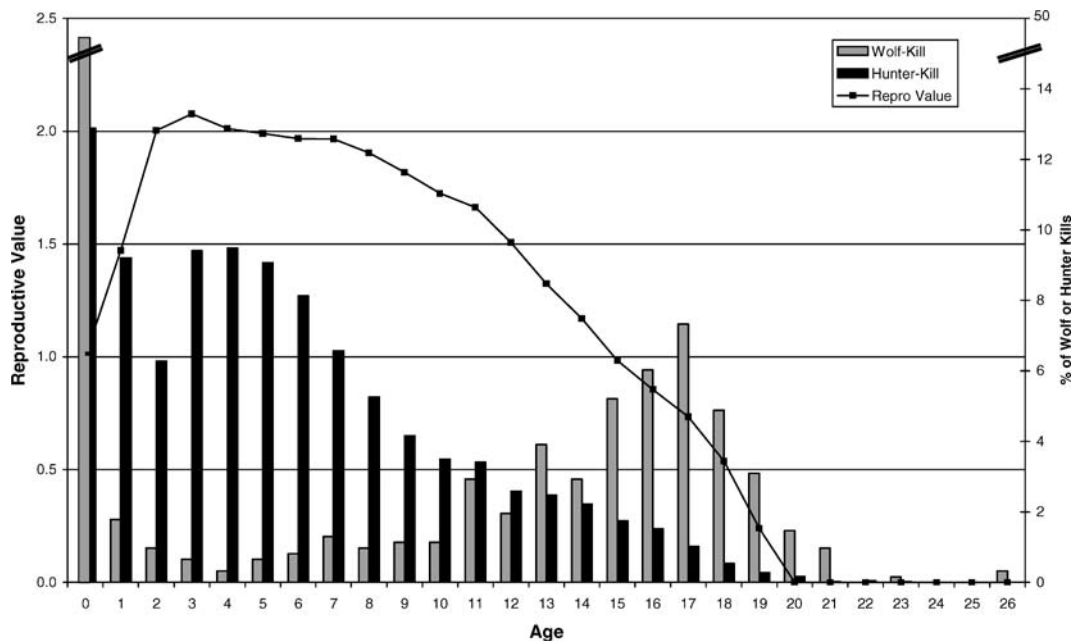
#### Analysis of Elk Age Structure

There was significant annual variation ( $P < 0.0001$ ,  $\chi^2 = 99.71$ , 15 df) in the age composition of female elk ( $n = 6,528$ ) harvested in the Gardiner Late Hunt from 1996–2001 (Table 4). The largest variation in annual proportions occurred in the yearling ( $P < 0.0001$ ,  $\chi^2 = 59.80$ , 5 df), 2–9 year-old ( $P < 0.0001$ ,  $\chi^2 = 55.75$ , 5 df), and calf ( $P = 0.0010$ ,  $\chi^2 = 20.62$ , 5 df) age classes, respectively. There was not a significant difference in the proportion of female elk aged  $\geq 10$  years ( $P = 0.3829$ ,  $\chi^2 = 5.28$ , 5 df). Calves comprised 11–13% of the female harvest from 1996–2000, and 18% in 2001 (Table 4). The large calf harvest in 2001 explained most of the variation in the calf proportions over our study period. The yearling age class had the greatest variation from year to year, and it comprised from 5–14% of the female harvest. Adult females comprised from 50–64% of the female harvest from 1996–2001.

## Discussion

#### Selection of Female Elk by Wolves and Hunters

Wolves and hunters selected female elk very differently (Figs. 2, 3). Although prime reproductive-aged females (2–9 yr old) are most abundant in the population, wolves selected and killed the vast majority of female elk from the more vulnerable calf and old ( $\geq 10$  yr) age classes. Wolf predation on the more vulnerable members of a prey species has been documented extensively (Mech 1970, Peterson 1977, Fuller and Keith 1980, Huggard 1993, Mech et al. 2001, Smith et al. 2004). The majority of hunter-killed females were adults from the largest age class present, 2–9-year-old females. When given the opportunity, hunters clearly selected for harvesting adult cow elk over calves



**Figure 3.** Reproductive values of female northern Yellowstone elk and age distributions of hunter (Gardiner Late Hunt, 1996–2001) and wolf-killed females (1995–2001). Note the scale change for the Y axis on the right side of the chart for wolf-killed calves (49% of total wolf-kills).

due to the larger amount of meat a cow provides. Most hunters can easily distinguish adult cow elk from calves based on size.

The selection pattern of wolves preying more heavily on calves and older elk than hunters is supported by other research in Canada (Carbyn 1983) and the northern Rockies (Boyd et al. 1994, Kunkel et al. 1999). Calves were over-represented in our wolf-kill data (49%) because we excluded adult elk that were not aged by counting cementum annulations. Calves comprised 43% of total kills during a study of Yellowstone wolf kill rates in winter from 1995–2000 (Smith et al. 2004). This number (43%) more accurately reflects the calf proportion of total wolf-killed elk.

### Reproductive Value and Total Reproductive Impact

Because we used a life table for female northern Yellowstone elk in the calculation of reproductive values, all the assumptions of life table analysis must apply. We assumed a stationary age distribution, constant  $l(x)$  and  $b(x)$  schedules and a closed population (Gotelli 2001). The age distributions of female elk in the northern Yellowstone population have remained relatively stable from 1996–2001 (Table 4). In reality, elk may immigrate or emigrate and  $l(x)$  and  $b(x)$  schedules are likely affected by density-dependent mechanisms. Pregnancy rates derived from blood tests of captured northern Yellowstone elk ( $n = 96$ ) were considerably higher (82% mean pregnancy rate) than the pregnancy rates used in our life table (62% mean pregnancy rate; L. D. Mech, United States Geological Survey, unpublished data). We used the Late Hunt-derived pregnancy rates because the sample sizes were considerably larger and encompassed more age classes than the captured sample. However, this may indicate that average pregnancy rates and, therefore, reproductive values for northern Yellowstone elk are higher than we reported.

The majority of hunter-killed elk (58.4%) were cows from the 2–9-year age class. By removing large numbers of female elk with reproductive values  $>1.0$ , the Gardiner Late Hunt exerts a much

greater total reproductive impact on the elk population than do wolves (Fig. 3; Table 3). Because most prime-age females are pregnant when harvested, the net effect is the immediate removal of 2 elk (the harvested cow and her calf) from the population, as well as the loss of the cow's future reproductive contribution to the population. Additionally, we estimated annual 2001 wolf predation for this index using winter kill rates, which are likely

**Table 3.** Index of total reproductive impact on female northern Yellowstone elk by the Gardiner Late Hunt and wolves in 2001.

Age	Reproductive value	Late hunt elk harvest	Hunt impact	Wolf-killed elk	Wolf impact
0	1.000	152	152	508	508
1	1.471	100	147	19	27
2	2.004	43	86	10	20
3	2.077	54	112	7	14
4	2.012	36	72	3	7
5	1.990	55	109	7	13
6	1.967	77	151	8	17
7	1.966	65	128	13	26
8	1.904	50	95	10	19
9	1.818	55	100	12	21
10	1.724	51	88	12	20
11	1.661	25	42	30	50
12	1.507	16	24	20	30
13	1.324	25	33	40	53
14	1.168	19	22	30	35
15	0.984	18	18	51	50
16	0.856	13	11	63	54
17	0.735	3	2	77	56
18	0.538	4	2	51	27
19	0.239	1	0	32	8
Total elk:		862		1,003	
Total reproductive impact:			1,394		1,055

<sup>a</sup> Reproductive values for elk  $\geq 20$  yr are 0.0, so they are not included in this calculation.

**Table 4.** Age distribution of female elk harvested in the Gardiner Late Hunt, 1996–2001.

	Year	Calf	Yearling	Adult (2–9)	Old (10+)
Number harvested	1996	111	134	504	201
% of female harvest		11.68	14.11	53.05	21.16
Number harvested	1997	242	152	1,193	367
% of female harvest		12.38	7.78	61.05	18.78
Number harvested	1998	105	46	586	180
% of female harvest		11.45	5.02	63.90	19.63
Number harvested	1999	158	104	753	224
% of female harvest		12.75	8.39	60.77	18.08
Number harvested	2000	73	65	339	126
% of female harvest		12.11	10.78	56.22	20.90
Number harvested	2001	152	100	435	178
% of female harvest		17.57	11.56	50.29	20.58
Total		841	601	3,810	1,276

greater than year-round kill rates due to elk vulnerability and snow depth in winter (Huggard 1993, Mech et al. 2001, Smith et al. 2004). As a result, the total reproductive impact due to wolves is probably lower than we reported.

The harvest of female elk with the greatest reproductive values in the Gardiner Late Hunt may have negative implications for calf production and recruitment in the future. Survival of adult females is vital to sustaining populations of long-lived vertebrate species, including elk (Eberhardt 2002). Adult female survival is likely to be  $\geq 0.95$  in populations that are not subject to human impact by hunting or other forms of lethal control (Eberhardt 2002). Houston (1982) estimated adult female elk survival for the northern Yellowstone herd at  $\sim 0.99$ . Garrott et al. (2003) estimated adult female survival of 0.97 for the Madison-Firehole herd in Yellowstone. We estimated survival probability at  $\sim 0.82$ – $0.92$  for prime-age adult females in the northern Yellowstone herd (Table 1). This lower survival probability was due to heavy selection of these age classes in the Gardiner Late Hunt.

The proportion of calves harvested by hunters increased from levels of 11–13% of the harvest from 1996–2000 to 18% of the harvest in 2001. Because the Late Hunt harvest reasonably represented the female elk population (or at the very least, the migratory females), there is no apparent calf decline in the population available to hunters. If wolf predation on calves is additive, the combination of hunters removing cows with high reproductive values and wolves preying heavily on calves may negatively affect recruitment.

Although a large proportion of wolf-kills are calves, this is not as important as one may intuitively think, in terms of future calf production. Female calves have a low reproductive value because newborns, by default, are assigned a reproductive value of 1.0. The reproductive value of newborns is discounted by the fact that a newborn may not achieve its maximum lifespan, and therefore will not produce its maximum potential offspring (Gotelli 2001). Therefore, it is likely that removal of females with the highest reproductive values has more of an impact on elk herd sustainability than removal of calves. This is especially true if wolf predation on calves mostly compensates for calf mortality by other factors. It remains unknown if calf mortality is additive or compensatory in the northern Yellowstone elk population.

### Analysis of Female Elk Age Structure

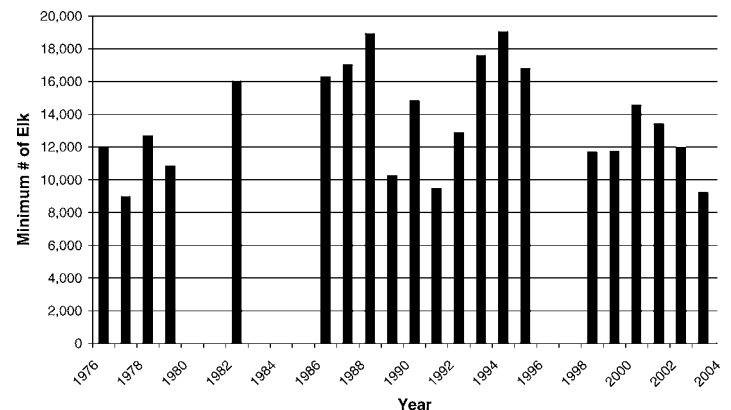
The age structure of female elk harvested in the Gardiner Late Hunt was relatively stable over our study (Table 4). Although there were significant differences in the proportion of yearlings and adults harvested from 1996–2001, we did not detect major instabilities in cow elk age distributions or undue impacts to particular year classes. Adult females made up the bulk of the hunter harvest each year. However, the proportion of adult females in the Gardiner Late Hunt harvest has fallen slightly each year since 1998; from 64% in 1998, to 61% in 1999, 56% in 2000, and 50% in 2001 (Table 4). Only long-term observation of elk population dynamics will reveal if this trend reflects fewer adult females in the population.

If wolves were affecting recruitment in a significant manner due to heavy calf predation, it should be observable in largely reduced cohorts in the youngest age classes, especially in the later years of the study period when wolf populations were higher. We did not observe this.

### Wolf Impact on Elk Abundance

Northern Yellowstone elk abundance did not decline markedly during our study period of 1995–1996 through 2001–2002 (Fig. 4). Since 1994 (pre-wolf reintroduction), elk population counts have declined at an overall average of approximately 6% per year (P. J. White, National Park Service, personal communication). Unadjusted aerial counts from 1976–2001 ranged from a low of 8,980 elk in winter 1976–1977 to a high of 19,045 in winter 1993–1994 (Lemke et al. 1998). That said, the elk population throughout the 1970s and early 1980s was probably artificially low because the elk herd was still recovering from the culling that occurred prior to implementing natural regulation in 1969.

In the last 2 decades, the greatest declines in elk abundance occurred in the winters of 1988–1989 and 1996–1997 (NRC 2002). These declines are attributed to a combination of harsh weather events and harvest in the Gardiner Late Hunt. There was a severe drought in the summer of 1988 followed by the 1988 fires and a harsh winter. More than 4,000 elk died from winter malnutrition in 1988–1989, with an additional 2,409 harvested in the Gardiner Late Hunt, for a population reduction of around 40% (Singer et al. 1989, Lemke et al. 1998). There was heavy elk mortality due to winter malnutrition again in 1996–1997 (Smith



**Figure 4.** Estimated minimum elk populations from Northern Yellowstone Cooperative Wildlife Working Group aerial surveys. Source data from Lemke et al. (1998) and Late Hunt Annual Harvest Reports (Lemke 1996–2001). No survey occurred in years with no bar. 1976 = winter of 1975–1976.

1998, NRC 2002), as well as a larger than average Late Hunt harvest ( $n = 2,465$ ) in early 1997 (Lemke 1997).

Unfortunately, no aerial counts were conducted in the winters of 1995–1996 or 1996–1997. The lack of elk counts for these years is problematic for 2 reasons. First, it is difficult to measure the extent of winter mortality in 1996–1997 without minimum population estimates immediately prior to this winter-kill event. Second, and arguably more important, there is no minimum count of northern Yellowstone elk for the first 2 years following wolf reintroduction.

The first post-wolf recovery count of northern Yellowstone elk occurred in winter 1997–1998 and estimated 11,692 elk (Fig. 4). The count increased in the presence of wolves to an estimated 14,538 elk in the winter of 1999–2000, and stood at 11,969 in the winter 2001–2002 count. Since that time, elk counts have declined to 9,215 elk in 2002–2003 and 8,335 elk in the 2003–2004 winter count. This is likely due to a combination of a 6-year drought, predation by wolves and other large carnivores, and human harvest (P. J. White, personal communication).

Limitation of the northern Yellowstone elk population by predation and hunting may reduce the potential for large winter die-offs such as those that occurred in 1988–1989 and 1996–1997. However, severe winters increase elk vulnerability to hunting and predation, so a reduction in elk numbers is a continuing possibility during harsh winters. As Boyce (1995) predicted, the most likely long-term biological effect of wolf predation on the elk herd is to hold the population at lower levels (5–25% lower), thereby reducing the impact of weather and other stochastic events on elk abundance. The most likely long-term social effect of lower elk populations is reduced hunter opportunity and a decline in the economic benefits associated with the Gardiner Late Hunt. Economic gains associated with opportunity for tourists to observe wolves in YNP are predicted to exceed those lost in reduced hunting opportunities (Duffield 1992).

## Management Implications

We recommend that future monitoring of northern Yellowstone elk should focus on calf recruitment and potential changes in age structure, especially among the females. A study of wolf-kill rates during summer months would help clarify whether the kill rates used in this analysis are accurate.

Because YNP has a large assemblage of predators (including humans), and cougars in Yellowstone kill elk at higher per capita rates than wolves (Murphy 1998, Smith and Guernsey 2002), managers should anticipate a drop in elk numbers and reduce the human harvest of elk outside the park to minimize the decline (Smith et al. 2004). A recent study in Glacier National Park documented a decline in elk due to the presence of multiple predators (Kunkel and Pletscher 1999). Cougars, humans, wolves, and bears were the largest causes of female elk mortality, respectively. The Nelchina caribou herd in Alaska declined from

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- 80,000 to under 10,000 animals over a 13-year period due to constant subsistence hunting and wolf predation pressure (Eberhardt and Pitcher 1992). Eberhardt et al. (2003) suggest that human harvest of elk outside Yellowstone may drive wolf–elk population trends. This reinforces the importance of monitoring Late Hunt harvests along with wolf–elk abundance in the future.
- Since the mid-1990s elk permit levels have been set using an Adaptive Harvest Management (AHM) approach that uses consistently collected biological and harvest information and established “management triggers” to move from “liberal” to “standard” to “conservative” hunting-season types, which are defined by the number of elk permits issued (T. Lemke, Montana Fish, Wildlife and Parks, unpublished report). Triggers that help direct hunting-season decisions include estimated elk abundance, number of elk that winter north of YNP, and number of elk that winter on or adjacent to the state-owned Dome Mountain Wildlife Management Area. Additional factors that are used to set season types include annual elk recruitment estimates, Late Season elk harvest rates, and environmental factors such as significant winter-kill events or drought.
- Since 1997, based on the AHM process, the Gardiner Late Hunt has gone from a liberal to a standard to a conservative hunting season type. Antlerless elk permits were incrementally reduced by 51% from 2,880 permits in 1997 to 1,400 permits in 2004. As a result of these hunting season changes the antlerless elk harvest decreased by 72% from 2,221 elk in 1997 to 620 elk in 2004. Based on an AHM process, the number of antlerless permits will be reduced further as needed to partially offset elk losses to wolves, other predators, and environmental factors. Continued use of the AHM process will be important in maintaining a healthy population of northern Yellowstone elk.
- Based on recent trends in total elk abundance, elk migration size, elk distribution, and calf recruitment, the Gardiner Late Hunt will likely remain in a conservative hunting season type for the next several years. Cooperation between NPS, MFWP, and other management agencies is critical to effectively monitor predation and hunting effects on the northern Yellowstone elk population.

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