

CHAPTER 25

Contrasting Wolf–Ungulate Interactions in the Greater Yellowstone Ecosystem

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Theme

Considerable research attention has focused on large herbivore population dynamics in protected natural areas to better understand the roles of resource limitation (a “bottom–up” process) and predation (a “top–down” process). This emphasis on landscapes with minimal human impact is particularly true for investigations of wolf–elk dynamics in the Rocky mountain states, where the vast majority of research occurs within the national park system. Although such studies largely avoid the confounding effects of humans, Andersen *et al.* (2006) argued that evaluation of large herbivore dynamics on multiple-use landscapes, where human influence is typically pervasive, is also needed. Initial investigations of this kind (Garrott *et al.* 2005) indicated that the effects

of wolves (*Canis lupus*) on elk (*Cervus elaphus*) dynamics could vary considerably within the same river drainage system and distances less than 40 km apart, making generalizations strictly from protected areas equivocal. Here, we expand this landscape approach to compare population dynamics among seven elk populations in the Greater Yellowstone Ecosystem, all with winter ranges within 115 km of each other and whose summer ranges partially overlap. Land ownership, land use, vegetation communities, large predator densities and management, and local landscape and environmental conditions vary considerably across this area. Similarly, elk harvest management strategies also vary and reflect different migratory patterns, harvest availabilities, and habitats of the elk populations. Our use of data collected extensively for management purposes, rather than intensively for research, was necessarily more descriptive compared to presentation of data collected intensively on one area. However, we believe information collected across multiple-use landscapes allows insights and conclusions not possible from one or a few intensively studied protected areas.

I. INTRODUCTION

Population dynamics of large herbivores can be influenced by an array of biotic and abiotic factors (Chapter 8 by Messer *et al.*, and Chapter 23 by Garrott *et al.*, this volume) and, particularly when predation is limiting, the collective attributes of the local landscape and climate can exert considerable influence on these dynamics (Chapter 21 by White *et al.*, and Chapter 24 by Garrott *et al.*, this volume). Consequently, the dynamics of a particular predator and their focal prey can be expected to vary across systems. Discerning the respective influences of resources and predation on large ungulates in temperate systems is often heavily confounded by human harvests (Figure 25.1) and habitat alteration (Eberhardt 1997). Therefore, most investigations occur in systems that are managed for resource protection and experience only minimal human interference. Nevertheless, most ungulate species are widely distributed throughout a mosaic of landscapes with different uses, ownerships, and policies, where human impacts are a pervasive and significant component. Insights gained from protected areas and generalized to these multiple-use areas may be misleading due to the significant differences in human influence. Thus, developing effective management plans necessitates an evaluation of ungulate dynamics in multiple-use landscapes.

Even in protected areas the spatial and temporal scales at which large herbivore population dynamics occur make evaluations particularly difficult. While experimentation is the strongest science, it is problematic at a landscape scale because true controls are rare, replicates are difficult to obtain, and experiments take years to complete (Hobbs and Hilborn 2006). Although there are notable exceptions, such as partially controlled field manipulations or treatments (Platt 1964, Romesburg 1981) that have been conducted at the landscape scale (*e.g.*, Boutin 1992, Krebs *et al.* 1995), their feasibility in most systems is limited. These limitations are obvious for national parks, which are managed to minimize human intervention, but also affect research on many other multiple-use public and private lands due to multiple land ownerships and the differing goals and expectations of different segments of the public. Furthermore, true experimentation is rarely possible when major influential species of study such as the wolf and grizzly bear (*Ursus arctos*) are protected from adverse effects under the Endangered Species Act.

Because true experiments are typically not feasible, biologists are often faced with the problem of how to obtain results useful for the planning and management decisions that will be made regardless of study method, whether the information was arrived at by the strong inference (deduction) of experimentation, or whether there is information available at all. Planned studies with random sampling and reasonable sample sizes can provide sound inferences (Cochran 1983, Eberhardt and Thomas 1991) and the method of induction can use the “general-purpose data” collected by “game agencies” to obtain reliable information (Romesburg 1981). Thus, we can gain reliable knowledge



FIGURE 25.1 A successful elk hunter on the Lower Madison winter range where late-season management hunts are conducted to reduce elk numbers (Photo by Julie Cunningham).

(Romesburg 1981) by repeating observational studies many times, in many places, to sequentially gain understanding of basic ecological processes (Eberhardt 2003).

Wolf restoration to the greater Yellowstone, central Idaho, and northwest Montana recovery areas has been spectacularly successful. Goals for numbers of breeding pairs and total wolves, along with distribution goals for the States of Idaho, Montana, and Wyoming were met by the end of 2002 (U.S. Fish and Wildlife Service *et al.* 2006). As a result, the U.S. Fish and Wildlife Service proposed delisting wolves in the northern Rocky Mountains and transferring management to state wildlife agencies pursuant to approved wolf management plans (72 Federal Register 36939). The increasing numbers and distribution of wolves make it imperative that state agencies managing wolves and game animals, and responding to livestock depredations, have the best available information on factors influencing wolf predation. Ideally, this information should be as broadly applicable as possible, gathered and synthesized across the range of wolves and ungulates densities as well as across a diversity of ecological and management situations.

Results presented elsewhere in this book for the Madison headwaters area represent substantial new knowledge of elk and wolf dynamics in Yellowstone National Park (Yellowstone). Previously, most research and attention was focused on elk and wolves that wintered in the northern portion of Yellowstone (*e.g.*, Houston 1982, White and Garrott 2005, Vucetich *et al.* 2005, Smith *et al.* 2006a, Varley and Boyce 2006). However, areas within Yellowstone are managed pursuant to preservation policies and under conditions that are quite different than those affecting elk and predators outside the park (though portions of the northern Yellowstone elk herd are subject to hunting when animals migrate outside the park during winter). Thus, management goals, population densities, hunting harvest, local climate, and other conditions vary substantially for both elk and wolves in Montana within short distances of central and northern Yellowstone. The interactions of wolves and elk could vary considerably depending on the ecological and human-influenced characteristics of the area they occupy (Garrott *et al.* 2005) and results determined for the central (Madison headwaters) and northern Yellowstone case studies might not be widely applicable.

In 2001, the Montana Department of Fish, Wildlife, and Parks, Montana State University, National Park Service, and U.S. Fish and Wildlife Service began a cooperative project to provide mutual assistance among some intensive studies of wolves and ungulates and initiate systematic collection and examination of past, present, and future “general-purpose data” (Romesburg 1981) for elk populations in southwestern Montana (Hamlin 2005). Our goal was to use population monitoring data routinely collected for many years before and after wolf restoration across a multiple-use landscape to provide insights that could contribute to management decisions regarding wolves and elk. We compared and contrasted vital rates such as yearling and adult pregnancy rates, calf survival and recruitment, and the survival of adult female elk among areas relative to the strength of influencing factors such as hunter harvest, weather, and levels of wolf and grizzly bear populations. Eberhardt (1977), Hanks (1981), and Gaillard *et al.* (1998) suggested that a decrease in physical condition through increased ungulate population densities (or other stressors) leads to the following sequential demographic changes: (1) increased juvenile mortality, (2) increased age at sexual maturity, (3) decreased fecundity of mature females, and (4) increased adult mortality. However, this sequence and its interpretation, especially for increased juvenile mortality, can be complicated by the presence of effective predators (Bergerud 1971, Beasom 1974, Keith 1974, Bergerud 1978, Stout 1982, Gasaway *et al.* 1983, 1992, Hamlin and Mackie 1989, Chapter 23 by Garrott *et al.*, this volume).

For many presentations, we will use numbers of wolves and grizzly bears per 1000 elk to represent the potential influence of this variable because predator to prey ratios are likely most ecologically relevant (Eberhardt 1997). We also compared population trends among the seven elk populations relative to these changes in vital rates and influencing factors. We believe conclusions based on this information will be useful to guide planning and management decisions throughout the current and potential future distribution of wolves in the northern Rocky Mountain region of the United States.

II. METHODS

A. Elk Populations and Study Site Descriptions

We assessed the status of elk on seven areas with different predator guilds and management paradigms in the greater Yellowstone area, including the Madison headwaters and northern winter range of Yellowstone National Park (northern Yellowstone), the Wall Creek Wildlife Management Area (Wall Creek) and Blacktail–Robb Ledford Wildlife Management Areas (Blacktail–Robb Ledford) of the Gravelly-Snowcrest mountains, Gallatin Canyon (Gallatin), Lower Madison drainage (Hunting District 362), and the Yellowstone Valley (Hunting District 314) in Montana (Figure 25.2). The relative proximity of the seven areas (Figure 25.2, most winter ranges within 80 km of each other, the furthest 115 km) resulted in similar broad-scale climate patterns. Thus, all areas experienced sustained drought since 1995 and relatively mild winters since 1998.

Preservation was the primary land use for areas used by the Madison headwaters and northern Yellowstone elk populations (Table 25.1). The Madison headwaters population remained in Yellowstone, but a portion of the northern Yellowstone elk population was subject to multiple-use management, including hunting, when elk seasonally migrated into Montana. The Gallatin Canyon elk population was subject to public multiple-use management, with preservation on some summer range but no significant agricultural influence. The Wall Creek and Blacktail–Robb Ledford elk populations were managed under public multiple-use, with surrounding areas of agricultural ownership. The Lower Madison and Yellowstone Valley elk populations wintered primarily on private agricultural lands (Figure 25.3). Thus, different levels of tolerance for wolves occurred among the seven areas. The Montana Department of Fish, Wildlife, and Parks collected elk demographic data in these areas for at least several decades prior to wolf reintroduction.

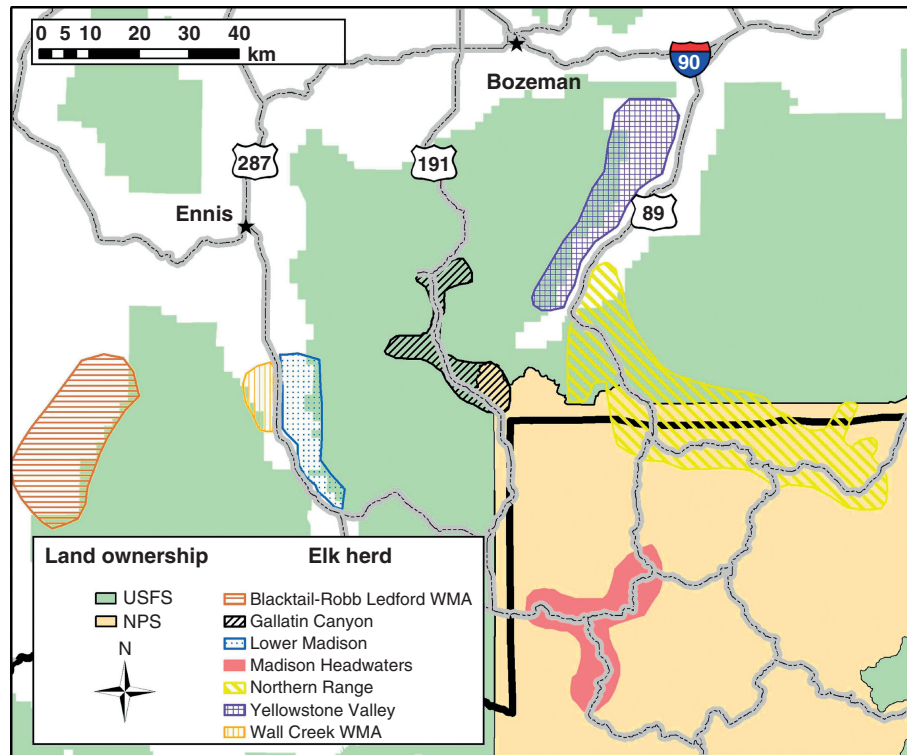


FIGURE 25.2 Proximity and landownership patterns of the winter ranges for seven elk herds in the greater Yellowstone area. White areas depict private lands.

Primary winter habitat for five of the seven elk populations was predominantly grasslands (Table 25.1, Figure 25.4), with inclusions of sagebrush (*Artemisia spp.*) steppe. Conifer forest occurred on the upper fringes of winter range. The Madison headwaters and Gallatin Canyon elk winter ranges (Figure 25.5) occurred within a predominantly conifer forest area, with limited inclusions of grasslands and sagebrush along some stream courses and meadows near thermal features in the Madison headwaters. Thus, the winter distribution of elk after wolf restoration was limited to smaller, predictable areas in the Madison headwaters and Gallatin Canyon areas compared to the other five areas (Chapter 18 by Gower *et al.*, and Chapter 21 by White *et al.*, this volume). These broad habitat differences among areas were also related to differences in winter severity faced by elk, with the most-severe winter conditions occurring in the Madison headwaters and Gallatin Canyon areas. Winter severity ranged from moderate to mild for the northern Yellowstone elk population, with severity decreasing to the north of the park. Winter severity was comparatively mild for the other four elk populations (Table 25.1).

Total range in estimated elk population size among the seven areas since wolf restoration was approximately 200–17,000 elk (Table 25.1). The smallest elk populations were in the Madison headwaters (200–600) and Gallatin Canyon (700–1500), while the largest population was in northern Yellowstone (6700–16,700). Elk numbers in the other four populations (1500–4800) ranged from 10–20 times greater than the low estimate for the Madison headwaters population and one-half to one-third of the lowest count for the northern Yellowstone population. Annual levels of hunter harvest also varied considerably among populations, from no harvest of the nonmigratory Madison headwaters population to an average harvest of 65% of the bulls and 15% of the cows from the Blacktail–Robb

TABLE 25.1 Description and comparison of landscape and ecological characteristics of 7 study areas in southwestern Montana and northwestern Wyoming (Yellowstone National Park)

Characteristics	Areas						
	Madison Headwaters	Northern Range	Wall Creek WMA	Blacktail–Robb Leford WMA	Gallatin Canyon	Lower Madison	Yellowstone Valley
Primary Winter Habitat	Conifer Forest	Grassland & Sage Steppe	Grasslands & Sage Steppe	Grasslands & Sage Steppe	Conifer Forest	Grasslands & Sage Steppe	Grasslands & Sage Steppe
Winter Severity	Severe	Moderate to Mild	Mild	Mild	Moderate	Mild	Mild
Land Ownership	Public—Preservation	Public—Preservation & Multiple Use	Public—Multiple Use	Public—Multiple Use	Public—Multiple Use	Private—Agricultural	Private—Agricultural
Winter Elk Counts	200–600	6700–16,700	1500–2700	1700–2700	700–1500	1500–3500	3000–4800
Hunting Pressure	None	Bulls—low (<10%), Cows—(2–13%) low recently	Bulls—High (50%), Cows moderate (10–12%)	Bulls—Highest (65%), Cows moderate to high (15%)	Bulls—High (45%), Cows (1–25%) low recently	Bulls—Moderate (30%), Cows (3–20%) lower recently	Bulls—High (40%), Cows moderate (10%)
Alternate Prey	High densities of bison	Moderate densities of bison, low of mule deer, pronghorn	Low densities of mule and white tail deer	Low densities of mule and white tail deer, pronghorn and moose	Low densities of mule deer and moose	Low densities of pronghorn and mule deer	High densities of white-tail deer and mule deer
Grizzly Bear Presence ^a	Highest: 105.7	Moderate: 9.25	Transients: rare	Transients: rare	High: 56.9	Low: 7.1	Low to moderate
Winter Wolf Presence ^b	Highest: 85.3	Moderate: 9.5	Transients: rare	Low: 2.6	High: 23.4	Low: 1.9	Low: 2.1

^a Highest estimated grizzly numbers per 1000 elk.

^b Highest estimated wolf numbers per 1000 elk.



FIGURE 25.3 Cattle being moved across private land elk winter range on the Lower Madison area toward elk summer range. Wolf depredations of livestock reduce tolerance for wolves on and near private lands (Photo by Julie Cunningham).



FIGURE 25.4 Elk winter range in the Lower Madison Valley, looking from the east side (typical of Lower Madison) to the west side (typical of the Wall Creek Wildlife Management Area). This habitat is also typical of Blacktail–Robb Ledford Wildlife Management Area, Yellowstone Valley, and the north portion of Yellowstone National Park (Montana Fish, Wildlife, and Parks photo by Craig Jourdonnais).

Ledford population. Hunter harvest for the other elk populations (Table 25.1) varied between these extremes, with harvests of cows decreasing to an average of 3% of estimated preseason numbers in the Gallatin Canyon and northern Yellowstone populations since 2004. More detailed descriptions of the characteristics of the seven study areas are provided in Appendix 25A.1, and more detailed descriptions for estimating elk numbers and population parameters are in Appendix 25A.2.



FIGURE 25.5 Elk winter range in the Gallatin Canyon (Montana Fish, Wildlife, and Parks photo by Craig Jourdonnais).

B. Estimates of Predator Numbers

The annual number of wolves estimated for each area and numbers killed in control actions or other known mortalities due to humans were determined from December numbers reported in the Cooperative Rocky Mountain Wolf Recovery Annual Reports (*e.g.*, U.S. Fish and Wildlife Service *et al.* 2007), Yellowstone National Park research reports (Smith *et al.* 2001, 2003, 2004a,b, 2005, 2006a, 2007, Smith and Guernsey 2002), and consultations with field biologists from Montana Fish, Wildlife, and Parks. After consultation with a Montana wolf management specialist (Mike Ross), we estimated wolf numbers by elk range each winter to fractions of 0.25 in some areas because some wolves and wolf packs used multiple elk ranges. For the Blacktail–Robb Ledford, we used Global Positioning System telemetry locations to estimate that the wolf pack spent 34% of its time with this elk herd and fractionalized annual wolf numbers for that pack accordingly. Similarly, intensive fieldwork in the Madison headwaters allowed estimation of wolf-days on the area and fractional wolf numbers equivalent to estimates for the other areas (Chapter 15 by Smith *et al.*, Chapter 16 and 17 by Becker *et al.*, this volume).

Grizzly bears have been implicated in substantial mortality of neonatal elk calves in this region (Singer *et al.* 1997, Barber-Meyer 2006, Creel *et al.* 2007). Thus, we attempted to quantify relative grizzly bear numbers by area and year. Our index of grizzly bear numbers represents relative differences among areas and years rather than accurate, absolute numbers. We used information presented in the annual reports of the Interagency Grizzly Bear Study Team (*e.g.*, Knight *et al.* 1990, Knight and Blanchard 1996, Haroldson 2006, Haroldson and Frey 2006) to construct our estimates. More detailed descriptions of estimating wolf and grizzly bear numbers and population parameters are in Appendix 25A.2.

C. Estimates of Elk Vital Rates

1. Pregnancy Rate

Hunters at the Gardiner (northern Yellowstone) and Gallatin check stations were asked to report the pregnancy, sex of fetus, and lactation status of their harvests during 1985–2007. The reported pregnancy rates are underestimates because hunters vary in their anatomical skills and, also, miss

some small fetuses. However, this underestimate should be consistent among years and yield a good relative annual index of pregnancy. Check station personnel at the Gardiner and Gallatin check stations also weighed hunter-harvested calves to the nearest pound and we converted these weights to kg for analysis. Male calves consistently weighed more (70.53 kg, 95% CI = 69.81, 71.25) than female calves (67.04 kg, 95% CI = 66.45, 67.63) and we adjusted female weights upward based on this average difference to construct an annual average sex-adjusted weight for all calves.

When adult female elk were captured to attach radio-transmitter collars on our study areas, we collected blood samples and used pregnancy-specific protein B (PSPB) assays to assess pregnancy status (Sasser *et al.* 1986). Earlier tests, where both blood samples and reproductive tracts were obtained (Palmisciano 1986) or blood samples and rectal palpation occurred (Hamlin and Ross 2002), indicated 100% accuracy ($n = 78$) for PSPB assays to estimate pregnancy.

The hunter-reported pregnancy data were binomial and required an analytical method accounting for nonnormal error structure. We used the logit-transform (on proportions) rather than logistic regression because, although sampling was random within years, it was nonrandom among years. For example, sample sizes for adult females from the northern Yellowstone population varied from 37 to 1456 among years and were related to factors that could affect pregnancy rates such as increased samples during severe winters and decreased sample sizes with increasing numbers of wolves and reduced hunting. For the January 2003 hunter-reported sample, there were no pregnancies among 19 yearlings. We used 0.01 (lower than any other year) as the pregnancy rate for logit-transformation. We used logistic regression to analyze pregnancy rates estimated using the PSPB assay because samples were random and similar in size among years. We used the R statistical package, version 2.5.0 (R Development Core Team 2006) for all analyses.

2. Elk Calf Recruitment

Montana Fish, Wildlife, and Parks biologists recorded total numbers and bulls during all aerial surveys of elk. Numbers of calves and cows were also recorded during many surveys. However, separate classifications of cows and calves were commonly conducted from the ground for many of the areas. When a mixture of techniques occurred, we used aerial counts to determine proportions of bulls and ground classifications to determine ratios of calves per 100 cows. These classifications were not available for a few years in the northern Yellowstone, Gallatin Canyon, and Lower Madison. However, age structure data were available from check stations. We did not directly use numbers of harvested calves and cows to estimate the ratio of calves per 100 cows in the populations because hunters may select against calves (Hamlin and Ross 2002). Rather, we used proportion of yearling cows in the next year's harvest (YC_{t+1}) to estimate the recruitment of female calves per 100 adult cows during the previous year. We added estimated recruited male calves (MC_{t+1}) to YC_{t+1} , where $MC_{t+1} = (YC_{t+1})(MC_t/FC_t)$. Thus, $(YC_{t+1} + MC_{t+1})$ per 100 cows ≥ 2 -years old = recruitment of total calves per 100 adult females (t). This estimate could be slightly lower than comparable classifications of calves per 100 cows because it included any mortality occurring between the end of March and the next hunting season. We assumed this mortality was low except during severe winters.

We used the average Palmer Drought Severity Index (PDSI) during May and June as an index of soil moisture conditions during the early growing season (Palmer 1968). The PDSI incorporates precipitation, temperature, and evapotranspiration, all correlated with production and nutritive quality of plants (Sala *et al.* 1988). Thus, we expected PDSI to be positively related to elk nutrition and elk calf survival because dry years (*i.e.*, low PDSI) would decrease plant production, thereby decreasing fat reserves for elk entering winter and resulting in lower calf survival.

All of our graphics display relationships relative to observed calves per 100 cows for ease of understanding. However, we used the proportional calf per cow ratio and logit-transformed this quantity for statistical analysis.

3. Adult Female Survival

Ages of hunter-harvested elk were estimated by eruption-wear (Quimby and Gaab 1957) and recorded at Montana Fish, Wildlife, and Parks check stations. Since 1989, incisors also were collected from elk >2 years of age for aging via examination of annuli in the cementum of incisor root tips (Hamlin *et al.* 2000). For years when only eruption-wear ages were available, and for portions of annual samples that included some elk aged by eruption-wear only among samples mostly consisting of incisor annuli aged elk, we constructed area and time period specific matrices (*e.g.*, Table 3 in Hamlin *et al.* 2000) to proportionally correct eruption-wear ages to their expected distribution as incisor determined ages. We then added incisor-aged and corrected eruption-wear ages for the time period samples. We natural-log transformed the age–frequency distributions of adult females recorded at check stations and fit linear regressions against age (Hamlin and Ross 2002, White and Garrott 2005). We used the slope of these regressions to estimate survival ($S = e^\beta$, where e = inverse of natural log and β = slope of the regression line). For years and areas when population trend did not indicate relative stability (Caughley 1977), we estimated rate of change in population size by regressing natural log of raw population counts against year to determine the instantaneous rate of change (r). We then adjusted age–frequency distributions by the equation-adjusted number of age $x = f_x e^{rx}$ (Caughley 1977). We then proceeded as above to use slopes of the regression of natural log of age distribution against age to determine the estimate of survival adjusted for population growth rate. We used the different time periods and areas as factors in multiple linear regression models (Program R) to test for differences in survival among periods by area and period, and allow interactions between $\ln(\text{count})$ and age. We compared periods, and areas within periods, using all-subsets regression. The P -value of the regression coefficients on the interaction terms represented the significance level of the difference between the survival rate for the periods and areas. The age–frequency technique for determining survival closely matched survival data determined by telemetry for elk in the Gravelly-Snowcrest mountains during 1989–1996 (Hamlin and Ross 2002). Also, the survival rate we determined by age structure for the northern Yellowstone during 2001–2006 (0.81) was similar to the rate estimated by telemetry (0.80) during March 2000 to February 2004 (Evans *et al.* 2006). Thus, the age structure technique for estimating survival appeared to be relatively accurate.

We used annual reports of the Montana Statewide Harvest Questionnaire (Cada 1985; Montana Fish, Wildlife, and Parks annual reports) to estimate hunter harvest by area as calves, adult females, and adult males. Additionally, annual reports were available for the mandatory check of northern Yellowstone elk harvested during late season hunts (T. Lemke, Montana Fish, Wildlife, and Parks, unpublished reports). More detailed descriptions of methods used to determine harvest by area, adjust for a year of missing data, and adjust for estimated wounding loss are available in Appendix 25A.2.

To estimate preseason adult female numbers for comparison to hunter harvest and wolf-kill rates, we multiplied raw post-season counts by correction factors for sightability (Appendix 25A.2) and used classification data to estimate the proportion or number that were adult females, calves, and males. To obtain the estimated preseason number of adult female elk, we added the estimated harvest of adult females to the estimated number of adult females and adjusted for estimated wounding loss (Appendix 25A.2).

We used estimates provided in Smith *et al.* (2004a) and Becker *et al.* (Chapter 17 by Becker *et al.*, this volume) to estimate total wolf-killed elk as 0.060 elk killed per wolf day during the 181 day (November 1–April 30) winter period and reduced summer kill rates (184 days, May 1–October 31) to 70% (0.042 elk killed per wolf day) of winter rates (Messier 1994). We used 25% (0.015 adult female elk killed per wolf day in winter and 0.0105 in summer) as the estimate for percent of wolf-kill that was adult females based on averages in reports for the northern Yellowstone (Smith *et al.* 2004a, 2005, 2006a, 2007), Gallatin Canyon (Creel *et al.* 2007), and Lower Madison (Hamlin 2005; R. Garrott, unpublished data). Thus, we estimated the number of adult female elk killed by wolves each year in each area as the $[(\text{number of wolves}) \times (0.015 \times 181)] + [(\text{number of wolves}) \times (0.0105 \times 184)]$.

III. RESULTS

A. Predator Numbers

Wolves first established in the northern portion of Yellowstone in 1995 and colonization proceeded to the Gallatin Canyon, Madison headwaters, Lower Madison, and Yellowstone Valley (Table 25.2). Wolves formally colonized the last of our seven areas (Blacktail–Robb Ledford) in 2000. Though a breeding pack did not establish at the Wall Creek Wildlife Management Area, transient wolves have been noted since 1999. Pack tenure was longest, and the maximum number of packs and wolves was highest, in northern Yellowstone, followed by the Madison headwaters and Gallatin Canyon (Table 25.2). As would be expected, wolf deaths due to agency control actions related to depredations were highest in private agricultural valleys and closely associated public lands (Table 25.2, average = 21–49% of wolves). Wolf deaths due to agency control actions ranged from 0 to 4% in the central and northern portions of Yellowstone to 11% on public land in the Gallatin Canyon where there were also no significant agricultural conflicts. Smith *et al.* (2006a) reported that during the first nine years after wolf restoration to Yellowstone, including the Madison headwaters and northern Yellowstone areas, wolf mortality in the park from all causes averaged 18% per year and dispersal averaged 28% per year, totaling 45% annual loss from the population. We do not have this type of information for the other areas, but based on numbers and growth rates, wolf mortality was much higher overall (at least 21–49% annual loss) in the agricultural valleys surrounding Yellowstone than inside the park or on adjacent public lands without agricultural conflicts.

The broad range of 0–85 wolves per 1000 elk among areas, and among years within areas (Table 25.2), is of major ecological significance in interpreting our results. Public lands managed primarily for preservation (*e.g.*, Yellowstone National Park) and public lands without agricultural conflicts (*e.g.*, Gallatin Canyon) reached the highest levels of 10–85 wolves per 1000 elk. In contrast, fewer than three wolves per 1000 elk were sustained in valleys with a significant agricultural component. In addition, the absolute and relative number of predators on elk varied substantially among the seven areas (Table 25.1). The ratio of wolves per 1000 elk reached the highest level in the Madison headwaters (85) and was four times greater than the second highest ratio (23) in the Gallatin Canyon. Wolves per 1000 elk in northern Yellowstone (10) were one-half the maximum ratio recorded for the Gallatin Canyon, with the other four areas reaching only minor levels (0–3) of wolves relative to the number of their main prey, the elk. Grizzly bears, which were determined to be a major predator of neonatal elk calves in the northern Yellowstone (Singer *et al.* 1997, Barber-Meyer 2006) and Gallatin Canyon (Creel *et al.* 2007) populations, increased in the Yellowstone ecosystem (Schwartz *et al.* 2007) coincident with wolf restoration. As with wolves, the index of grizzly bear numbers per 1000 elk reached the highest levels in the Madison headwaters (106), followed by the Gallatin Canyon (57; Table 25.1). The index indicated relatively moderate levels of grizzly bears per 1000 elk occurred in northern Yellowstone (9), with lower numbers in the Lower Madison (7) and low to rare numbers elsewhere (Table 25.1). Alternate prey for these predators is relatively low on most areas (Table 25.1), with fairly high densities of harder to kill bison (*Bison bison*) in the Madison headwaters and northern Yellowstone areas and relatively high densities of mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) in the Yellowstone Valley.

B. Pregnancy Rate

Hunter-reported pregnancy rates were determined from records for 1714 yearling female elk in northern Yellowstone during 1985–2005. Annual yearling pregnancy rates were not related to numbers of wolves per 1000 elk during the prior winter ($R^2 = 0.08$, $F_{1,19} = 1.74$, $P = 0.20$, Figure 25.6A) or prior

TABLE 25.2 Description and characteristics of the status of wolves on 7 study areas in southwestern Montana and northwestern Wyoming (Yellowstone National Park), 1995–2007

	Areas							
		Madison Headwaters	Northern Range	Wall Creek WMA	Blacktail–Robb Ledford WMA	Gallatin Canyon	Lower Madison	Yellowstone Valley
Wolf pack characteristics	Year of Wolf Colonization	1998 ^a	1995	Transients	2000	1996	1999	1999 ^a
	# Packs ^b	1 to 3	5 to 10	None	1 to 2	1 to 3	1	1 to 2
	# Wolves ^c	30 to 40	21 to 106	Transients	3 to 14	2 to 19	5	2 to 11
	Average wolf loss to control actions	None (0%)	None to Low (4.3%)	Transients	Highest (48.5%)	Low (10.9%)	High (33.5%)	Moderate (21.2%)
	Maximum pack tenure	8 years	11+ years ^d	None	5 years	10 years ^e	2 years	2.5 years
	Range in Wolves:1000 elk (time adjusted)	0.5–85.3	1.0–9.5	Transients	0.3–2.6	1.0–23.4	0.5–1.9	0.1–2.1

^a Some use by transient wolves earlier.

^b Maximum number of packs in a year.

^c The total number of wolves with a home range that crossed the specific wintering elk populations.

^d There are two packs in the northern range that have existed since reintroduction: the Leopold and Druid packs.

^e The Chief Joseph pack began in 1996 with little territory outside YNP, but gradually increased presence outside YNP in the Gallatin National Forest with time. The Chief Joseph pack was counted as a southwestern Montana pack in 2005 and 2006.

summer ($R^2 = 0.02$, $F_{1,19} = 0.44$, $P = 0.51$). Also, annual hunter-reported pregnancy rates for 13,750 female elk ≥ 2 -years old in northern Yellowstone during 1985–2007 and 812 female elk ≥ 2 -years old in the Gallatin Canyon during 1989–2004 were not correlated with the number of wolves per 1000 elk the previous winter ($R^2 < 0.01$, $F_{1,36} = 0.01$, $P = 0.91$, Figure 25.6B) or previous summer ($R^2 < 0.01$, $F_{1,36} = 0.001$, $P = 0.97$). Pregnancy rates determined using PSPB assays (northern Yellowstone, $n = 167$; Gallatin Canyon, $n = 62$; and Lower Madison, $n = 59$) for all ages of elk across three of our elk populations were not significantly related to numbers of wolves per 1000 elk in the winter prior to conception ($\beta_w = 0.0997$, $SE = 0.063$, $P = 0.11$, Figure 25.6C) or during the prior summer ($\beta_s = 0.0854$, $SE = 0.057$, $P = 0.14$). A possible 32% decrease in pregnancy rate occurred on the Madison headwaters area during the post-wolf period (Chapter 23 by Garrott *et al.*, this volume), but results were equivocal.

C. Elk Calf Recruitment in Relation to Wolves and Grizzly Bear

Recruitment of elk calves across all seven areas, as indexed by ratios of calves per 100 cows observed in late winter or spring, decreased exponentially as the numbers of wolves per 1000 elk, grizzly bears per 1000 elk, and combined wolves and grizzly bears per 1000 elk increased (Figure 25.7A–C). Analysis with logit-transformed ratios of calves per 100 cows indicated a significant correlation with wolves per 1000 elk ($R^2 = 0.47$, $F_{1,110} = 97.3$, $P < 0.001$), grizzly bears per 1000 elk ($R^2 = 0.56$, $F_{1,90} = 114$, $P < 0.001$), and wolves and grizzly bears per 1000 elk ($R^2 = 0.60$, $F_{3,88} = 46.7$, $P < 0.001$). These statistics excluded the data from 1989 and 1997 when the effects of extensive fires and a severe winter, respectively, resulted in high malnutrition and starvation. However, the relationships remained significant when 1989 and 1997 were included (wolves per 1000 elk: $R^2 = 0.38$, $F_{1,122} = 74.8$, $P < 0.001$; grizzly bears per 1000 elk: $R^2 = 0.45$, $F_{1,100} = 82.1$, $P < 0.001$; and wolves and grizzly bears per 1000 elk: $R^2 = 0.49$, $F_{3,98} = 31.4$, $P < 0.001$). The increase in numbers of wolves and grizzly bears was coincident, so that they covaried strongly ($R^2 = 0.71$, $F_{1,107} = 261.4$, $P < 0.001$) and interpretation of relative effects is problematic. However, regional studies determining elk calf mortality based on telemetry indicate that mortality of calves due to bears is almost entirely within the first 45 days of life (Singer *et al.* 1997, Barber-Meyer 2006, Creel *et al.* 2007, Zager *et al.* 2007b) and mortality due to wolves continues through the year.

D. Elk Calf Recruitment in Relation to Condition, Drought, and Forage

Annual mean weights recorded for 1906 northern Yellowstone elk calves harvested during 1985–2005 late hunts were generally at or above the long-term mean after wolf restoration (Figure 25.8), indicating no wolf-induced decreases in nutrition. Further, variation in nutritional level did not affect calf survival because numbers of calves per 100 cows (logit-transformed) in spring were not positively related to weights of harvested calves ($\beta_{cw} = 0.012$, $SE = 0.024$, $R^2 = 0.0135$, $P = 0.62$, Figure 25.9).

There was a significant positive relationship between the regional PDSI and recruitment of elk calves (*i.e.*, low PDSI = dry years and lower calf recruitment) as indexed by logit-transformed ratios of calves per 100 cow in spring across our seven elk populations during 1968–2007 ($\beta_{all} = 0.098$, $SE = 0.019$, $R^2 = 0.14$, $P < 0.001$), but residuals were large and predictability low (Figure 25.10). The relationship remained positive after data were partitioned into areas and years when wolves and/or grizzly bears were greater than four per 1000 elk ($\beta_{great} = 0.069$, $SE = 0.039$, $R^2 = 0.07$, $P = 0.08$) or less than four per 1000 elk ($\beta_{less} = 0.025$, $SE = 0.014$, $R^2 = 0.02$, $P = 0.08$). Other factors affecting calf survival apparently overwhelmed regional drought effects or these effects did not affect nutrition sufficiently to

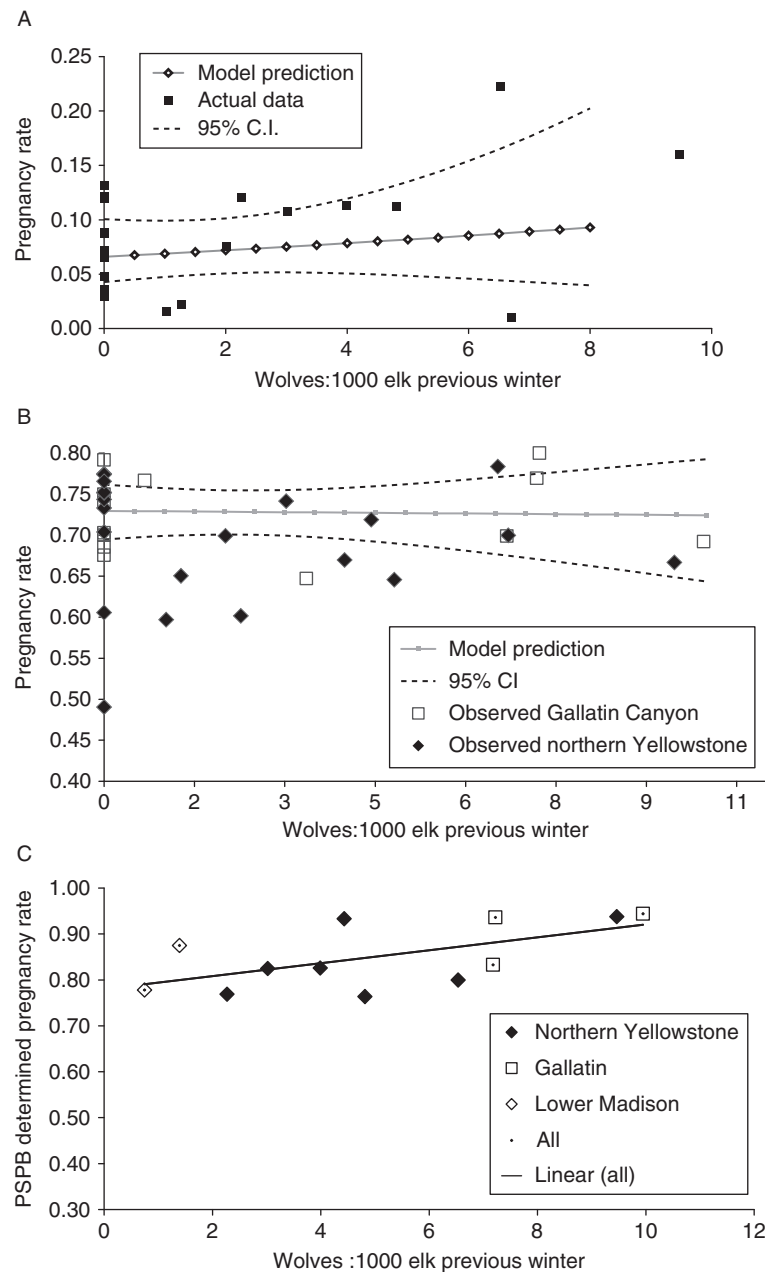


FIGURE 25.6 Pregnancy rates of elk in relation to number of wolves:1000 elk on winter range. Panel A—hunter-reported pregnancy rate for yearling females migrating outside the northern portion of Yellowstone National Park during winter ($n = 14-250$). Panel B—hunter-reported pregnancy rate for females ≥ 2 -years-old outside the northern portion of Yellowstone National Park ($n = 37-1456$) and in the Gallatin Canyon ($n = 11-114$). Panel C—pregnancy rate determined by PSPB for all female elk outside the northern portion of Yellowstone National Park ($n = 15-40$), in the Gallatin Canyon ($n = 12-32$), and in the Lower Madison areas ($n = 27-32$).

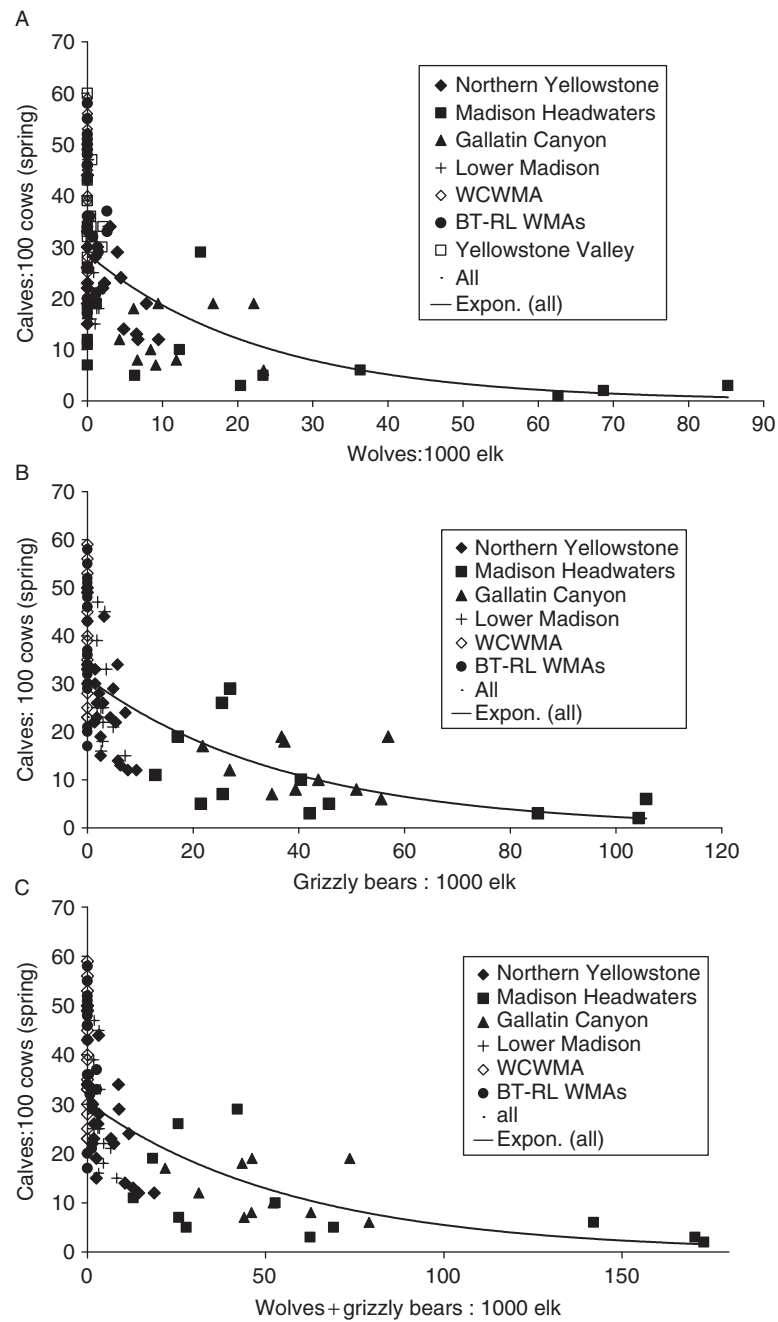


FIGURE 25.7 Recruitment rate (calves:100 cows) of elk in seven populations in relation to numbers of wolves and/or grizzly bears:1000 elk (excluding 1989 and 1997). Panel A—calves:100 cows recruited relative to numbers of wolves:1000 elk on winter range for 7 elk populations, 1986–2007. Panel B—calves:100 cows recruited relative to numbers of grizzly bear:1000 elk on winter range for 6 elk populations (Yellowstone Valley not included), 1986–2006. Panel C—calves:100 cows recruited relative to numbers of wolves and grizzly bear:1000 elk on winter range for 6 elk populations (Yellowstone Valley not included), 1986–2006.

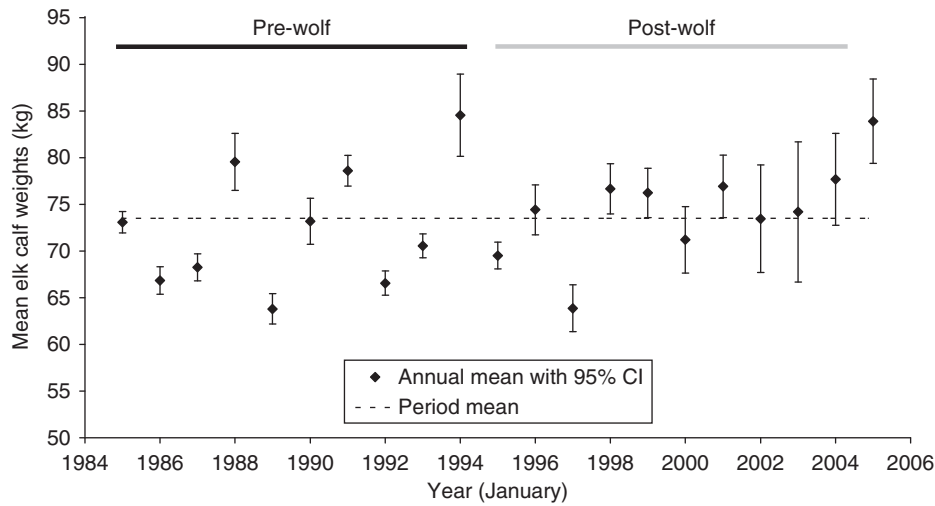


FIGURE 25.8 Mean weight (kg) of calves harvested during the late hunt for northern Yellowstone elk during 1985–2005 ($n = 12$ –253).

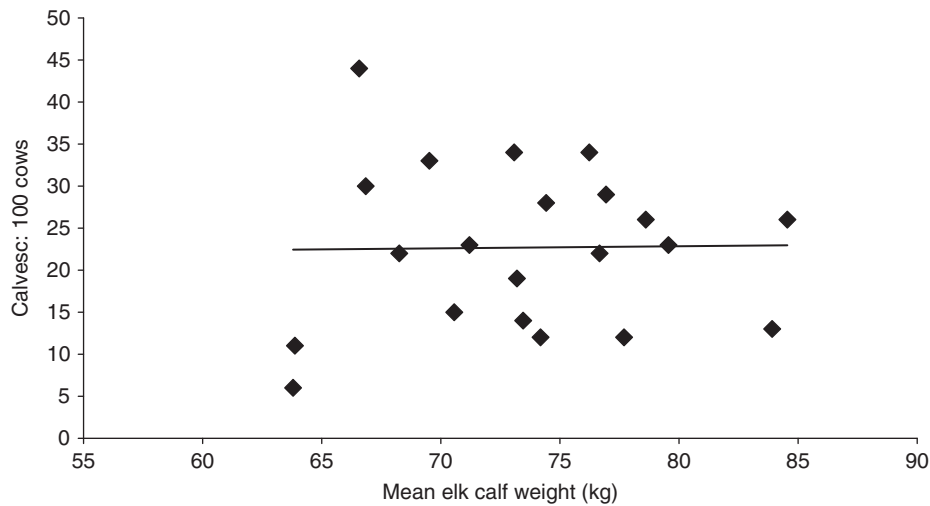


FIGURE 25.9 Recruitment rate (calves:100 cows) of elk calves relative to mean weight (kg) of elk calves recorded in early winter during the late hunt for northern Yellowstone elk, 1985–2005.

result in a strong calf survival response, even in areas with few or no wolves or grizzly bears. This conclusion also was indicated for the Madison headwaters, where the data supported constant nutrition for elk during the pre-wolf and post-wolf drought period (Chapter 22 by White *et al.*, this volume). The lack of a strong drought effect was not unexpected because the recent period of drought was similar across our entire area of study. Also, our findings suggest the effects of predation may have exceeded the effects of moisture and nutrition because areas and years with fewer than four wolves and/or grizzly bears per 1000 elk had significantly higher ratios of calves per 100 cows than areas and

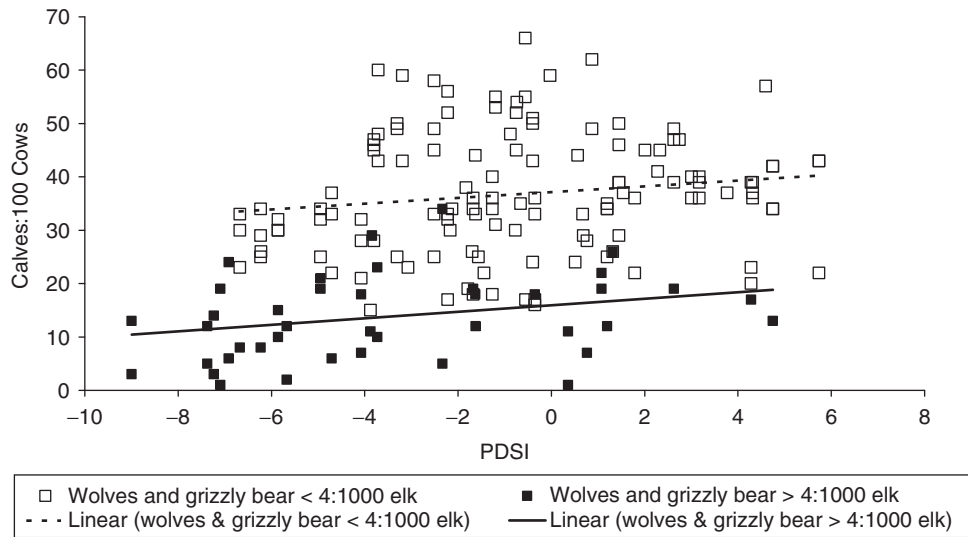


FIGURE 25.10 Recruitment rate of elk calves (calves:100 cows) across seven elk populations relative to the average PDSI during May and June of their birth year and relative to numbers of wolves and grizzly bear per 1000 elk in their herd range, 1968–2007. Yellowstone Valley not included for grizzly bear indexes.

years with greater than four wolves and/or grizzly bears per 1000 elk, regardless of the drought severity level (Welch 2-sample t -test, $t = 9.9905$, $P < 0.001$, Figure 25.10).

E. Adult Female Elk Survival

Survival estimates for adult females ranged from 0.76 to 0.88 among areas and periods for the four areas with data to estimate survival based on age structure. Survival of adult females was generally lower during the post-wolf period (Figure 25.11), but only consistently for elk in the Gallatin Canyon. Survival of adult females in the northern Yellowstone and Gravelly-Snowcrest mountains was lower during the 1997–2000 period, which included effects of the relatively severe winter of 1996–1997. For the Lower Madison area, adult female survival was significantly higher ($P < 0.001$) during the 2001–2006 post-wolf period compared to the 1989–1996 pre-wolf period, but this coincided with a substantial reduction in hunting pressure (Table 25.3), indicating hunting effects on adult female survival.

Survival estimates for adult female elk in northern Yellowstone during the 2001–2006 post-wolf period were not significantly different ($P \geq 0.19$) than during the 1983–1988 and 1989–1996 pre-wolf periods (Figure 25.11), despite a reduction in hunting mortality after 2003 (Table 25.3). Survival for adult female elk in the Gallatin Canyon was not significantly different among pre-wolf periods (1973–1975, 1983–1988, and 1989–1996, $P \geq 0.19$), but was significantly lower ($P \leq 0.004$) during the 2001–2006 post-wolf period (Figure 25.11), which included a reduction in hunting mortality after 2003 (Table 25.3). For the Gravelly-Snowcrest mountains, including the Wall Creek and Blacktail–Robb Ledford Wildlife Management Areas, survival of adult female elk was not different between the pre-wolf (1989–1996) and post-wolf (2001–2006) periods ($P = 0.41$), but survival during 1997–2000 was significantly lower ($P = 0.004$) than during both other periods (Figure 25.11). Survival of adult females decreased during the post-wolf period in the Madison headwaters compared to the pre-wolf period (Chapters 11 and 23 by Garrott *et al.*, this volume).

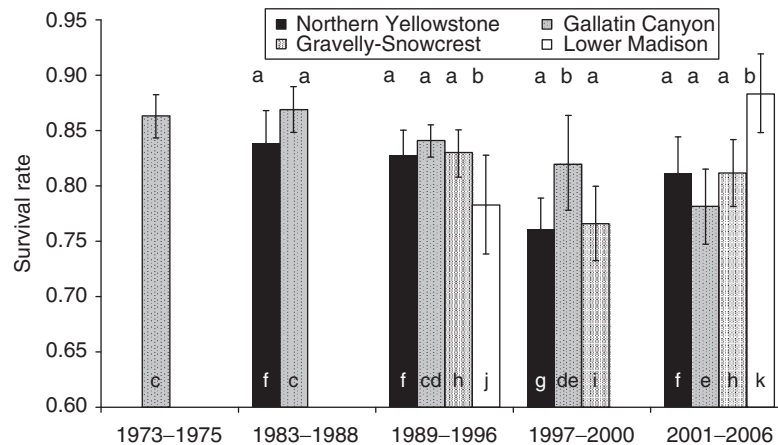


FIGURE 25.11 Estimated survival rate of adult female elk by time period and area as determined by age structure, 1973–2006. Different letters at top (a, b) represent significant differences ($P \leq 0.05$) among areas within time periods. Different letters at bottom (c–k, within bars) represent significant differences ($P \leq 0.05$) among time periods within areas.

F. Hunter Harvest and Estimated Wolf-Kill of Adult Female Elk

There was no hunter harvest of adult females or other elk for the Madison headwaters population except for those that dispersed to other populations (Chapter 18 by Gower *et al.*, this volume). Hunter harvest of adult female elk in northern Yellowstone varied considerably among years (Table 25.3, Figure 25.12A) with snow conditions and permit levels. We did not have age structure data to calculate survival for the adjacent Yellowstone Valley population, but hunter harvest rates of adult females were generally always higher than for the northern Yellowstone population. Estimated hunter harvests of adult females averaged 14% (range 8–21%) of estimated preseason populations in the Yellowstone Valley during 1989–1996, 11% (range 8–14%) during 1997–2000, and 10% (range 9–12%) during 2001–2003. Estimated hunter harvest of adult females in the Gallatin Canyon was generally high prior to 2001 (Table 25.3, Figure 25.12B). Except for an increase during 2003–2004 (Figure 25.12B), hunter harvest as a percent of the estimated preseason Gallatin Canyon adult female elk population decreased after 2000 (Table 25.3). We believe that the harvest estimates we portray for the Gallatin Canyon are overestimates to some degree, and estimates for the Lower Madison are slight underestimates, because some of the adult females harvested in the Gallatin Canyon were migratory to Madison Valley wintering herds (including the Lower Madison). Though hunter harvests of adult female elk in the Gravelly-Snowcrest Mountains (Wall Creek and Blacktail–Robb Ledford) decreased during 2001–2006 compared to historic levels (Table 25.3), they remained higher than for other areas. Based on historical trends in hunter harvest (Hamlin and Ross 2002), the harvest rate for the Blacktail–Robb Ledford population would have been higher than the Gravelly-Snowcrest average (Table 25.3) and the harvest rate for the Wall Creek population lower than the average.

Estimates of adult female elk killed by wolves were less than 2% of pre-hunting season numbers for all areas except the Gallatin Canyon, northern Yellowstone, and Madison headwaters areas (Table 25.3). The recent reduction in harvest mortality has not reduced overall mortality of adult females in the northern Yellowstone and Gallatin Canyon populations (Table 25.3, Figure 25.12A and B). Kills by wolves and deaths due to other factors (e.g., other predators, malnutrition/winter-kill, accidents, disease) appear to have replaced the reduced deaths due to hunting (Table 25.3). Hunter harvests of adult females in northern Yellowstone and the Gallatin Canyon are currently at insignificant levels, but further years of data collection will be necessary to determine if survival will increase in the face of significant wolf presence.

TABLE 25.3 Rates and causes of mortality for adult female elk and comparison of average recruitment of calves with replacement level necessary for stable populations on four areas in southwestern Montana and northwestern Wyoming, 1983–2006

Area	Period	Mortality Rate (M) from					Mortality Rate					Average Recruitment		
		Age Structure	Hunting	Wolf-kill	Other ^a	% Hunting	% Wolf-Kill	% Other ^a	Calves:100 Cows to replace Mortality ^b	Calves:100 Cows Observed	Calves:100 Cows Observed			
Gallatin	1989–1996	0.16	0.18 ^c	0.00	0	100 ^c	0	0	32	22				
	1997–2000	0.18	0.18 ^c	0.04	0	100 ^c	22	0	37	16				
	2001–2006	0.22	0.07 ^c	0.09	0.06	32 ^c	41	27	47	10				
Lower Madison	1989–1996	0.22	0.20	0	0.02	91	0	9	47	38				
	1997–2000		0.07	0.01										
	2001–2006	0.12	0.07	0.01	0.04	58	8	34	23	20				
Gravelly-Snowcrest ^d	1989–1996	0.17	0.15	0	0.02	88	0	12	34	46				
	1997–2000	0.23	0.16	0.01	0.06	70	4	26	50	36				
	2001–2006	0.19	0.10	0.01	0.08	53	5	42	39	30				
Northern Yellowstone	1983–1988	0.16	0.05	0	0.11	31	0	69	32	31				
	1989–1996	0.17	0.07	0.01	0.09	41	6	53	34	25				
	1997–2000	0.24	0.11	0.02	0.11	46	8	46	53	23				
	2001–2006	0.19	0.05 ^e	0.04 ^e	0.10	26	21	53	39	17				

^a Other = winter-kill/malnutrition, other predators, accidents, disease, etc.

^b Replacement = $((M/0.6)/(1-M)) \times 100$. An average 0.6 of recruited calves have been female. M = proportion of cows to replace, M/0.6 = total calves of both sexes, and 1-M = surviving cows.

^c Because an unknown proportion of harvested elk were migrating through to Madison Valley winter ranges, estimated mortality rate to the Gallatin population from hunting is likely high.

^d Estimated mortality rate from age structure only available for entire Elk Management Unit. Estimates for hunting and wolf-kill an average of only WCWMA and BT-RL WMAs.

^e Hunter harvest decreased throughout the period and wolf-kill increased to exceed hunter-kill.

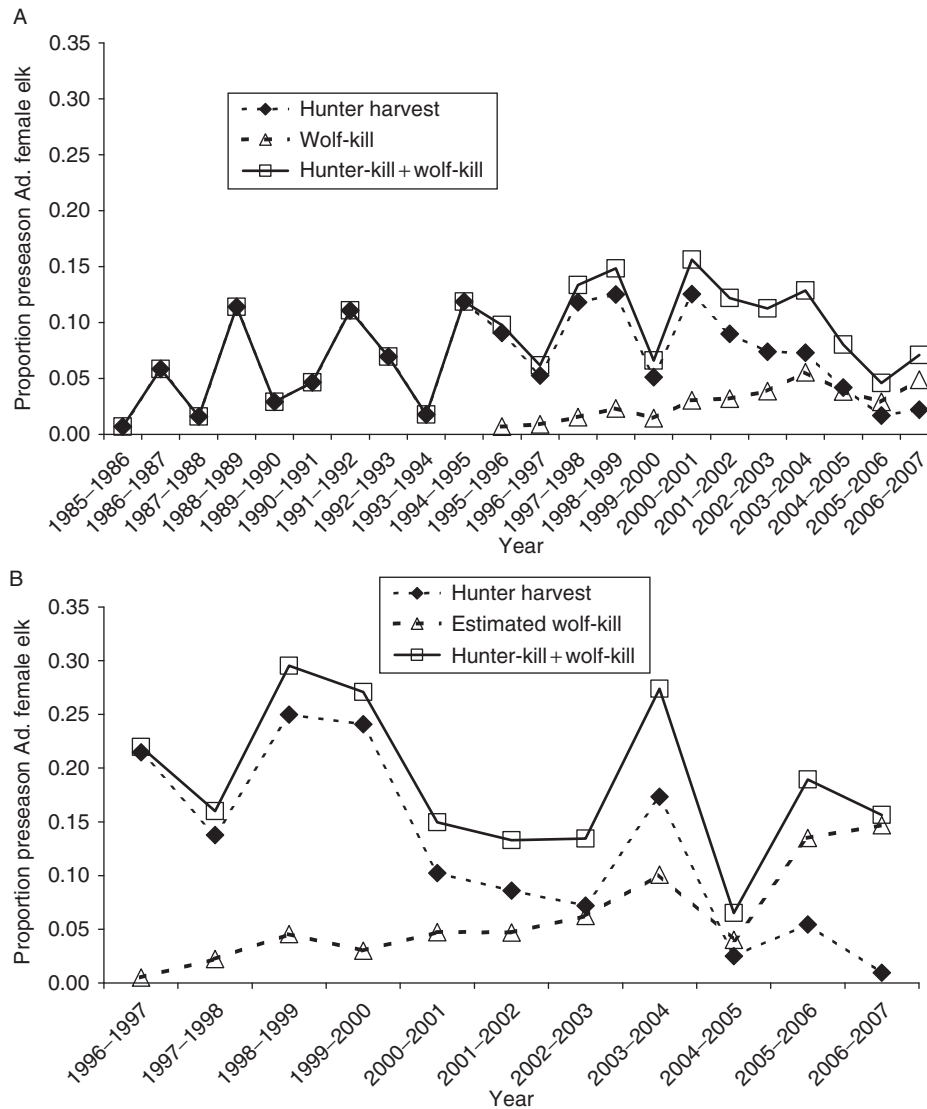


FIGURE 25.12 Estimated proportion of preseason adult female elk population killed by hunters and wolves. Panel A—estimated proportion of preseason adult female elk in the northern Yellowstone population killed by hunters (1985–2007), by wolves (1995–2007), and total off-take to both causes (1985–2007). Panel B—estimated proportion of preseason adult female elk in the Gallatin Canyon population killed by hunters, by wolves, and total off-take due to both causes (1996–2007).

G. Elk Population Trend

Elk populations in most of Montana and the greater Yellowstone area have increased substantially since the 1940s, with some exceptions. Long-term trends were increasing for five of the seven populations we examined, with a downward trend for the Gallatin Canyon and Madison headwaters elk populations (Figure 25.13). Thus, our seven elk populations have mirrored regional long-term trends.

The long-term trend for the Madison headwaters elk population (Figure 25.13A, Chapters 11 and 23 by Garrett *et al.*, this volume) indicated relative long-term stability with a recent decrease following

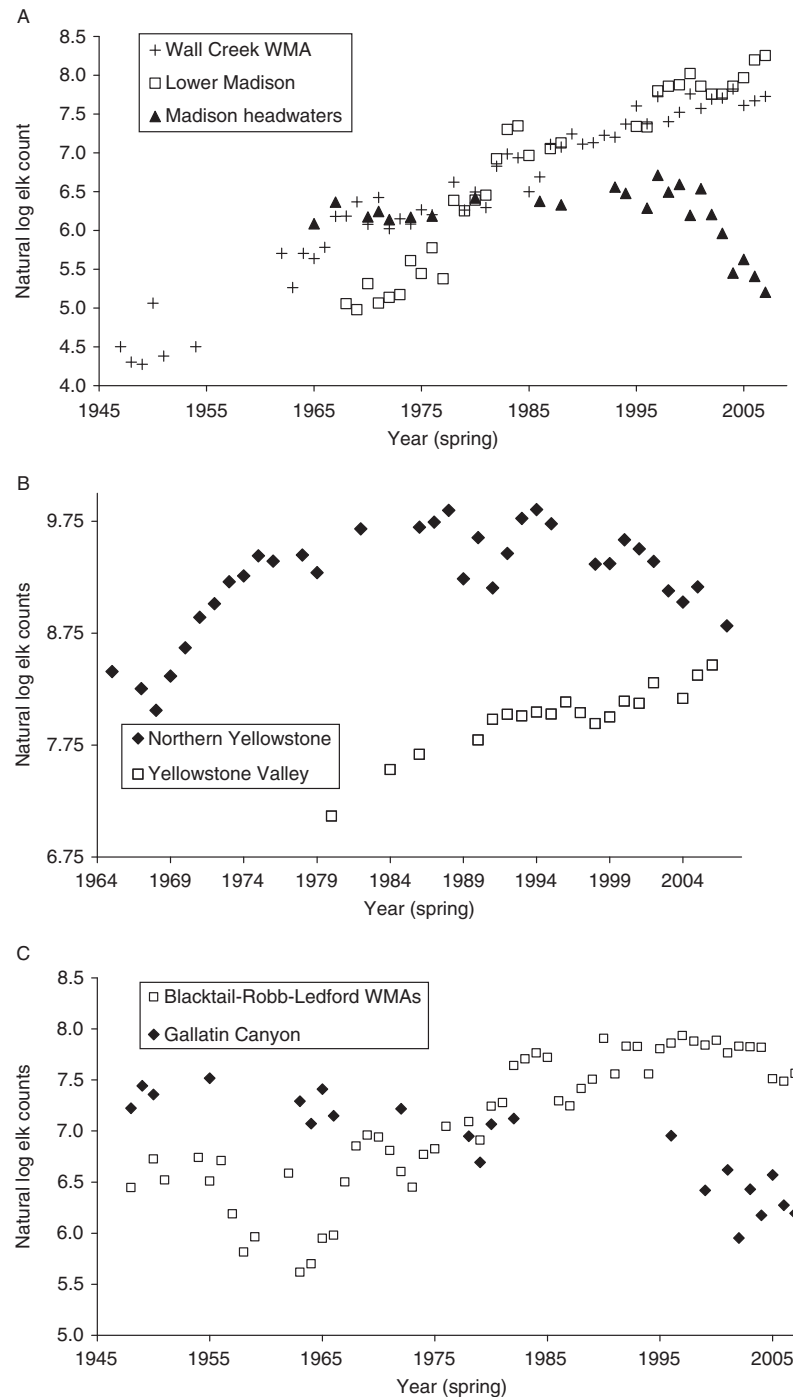


FIGURE 25.13 Long-term trend of elk population counts (natural log-transformed) for our seven study populations, 1947–2007. Panel A—trend of natural log-transformed counts of elk in Madison Valley populations: Madison headwaters, Lower Madison, and the Wall Creek Wildlife Management Area. All populations are within approximately 40 km. Panel B—trend of natural log-transformed counts of elk in Yellowstone Valley populations. The northern end of the northern Yellowstone elk winter range and southern end of the Yellowstone Valley winter range are immediately adjacent. Panel C—trend of natural log-transformed counts of elk in the Gallatin Canyon and the Blacktail–Robb–Ledford Wildlife Management Area.

wolf recolonization, whereas there is a continuing increasing trend for elk wintering in the Lower Madison and an increasing trend with recent stability for the Wall Creek population. Both of these populations are only 40 km downstream from the Madison headwaters (Figure 25.13A, Garrett *et al.* 2005). The northern Yellowstone elk population (Figure 25.13B) increased from lows after intense culling during 1961–1968 to a peak in the mid-1990s and has decreased since that time. Elk counted in the immediately adjacent Yellowstone Valley population have continued to increase since 1980 (Figure 25.13B), exceeding Montana Fish, Wildlife, and Parks objective levels. Similar to the close-proximity Madison River elk populations, the two Yellowstone River populations in close proximity displayed differing population trends. The Gallatin Canyon elk population showed relative long-term stability, perhaps with a slight decrease through the 1980s. A reduction in long-term numbers from about 2500 to 1500 elk counted was an objective of Montana Fish, Wildlife, and Parks and late hunts were held, after elk migrated from Yellowstone. Recently, the Gallatin population has decreased substantially below objective (Figure 25.13C), and late hunts ceased in 2004 with only youth allowed to hunt antlerless elk during the general season. The elk population wintering on the Blacktail–Robb Ledford increased substantially since the 1960s. However, population growth has slowed or stabilized recently (Figure 25.13C), in line with Montana Fish, Wildlife, and Parks management objectives of a reduction in numbers through harvests.

Population growth rate estimates during 1994–2007 support these differing population trends among the seven areas (Figure 25.13), with substantial decreases in the Madison headwaters ($r = -0.085$, $\lambda = 0.919$), Gallatin Canyon ($r = -0.077$, $\lambda = 0.926$), and northern Yellowstone ($r = -0.070$, $\lambda = 0.933$) populations. Elk populations wintering in the Lower Madison ($r = 0.074$, $\lambda = 1.077$) and Yellowstone Valley ($r = 0.032$, $\lambda = 1.033$) increased during the post-wolf period. Elk populations on the Wall Creek ($r = 0.018$, $\lambda = 1.019$) and Blacktail–Robb Ledford ($r = -0.019$, $\lambda = 0.982$) were relatively stable (Figure 25.13).

IV. DISCUSSION

We detected strong demographic differences among the elk populations from the seven different areas examined during this study that we interpret were due to varying site-specific effects of predation, land use and management regimes, and landscape characteristics. The close geographic proximity between sites allowed for similar influential effects of broad-scale climatic patterns such as drought. Conversely, predator densities, moderated by land management practices and local climatic and landscape conditions, varied considerably among elk populations and the effect of wolves was best described by predator:prey ratios. Decreases in elk calf recruitment with increasing predator:elk ratios were the most pronounced demographic effect and contributed most significantly to population trends within sites. Other demographic parameters such as adult female survival were negatively affected by predator densities. However, pregnancy rates, nutrition, and calf weights were not related to predator:elk ratios. Consequently, these comparative results illustrate that management actions cannot be applied universally over a large geographical scale.

Based on average progesterone concentrations in fecal samples, Creel *et al.* (2007) argued that pregnancy rates decreased with increasing ratios of wolves to elk as a consequence of elk behavioral responses to wolf predation risk. However, the data reported here from directly observed pregnancy rates reported by hunters (Figure 25.6A and B) and PSPB assays of blood samples (Figure 25.6C) that were collected from many of the same elk populations during the same time periods sampled by Creel *et al.* (2007), did not find evidence for such a decrease. Post-wolf pregnancy rates, as estimated using PSPB assays on samples from northern Yellowstone, Gallatin Canyon, and Lower Madison elk (Figure 25.6C) were equal to, or higher, than the average 80.7% pre-wolf pregnancy rate for all elk (including yearlings) reported for seven elk populations across Montana (Hamlin and Ross 2002).

These results are not surprising because reductions in pregnancy are unlikely to occur unless nutritional limitation, including by stress or disruption of foraging, becomes severe (Fowler 1981, Gaillard *et al.* 1998, Eberhardt 2002). Zager *et al.* (2007a) also found that elk pregnancy rates in Idaho were within the normal species range regardless of predator abundance. Fecal hormone assays suggested a post-wolf decrease in pregnancy rates in the Madison headwaters. However, ancillary data from sightings of radio-collared cows with calves-at-heel, fall calf:cow ratios, and serum PSPB and progesterone assays provided convincing evidence that the extremely low pregnancy assessments for these years were erroneous (Chapter 23 by Garrott *et al.*, this volume). Many of the Madison headwaters fecal samples were assayed in the same lab and frequently intermixed with the fecal samples reported in Creel *et al.* (2007). We are not certain of the reasons for the discrepancy between pregnancy assessments presented by Creel *et al.* (2007) and this study, but suggest some unexplained failure of the fecal hormone assays for progesterone (*e.g.*, physiological binding of metabolic by-products of progesterone in the gut or interference by them such that progesterone was not recognized in the enzyme immunoassays; Chapter 23 by Garrott *et al.*, this volume). The results reported in Creel *et al.* (2007) may also have been confounded with the use of fecal samples that likely included calves, immature females, and males not adequately identified and censored with the procedures used in that study.

Survival of elk calves appeared to be the vital rate most affected by increasing numbers of wolves and the coincident increase in grizzly bears relative to numbers of elk (Figure 25.7). Also, relative numbers of predators to prey appeared to be more important than absolute numbers of predators in affecting elk calf survival. Thus, the lowest survival of elk calves occurred in the smaller elk populations (Madison headwaters and Gallatin Canyon) with relatively high numbers of both wolves and grizzly bears. These two elk populations also occurred in areas with the greatest mixture of conifer cover and scattered small openings, the overall greatest level of landscape heterogeneity, and most severe snow conditions. This increased edge and restricted winter distribution of elk possibly made searches for, and killing of, prey easier for wolves (Bergman *et al.* 2006, Chapter 24 by Garrott *et al.*, this volume). Regional studies of neonatal elk calf survival indicated that predation by bears accounted for most mortality during the first 30–45 days (Singer *et al.* 1997, Barber-Meyer 2006, Creel *et al.* 2007, Zager *et al.* 2007b). Predation by wolves occurred through the year, perhaps increasing after calves became more active and visible.

Zager *et al.* (2007b) concluded from a study employing experimental manipulation of predator numbers and control areas that predation of elk calves, primarily by black bears (*U. americanus*) and mountain lions (*Puma concolor*), was largely additive. Our information indicated that nutritional factors played little or no role in elk calf mortality (Figures 25.8–25.10), which also indicated that most or much of elk calf mortality resulting from predation in the post-wolf period was likely additive. Likewise, nutritional effects were not detected during intensive studies of the Madison headwaters elk population (Chapter 22 by White *et al.*, and Chapter 23 by Garrott *et al.*, this volume). A correlative analysis indicated that ratios of calves per 100 cows in northwestern Wyoming were depressed to the greatest extent within herds with the greatest wolf presence (Wyoming Game and Fish Department 2007). Smith *et al.* (2006b), however, suggested that increasing predation of elk calves in the Jackson elk herd during 1990–1992 and 1997–1999 was partially compensatory because of nutritional factors, though mortality rates were lower there than reported for northern Yellowstone (Singer *et al.* 1997, Barber-Meyer 2006) or Gallatin Canyon (Creel *et al.* 2007). Thus, conclusions are generally similar regarding the effects of predation on elk calf survival across a variety of study approaches and within the broader area of wolf restoration.

Other information also indicated that it was unnecessary to invoke reduced pregnancy as a cause for low observed elk calf survival because observed normal pregnancy rates combined with telemetry-determined mortality rates explained observed survival. Average pregnancy rates for northern Yellowstone elk during 2000–2006 were estimated at 82% using the PSPB assay. Approximate average annual mortality of neonatal elk calves during 2003 through 2005 (Barber-Meyer 2006) was 76%, with approximately 58% of mortality attributed to bears, 16% to wolves, 19% to other unidentified predators (including unidentified wolves and bears), 5% to natural causes, and 2% to hunting.

Thus, for every 100 cows, 82 calves were born, 62 (82×0.76) died during the year, and 20 were recruited into the population. Average observed recruitment during 2003–2004 through 2005–2006 for northern Yellowstone elk was 16 calves per 100 cows. Thus, the observed low recruitment level was substantially explained by observed normal pregnancy rates and telemetry-determined calf mortality rates when also considering normal sampling error inherent in determinations of pregnancy, mortality rates of calves and cows, and spring classifications of calves per 100 cows.

Survival of adult females in most large mammal populations is generally high without human harvest (Eberhardt 2002). For example, annual survival of adult female elk averaged 0.83 during 1989–1996 in the Gravelly-Snowcrest mountains (Wall Creek and Blacktail–Robb Ledford), and 91% of this mortality was hunting related (Hamlin and Ross 2002). High survival rates in the absence of hunting (0.015 natural mortality in Gravelly-Snowcrest mountains) allows for limited operation of compensation in adult female mortality at densities below resource limitation (Nichols 1991). Thus, both human harvest and increased predation would likely decrease adult female survival, especially given the mild winter conditions in the region since 1997.

Survival of adult female elk was significantly lower in the Gallatin Canyon after wolf colonization compared to the pre-wolf period (Figure 25.11, Table 25.3), despite a reduction in hunting mortality to less than 3% of preseason numbers after 2003. Survival of adult female elk was also significantly lower in the Madison headwaters area following wolf colonization (Chapters 11 and 23 by Garrott *et al.*, this volume). For the other areas, adult female survival was not significantly lower during the post-wolf period (Figure 25.11, Table 25.3). High rates of hunter harvest, mortality during the relatively severe winter of 1996–1997, and low recruitment contributed to decreasing elk populations in the Gallatin Canyon and northern Yellowstone during the early post-wolf years (Figures 25.12 and 25.13, Table 25.3). However, adult female survival did not increase in northern Yellowstone after a reduction in hunting mortality to less than 3% of preseason numbers following 2003–2004. An increase in the estimated kill by wolves (Figure 25.12, Table 25.3) suggested that, similar to the Gallatin Canyon and Madison headwaters populations (Chapter 23 by Garrott *et al.*, this volume), some wolf-kills of adult female elk were additive to other sources of mortality, at least after 2003.

Observed vital rates and their relative changes (Table 25.3) generally explained elk population trends (Figure 25.13). Recruitment of calves was consistently low in historical terms during the post-wolf (and increased grizzly bear) period, and substantially below replacement levels for concurrent adult female mortality in the Madison headwaters, Gallatin Canyon, and northern Yellowstone populations. This consistently low recruitment of calves during the post-wolf period appeared to be the major factor influencing population trends. Recruitment of calves decreased somewhat during the post-wolf period on the other areas, but not to the extent observed in the high wolf and bear areas (Table 25.3). Elk populations were stable to increasing in the Wall Creek, Blacktail–Robb Ledford (Gravelly-Snowcrest mountains), Lower Madison, and Yellowstone Valley areas where ratios of wolves and/or grizzly bears per 1000 elk did not consistently exceed about 4–5 per 1000 elk. Thus, the presence of wolves and/or grizzly bears does not automatically signify significant consequences for elk populations, which can sustain at least moderate hunter harvest with low levels of wolf and bear predation.

Our conclusions are similar to those of many other studies of wolf-bear-ungulate systems in the north temperate region (Van Ballenberghe 1987, Ballard 1991, Gasaway *et al.* 1992, Crête 1998, 1999, Kunkel and Pletscher 1999, Hebblewhite *et al.* 2002, 2005). However, our findings do not support the conclusion of Vucetich *et al.* (2005) that hunting and weather alone explain the decrease in the northern Yellowstone elk. Their analysis through spring 2004 did not have the benefit of insight provided by the more recent reductions in hunter harvest. Also, their use of raw elk counts, uncorrected by sightability estimates, in combination with estimates of actual harvest overestimated the effects of hunting by 25–60%. We do not imply that hunting was not an important source of mortality, only that it was overestimated and other mortality sources, including the unexamined portion contributed by wolves and bears, are necessary to explain the observed population trend. High hunter harvest during 1997–2004 was implemented by Montana Fish, Wildlife, and Parks to reduce elk numbers wintering in

Montana to population objectives and, as intended, contributed to a significant decrease in the northern Yellowstone elk population. Population modeling that included effects of wolves along with winter severity/forage production and hunting (Varley and Boyce 2006) estimated about equal contributions by wolves and hunting (~38% each) and a contribution of approximately 23% by winter severity/forage production to the decrease in elk numbers in northern Yellowstone. The impact of bears on neonatal mortality of elk calves has generally been unaddressed in all models to date and should be considered in the future (Barber-Meyer 2006).

The effects of wolf restoration on elk populations in Montana and Yellowstone National Park have varied considerably by area, habitat, landownership, and management objectives. In Yellowstone and other public lands with few agricultural conflicts (e.g., Gallatin Canyon), wolves increased to high densities relative to elk numbers. Also, grizzly bear numbers simultaneously increased where conflicts with humans were minimal. In these situations, elk numbers have decreased. In contrast, on public multiple-use lands surrounded by private agricultural lands, and in valleys that contain largely private agricultural ownership, wolves have consistently depredated domestic livestock and been intensively controlled. Though wolves have persisted in these areas, regular control actions have maintained them at low absolute numbers and, also, low numbers relative to elk. We did not detect significant effects of wolves on numbers of elk in these areas. In fact, elk populations have remained above Montana Fish, Wildlife, and Parks objective levels in the agricultural valleys of Montana.

The differences we observed in the effects of wolves on elk populations and agricultural operations across our study region adds to the caution by Garrott *et al.* (2005) that one management prescription will not apply in all areas. Montana Fish, Wildlife, and Parks and the public will need to consider ecological factors such as predator to prey ratios, calf survival, and adult female survival in determining appropriate hunting regulations for elk. Similar factors should be considered in any management of wolves in which Montana, Idaho, and Wyoming becomes involved. Landscape, social, and economic factors will also be important in determining viable and realistic management options for both wolves and elk. Where elk numbers are above population objectives in agricultural environments, wolves are unlikely to contribute significantly to elk population reduction and varying strategies to increase hunter harvest will be necessary. However, where elk populations are small and wolf and other predator numbers are high, hunter harvest regulations must carefully consider potential “surplus” levels. These types of areas may support some regulated hunter harvest of wolves. However, land ownership type, management objectives, and social considerations will be important in determining management options for wolves.

Our investigational process was observational and correlative and, therefore, there are limitations to the strength of our conclusions (Boutin 1992). However, preliminary results from a more experimental, manipulative, multiple-area approach in the region (Zager *et al.* 2007b) indicate similar conclusions to our correlative approach. We believe that we have contributed to increasing reliable knowledge (Romesburg 1981) by repeating observational studies on a broader landscape scale (*i.e.*, many places; Andersen *et al.* 2006) to aid in the sequential gain in understanding of ecological processes (Eberhardt 2003). Also, we believe that our results and conclusions can aid in the management of both wolves and elk as the process of gaining reliable knowledge continues.

V. SUMMARY

1. We documented the effects of wolf restoration on elk populations in the greater Yellowstone area, which varied considerably with variations in ecological, landscape, and land use factors.

2. We found no correlation between wolf:elk ratios and the proportion of adult cows pregnant. Pregnancy rates were uniformly high for all herds, approaching the maximal levels that could be expected for this species. Thus, reduced pregnancy was unlikely to have substantially contributed to low indices of recruitment (*i.e.*, ratios of calves per 100 adult females) observed in some herds after wolf establishment.
3. We found a strong negative correlation between the ratio of predators to prey and indices of calf recruitment and attribute this relationship to additive predation effects that reduced calf survival below levels that would have been experienced in the absence of predators.
4. There was some evidence the survival of adult female elk decreased at high numbers of wolves relative to elk, and that a portion of this increased mortality was likely additive to other causes.
5. Elk populations decreased in areas where combined high numbers of wolves and grizzly bears occurred in relation to numbers of elk. However, elk populations remained stable or increased where consistently low numbers of wolves and/or grizzly bears coexisted with elk and moderate levels of hunter harvest occurred.
6. The effects of wolves on elk populations varied depending on the predominant land use. Wolves reached high numbers relative to elk populations where preservation was the main land use (*e.g.*, Yellowstone) and/or there were few conflicts with agricultural activities (*e.g.*, Gallatin Canyon). However, in areas where agriculture was the predominant land use, consistent depredations by wolves resulted in control actions that maintained low wolf to elk ratios.

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APPENDIX

Appendix 25A.1

Description of Study Areas

We assessed the status of elk on seven areas with different predator guilds and management paradigms in the greater Yellowstone area of the western United States, including: the Madison headwaters (Madison-Firehole, MF) and Northern Range (NR) areas of Yellowstone National Park (YNP), the Wall Creek Wildlife Management Area (WCWMA) and Blacktail–Robb Ledford Wildlife Management Areas (BT-RL WMAs) of the Gravelly-Snowcrest Mountains, Gallatin Canyon (Gallatin), Lower Madison drainage (HD 362), and the Yellowstone Valley (HD 314) in Montana (Figure 25.2). The relative proximity of the 7 areas (most winter ranges within 80 km of each other, the furthest 115 km) results in similarities in broad climate patterns. Thus, all areas have experienced the recent period of drought and mild winters.

The Madison headwaters range is well described elsewhere in this book (Chapters 11 and 23 by Garrott *et al.*, this volume). It supported 200–600 elk along the confluence of the Firehole and Gibbon rivers and the uppermost stretches of the Madison River. This nonmigratory herd was managed under the National Park Service's policy of natural regulation, whereby elk were not culled and numbers fluctuated in response to weather, predators, and resource limitations (Cole 1971, Chapters 11 and 23 by Garrott *et al.*, this volume). Snow depths and winter conditions are the most severe of the 7 areas discussed here. Coniferous forest covered 82% of this range, half of which burned during summer 1988. The remainder consisted of meadows (14%) and geothermal areas (4%) that reduced snow depths for wintering ungulates (Garrott *et al.* 2003). Approximately 1500–2000 ungulates wintered in

the area, 66% of which were bison (*Bison bison*) and 34% of which were elk. One wolf pack became resident in 1997 and by 2002 there were multiple packs totaling 30–40 animals.

The NR (Figure 25.2) has recently supported 6000–14,000 elk along a decreasing elevation gradient extending approximately 60 km along the Yellowstone River (Houston 1982, Lemke *et al.* 1998). These migratory elk were managed under the National Park Service's policy of natural regulation (Cole 1971). However, portions of the population that winter outside YNP boundaries have been subjected to varying levels of late season hunter harvest in Montana. Lower-elevation vegetation was primarily grassland and sagebrush steppe, with coniferous forests interspersed at higher elevations (Houston 1982). Other ungulates on this range included <150 bighorn sheep (*Ovis canadensis*), 700–1000 bison, <50 moose (*Alces alces*), <300 mule deer (*Odocoileus hemionus*), and 200–300 pronghorn (*Antilocapra americana*). The number of wolves residing in this area increased from 21 in 1996 to a high of 106 in 2003 (Smith *et al.* 2005). Hunter harvest of bulls is generally low, with the exception of 1991, when heavy harvest of bulls occurred as they migrated out of YNP due to early season snow conditions. Harvest of antlerless elk has varied considerably, from 1200–2400 during 1988–1989, 1994–1995, 1997–1998, 1998–1999, and 2000–2001 (10–13% of preseason estimates) to less than 140 antlerless elk during 2005–2006 and 2006–2007 (2%). An overall average antlerless harvest since 1986 is 6–7% of the preseason antlerless population.

The Wall Creek Wildlife Management Area (Figure 25.2) supported 1500–2700 migratory elk during winter on the west side of the Madison River Valley directly across the river from the Lower Madison drainage winter range (HD 362). This area was primarily managed to provide winter range for elk, though a rest-rotation cattle grazing system was also implemented in 1984. Vegetation on wintering areas was primarily open grassland benches and footslopes, which were kept relatively snow-free during most winters by strong winds. Summer and fall ranges throughout the Gravelly-Snowcrest mountains are a relatively open mixture of coniferous forests and grass-forb meadows (Hamlin and Ross 2002). Elk were the predominant ungulate, with less than 50 each of mule deer, white-tailed deer (*O. virginianus*), and pronghorn antelope also using the wintering area. Compared to elk, numbers of these species also are relatively low on summer and fall range, but additionally, a few moose occur on summer and fall range. Wolves were only transitory on the wintering area. Their attempts to establish a den site have been unsuccessful thus far for various reasons. However, wolves are established on summer and fall range of this population. The elk herd is relatively intensively hunted (10–12% of antlerless and about 50% of adult males, Hamlin and Ross 2002) to prevent long-term damage to vegetation and minimize complaints from private landowners.

The Blacktail–Robb Ledford Wildlife Management Areas (Figure 25.2) generally supported 1700–2700 elk during winter. Snow depths on winter range were generally low because periodic high winds blew much of the ridge top areas clear of snow during much of winter. Most of the valley and foothills were grassland with some inclusions of sagebrush. Similar to elk wintering on the WCWMA, elk on this area are scattered throughout a mixture of relatively open forests in the Gravelly-Snowcrest and Centennial mountains during summer and fall (Hamlin and Ross 2002). Elk comprised >85% of the wintering ungulate community. The remainder consisted of primarily mule deer, with a few white-tailed deer, pronghorn antelope, and moose. Up to 2 wolf packs totaling 3–14 wolves have used the area in a transitory manner since 2000. Locations from a pack member with a Global Positioning System radio-transmitter collar in 2005–2006 (5 wolves) indicated that about 34% of its time during winter was spent on and near the Blacktail–Robb Ledford WMAs. Some control of wolves because of conflicts with livestock has occurred in most years on and near this area. Hunter harvest of elk may average higher here than all the other areas, averaging about 15% of antlerless elk and 60% of antlered elk (Hamlin and Ross 2002).

The Gallatin Canyon range (Figures 25.2 and 25.5) historically supported 1000–3000 elk in the Daly/Tepee Creek, Porcupine Creek (including the Porcupine WMA), and Taylor Fork drainages on a combination of national forest, national park, private, and state lands. Recently, less than 1000 elk were counted during aerial trend flights. Snow depths on winter ranges here are lower than in the Madison headwaters,

but higher than all other areas described here. Valley bottoms were primarily sagebrush and grassland, with small riparian zones, coniferous forest, and small meadows on the slopes above (Creel and Winnie 2005). Elk comprised >90% of the wintering ungulate community, with the remainder consisting of about 50 moose, <100 mule deer, and a few white-tailed deer. At least one wolf pack totaling 8–13 wolves frequented this range since 1996–1997, though their presence was often transitory (Smith *et al.* 2005). In 2005 and 2006, 2 other wolf packs (6–10 wolves) also used the area on a consistent, but transitory basis. Some wolves in these packs were controlled when they moved into the Madison or Yellowstone Valleys and depredated livestock. Hunters harvested an average of 150 bull elk annually (about 45%) during 1994–2006. Harvest of antlerless elk averaged about 200 annually (about 15%) during 1994–1999, about 75 annually (about 8%) during 2000–2003, and was less than 30 annually (about 3%) during 2004–2006.

The Lower Madison drainage (HD 362, Figure 25.2 and 25.4), approximately 40 km downstream from the Madison headwaters range (Garrott *et al.* 2005) and directly east of and across the Madison River from the WCMWA, supported 1500–3500 migratory elk. This wintering area is a matrix of private (86%) and public (14%) lands managed primarily for livestock production, with 95% of the area supporting livestock at some time during the year. Average snow depth was low due to high winds that reduced snow accumulation (Gude *et al.* 2006). Grasslands comprised 58% of the area, with the remainder consisting of montane and riparian forests (32%) and sagebrush steppe (10%). Ungulates wintering in the area included 90% elk, 6% pronghorn, and 4% mule deer. Similarly, only low-moderate numbers of these other ungulates, including a few moose, occur on summer and fall range. Summer and fall range is a mixture of coniferous forest and meadows at higher elevations in the Madison-Hilgaard Range, western YNP, and portions of Idaho (Grigg 2007). One wolf pack became resident to the winter range in 1999, but the area never supported more than a single pack totaling 5 animals due to poor recruitment, low adult survival, and control due to livestock depredation (Garrott *et al.* 2005). Some other wolf packs, including some associated with the Gallatin elk herd, have also used the area on a transitory basis. Hunter harvest of bull elk varied from 100–200 annually (about 30%) during 1996–2006. Harvest of antlerless elk varied from 350–550 during the early 1990s (about 20%), to 50–100 (about 3%) during 1994–1996 and 160–320 annually (about 7%) during 1997–2006.

The western portion of the Yellowstone Valley is outside YNP, just northwest of the northern end of the NR, extending north to near Livingston, Montana (Figure 25.2). Winter range is mostly private lands and consists of open grasslands and foothills that are relatively snow-free during most winters due to strong winds. Summer and fall range includes much National Forest lands in the Gallatin range that are a mixture of coniferous forest and meadows. Little is known of extent of summer range for this population, but elk wintering in the southern portion of this area may overlap with portions of the Gallatin and NR herds in YNP during summer. During the period since wolf restoration, 3000–4800 elk were counted during aerial trend counts of this population. We do not have comparable population size information for mule deer and white-tailed deer, but annual harvests of each species are about 85% and 67%, respectively, of annual elk harvest. This indicated that the Yellowstone Valley has a greater complement of other small ungulates in proportion to elk than the other 6 areas studied. Hunter harvest of bull elk ranged from about 170–450 since 1996 (about 40%) and harvest of antlerless elk has ranged from about 250–425 annually (about 9%).

Appendix 25A.2

Methods

Predator Numbers

The annual number of wolves estimated for each area and numbers killed in control actions or other known mortalities due to humans were determined from December numbers reported in the Cooperative Rocky Mountain Wolf Recovery Annual Reports (*e.g.*, U.S. Fish and Wildlife Service *et al.* 2007),

YNP research reports (Smith and Guernsey 2002; Smith *et al.* 2001, 2003, 2004a,b, 2005, 2006a, 2007), and consultations with field biologists from Montana Fish, Wildlife, and Parks. After consultation with Montana wolf management specialist Mike Ross, we estimated winter wolf numbers by elk range to fractions of 0.25 in some areas because some wolves and wolf packs used multiple elk ranges. For the Blacktail–Robb Ledford, we used Global Positioning System telemetry locations to estimate that the areas wolf pack spent 34% of the time with this elk herd and fractionalized annual wolf numbers for that pack accordingly. Similarly, intensive fieldwork in the Madison headwaters allowed estimation of wolf-days on the area and fractional wolf numbers equivalent to estimates for the other areas (Chapters 15 by Smith *et al.*, Chapter 16 and 17 by Becker *et al.*, this volume).

Since restoration, estimated numbers of wolves (time adjusted) associated with our 7 elk populations (at least during winter) have ranged from: NR (21–106); Madison headwaters (0.4–23.7); Gallatin Canyon (1.5–17.75); Yellowstone Valley (0.5–10.5); BT-RL WMAs (1.01–10.03); Lower Madison (2–7); and WCWMA (minor transient use).

Wolf population growth rate relative to elk numbers followed an increasing linear trend for wolves associated with Madison headwaters ($r = 0.45$, $\lambda = 1.57$), Gallatin Canyon ($r = 0.23$, $\lambda = 1.26$), and Northern Range elk ($r = 0.18$, $\lambda = 1.20$). A minor increasing linear trend occurred ($r = 0.07$, $\lambda = 1.07$) for wolves associated with the Lower Madison elk, but total numbers were small (2–7). Numbers of wolves:1000 elk associated with the BT-RLWMAs and Yellowstone Valley increased to 2003–2004 and then declined. No wolves directly associated with the WCWMA elk wintering area have successfully dened and established a pack. Minor transient use of the WCWMA has occurred by wolves associated with the immediately adjacent Lower Madison elk population and other unknown wolves, and minor numbers of wolf-killed elk were observed. Similarly, relatively small numbers of wolves occur on summer/fall range of elk wintering on WCWMA (mostly wolves associated with BT-RL WMAs during winter).

Although absolute numbers of wolves on the Northern Yellowstone elk range were far above all other areas (peak = 106, next highest area = 23.7), numbers of wolves:1000 elk were highest on the Madison headwaters (peak = 85.3:1000), Gallatin Canyon (peak = 23.4:1000), followed by the NR (peak = 9.5:1000). Wolves:1000 elk on the other areas ranged from “none” to 2.6 wolves:1000 elk.

Numbers of grizzly bears also have made a remarkable recovery in the GYA from an estimated 136 (82–233) in 1974 (Craighead *et al.* 1974) to a minimum estimate of 405 in 2006 (Schwartz *et al.* 2007). Because bears, especially grizzly bears, have been implicated in substantial mortality of neonatal elk calves in this region (Singer *et al.* 1997, Barber-Meyer 2006, Creel *et al.* 2007), we thought it important to attempt to quantify relative grizzly bear numbers by area and year. Our index of grizzly bear numbers represents relative differences among areas and years rather than accurate, absolute numbers. We used information presented in the annual reports of the Interagency Grizzly Bear Study Team (e.g., Knight *et al.* 1990, Knight and Blanchard 1996, Haroldson 2006, Haroldson and Frey 2006) to construct our index. Annual sightings of unduplicated females with cubs-of-the-year (COY) were a good predictor of the minimum population estimate for the entire Greater Yellowstone ecosystem ($y = 7.5861x + 56.363$, $R^2 = 0.85$). Therefore, we used map locations of initial sightings of females with COY in the IGBST annual reports to partition sightings within elk calving/summer range among four of our study areas: the Gallatin Canyon, Northern Yellowstone, Lower Madison, and Madison headwaters. Bear Management Units (BMUs) 1 and 2 represented the Gallatin elk range, BMUs 3, 4, 5, 8, and 9 the Northern Yellowstone, BMUs 11 and 12 the Lower Madison, and BMUs 10 and 13 the Madison headwaters. Some sightings occurred on or near BMU boundaries and we divided those fractionally among the areas. A high proportion of the sightings in BMU 10 (Madison headwaters) occurred near the eastern boundary. Thus, it is likely that grizzly bear numbers affecting the Madison headwaters elk calves may be somewhat overestimated in our index. However, to maintain consistency of application of technique to all areas we included (or fractionalized) all BMU 10 sightings in the Madison headwaters estimate. To help smooth estimates, we summed the proportions that females with COY in our four areas comprised of the entire GYA each year and multiplied the average

(42.4%) times the GYA annual minimum estimate to obtain a minimum annual total bear estimate for our 4 areas (4AAME). Further, because of the relatively long reproductive cycle of bears, we used a 3-year-running average (RA) of females with COY (3YRACOY) to smooth the calculated estimated bear numbers. To construct the 3-year-RA for 1987 and 1988, we assumed that system-wide bear numbers in 1985 and 1986 were equal to those in 1987. Estimated annual numbers of grizzly bears by area was: $(3YRACOY \text{ area} / \sum 3YRACOY \text{ all 4 areas}) \times 4AAME$. Similar to wolves, from this estimate, we calculated estimated number of grizzly bears:1000 elk by area and year.

Our estimated numbers for 1985–2006 ranged from 6–24 grizzly bears for the Madison headwaters, 32–104 for the Northern Yellowstone, 18–45 for the Gallatin Canyon, and 3–21 for the Lower Madison. Relative to elk numbers, however, peak numbers were 105.7 grizzly bears:1000 elk in the Madison headwaters, 56.9:1000 in the Gallatin Canyon, 9.25:1000 on the NR, and 7.1:1000 in the Lower Madison. Estimated rates of population increase from 1985–2006 were: Madison headwaters ($r = 0.099$, $\lambda = 1.10$), Gallatin Canyon ($r = 0.087$, $\lambda = 1.09$), Northern Yellowstone ($r = 0.087$, $\lambda = 1.09$), and Lower Madison ($r = 0.029$, $\lambda = 1.03$). We had no method to estimate grizzly bear numbers for the Yellowstone Valley because females with COY were not recorded there. We believe that the southern portion would be similar to the Gallatin Canyon, the middle portion similar to the Lower Madison, and the northern portion would contain no or few bears. Single grizzly bear are sometimes observed in the Gravelly-Snowcrest Mountains (WCWMA and BT-RL WMAs) but females with COY have not been observed there in historic times.

We had no data to estimate levels of other predators (black bear, mountain lions, coyotes) and assumed that they were at relatively the same level for all areas.

Pregnancy, early calf survival, and condition

Hunters at the Gardiner (Northern Yellowstone) and Gallatin check stations were asked to report the pregnancy, sex of fetus, and lactation status of their harvest. Although the pregnancy rates reported may be underestimates because hunters vary in their anatomical skills and also miss some small fetuses, this underestimate should be consistent among years and yield a good relative annual index of pregnancy. Check station personnel at the Gardiner and Gallatin check stations also weighed hunter-harvested calves to the nearest pound and we converted these weights to kg for analysis. Male calves consistently weighed more than female calves and we adjusted female weights upward based on this average difference to construct an annual average sex-adjusted weight for all calves.

When adult female elk were captured to attach radio-transmitter collars on our study areas, we collected blood samples and used pregnancy-specific protein B (PSPB) assays to assess pregnancy status (Sasser *et al.* 1986). Earlier tests, where both blood samples and reproductive tracts were obtained (Palmisciano 1986) or blood samples and rectal palpation occurred (Hamlin and Ross 2002), indicated 100% accuracy for PSPB assays to estimate pregnancy ($n = 78$).

The hunter-reported pregnancy data were binomial and required an analytical method accounting for nonnormal error structure. We used the logit-transform (as proportions) rather than logistic regression because, although sampling was random within years, it was nonrandom among years. For example, sample sizes for adult females from the northern Yellowstone population varied from 37–1456 among years and were related to factors that could affect pregnancy rates such as increased samples during severe winters and decreased sample sizes with increasing numbers of wolves. For the January 2003 hunter-reported sample, there were no pregnancies among 19 yearlings. We used 0.01 (lower than any other year) as the pregnancy rate for logit-transformation. We used logistic regression to analyze pregnancy rates estimated using the PSPB assay because samples were random and similar in size among years. We used R version 2.5.0 (R Development Core Team 2006) for all analyses.

We used the average PDSI during May and June as an index of soil moisture conditions during the early growing season (Palmer 1968). The PDSI incorporates precipitation, temperature, and

evapotranspiration, all correlated with production and nutritive quality of plants (Sala *et al.* 1988). Thus, we expected PDSI to be positively related to elk nutrition and elk calf survival (*i.e.*, wet years and high PDSI = higher nutrition and elk calf survival).

All of our graphics display relationships relative to observed calves per 100 cows for ease of understanding. However, for statistical analysis, we logit-transformed calf:100 cow ratios as proportions.

Elk Population Size and Composition

Montana Fish, Wildlife, and Parks biologists conducted population trend counts for elk annually by using fixed-wing Piper Super Cub aircraft and Bell Jet Ranger helicopters. Counts were conducted as near as possible to the same mid-late winter time period each year. However, counts were not accomplished in some years due to weather conditions and scheduling conflicts. We recognize that single annual counts are particularly subject to substantial sampling variation among years, but variances of measurement errors of counts on the WCWMA, BT-RL WMAs, and NR were relatively small (Wang *et al.* 2006). For some analyses we present differences in natural log transformed raw counts, without corrections for missing years (r , Caughley 1977, $\lambda = e^r$), as measures of rates of change directly comparable among time periods. Where only a few years of missing counts occurred, for some other analyses we estimated the data for the missing year as the midpoint between the preceding and succeeding year. Where some indication of “true population size” was necessary (such as determining harvest rates where harvest estimates are of “true” numbers) and calculating predator:prey ratios, we used established correction factors to roughly estimate “true” population size.

For the Madison headwaters elk population, we used census figures reported elsewhere in this book (Chapters 11 and 23 by Garrott *et al.*, this volume). For the northern Yellowstone population, we used correction factors and estimates provided by Coughenour and Singer (1996) and Singer *et al.* (1997) through 1991–1992. After that period, we used the mean corrections factors established by sightability surveys (Coughenour and Singer 1996) to adjust counts upward by a factor of 1.322 (76% observed) during good survey conditions and 1.863 (54% observed) during poor survey conditions. For the WCWMA and BT-RL WMA populations, we used correction factors of 1.25 (80% observed) during good survey conditions, 1.67 (60% observed) during poor survey conditions, and 1.43 (70% observed) for average conditions (Hamlin and Ross 2002). These ranges were very similar to corrections determined for the Northern Yellowstone population (Coughenour and Singer 1996). For 1990 and 2005, when aerial counts were not conducted on the WCWMA, we used the high ground counts conducted by MFWP to represent the expected aerial count. Historically, aerial counts on this area averaged 110% of high ground counts conducted near the same time (Hamlin and Ross 2002). For 2003, when no aerial count was conducted on the BT-RL WMAs, we estimated the aerial count as the average of the prior and following year. For the Lower Madison and Yellowstone Valley, where terrain and cover conditions are similar to WCWMA and BT-RL WMAs, we used 1.25 (80% observed) as the correction factor for all years. For the Gallatin, aerial counts were not available for the period 1982–1995 and we used only counts from 1996 to 2007 for comparisons. For 1997, 2000 and 2002, when counts were not conducted, we estimated the aerial count as the average of the prior and following year. Because the Gallatin winter range has a greater portion of timber cover than the other Montana winter ranges, we used 1.43 (70% observed) as the correction factor for all years when estimating the “true” population.

Total numbers and bulls were recorded for all aerial counts of elk; for many, numbers of calves and cows were also recorded. However, for many areas and years, separate classifications of cows and calves were conducted from the ground. Where a mixture of techniques occurred, we used aerial counts to determine proportions of bulls and ground classifications to determine calf:100 cow ratios. For a few years in the Northern Yellowstone, Gallatin, and Lower Madison, calf:100 cow classifications were not available, but age structure data were available from check stations. We did not directly use calves:100 cows harvested to estimated calves:100 cows because hunters may select against calves

(Hamlin and Ross 2002). For those years, we used proportion of yearling cows in the next years harvest (YC_{t+1}) to estimate the previous years female calf:100 adult cow recruitment. To YC_{t+1} we added estimated recruited male calves (MC_{t+1}), where $MC_{t+1} = (YC_{t+1})(MC_t/FC_t)$. Thus, $(YC_{t+1} + MC_{t+1}):100$ cows ≥ 2 -years = recruitment of total calves per 100 adult females (t). This estimate could be slightly lower than comparable calf:100 cow classifications because it included any mortality occurring between the end of March and the next hunting season. We expect this mortality to be low in most years excepting those with severe winters.

To estimate pre-season adult female numbers for comparison of hunter harvest and wolf-kill rates, we multiplied raw post-season counts by correction factors for sightability and used classification data to estimate the proportion/number that were adult females, calves, and males. To this estimate for adult females, we added estimated harvest of adult females, adjusted for estimated wounding loss (see later), which became the estimated pre-season numbers of adult female elk.

Adult Female Elk Survival

Ages of hunter-harvested elk were estimated by eruption-wear (Quimby and Gaab 1957) and recorded at MFWP check stations. Increasingly since 1989, incisors also were collected for elk over 2 years of age and ages determined by examination of annuli in the cementum of incisor root tips (Hamlin *et al.* 2000). For years when only eruption-wear ages were available and for portions of annual samples that included some elk aged by eruption-wear only among samples mostly consisting of incisor annuli aged elk, we constructed area and time period specific matrices (*e.g.*, see Table 3, Hamlin *et al.* 2000) to proportionally correct eruption-wear ages to their expected distribution as incisor determined ages. We then added incisor-aged and corrected eruption-wear ages for the time period samples. We natural log transformed the age–frequency distributions of adult females recorded at check stations and fit linear regressions against age (Hamlin and Ross 2002, White and Garrott 2005). We used the slope of these regressions to estimate survival ($S = e^\beta$, where e = inverse of natural log and β = slope of the regression line). For years and areas when population trend did not indicate relative stability (Caughley 1977), we estimated rate of change in population size by regressing natural log of raw population counts against year to determine instantaneous rate of change (r). We then adjusted age–frequency distributions by the equation, adjusted number of age $x = f_x e^{rx}$ (Caughley 1977). We then proceeded as above to use slopes of the regression of natural log of age distribution against age to determine the estimate of survival adjusted for population growth or decline. To test for differences in survival among periods by area and period we used the different time periods and areas as factors in multiple linear regression models (Program R) allowing interactions between $\ln(\text{count})$ and age. We compared periods to each other and areas within periods to each other using all-subsets regression. The P -value of the regression coefficients on the interaction terms represented the significance level of the difference between the survival rate for the periods and areas. The age structure technique for estimating survival appears to be relatively accurate. During 1989–1996, for the Gravelly-Snowcrest Mountains, the age–frequency technique for determining survival closely matched survival data determined by telemetry (Hamlin and Ross 2002). Also, survival we determined by age structure for the Northern Yellowstone during 2001–2006 (0.81, this study) was the same as telemetry-determined survival (0.80) during March 2000 to February 2004 (Evans *et al.* 2006).

Hunter Harvest

We used annual reports of the Montana Statewide Harvest Questionnaire (SWHQ, Cada 1985, MFWP annual reports) to estimate hunter harvest as calves, adult females, and adult males. Additionally, for the Northern Yellowstone, annual reports were available for the mandatory check of late season elk harvest (T. Lemke, MFWP unpublished reports). Only raw results from the hunter questionnaire

sample, without multiplication by expansion factors, were issued for 1998. No elk harvest report was issued for 1997. For 1998, we averaged expansion factors reported for each hunting district in the 1996 and 1999 reports and multiplied those by the reported raw figures to estimate 1998 harvest. To estimate harvest for 1997 we used linear regression of harvest recorded at check stations against harvest estimated by the SWHQ for prior and subsequent years to estimate expected 1997 SWHQ harvest. For HD 314, where no check station was available, we used the mean estimate from all other areas to estimate SWHQ harvest (1997 SWHQ harvest = 0.471×1996 SWHQ harvest).

Hamlin and Ross (2002) reported that to account for wounding loss in the Gravelly-Snowcrest Mountains, it was necessary to multiply kill reported by the SWHQ by 1.22 for antlerless elk and by 1.1 for bulls. This figure likely varies among areas, years and conditions. Here, to estimate total loss due to hunting, we multiplied SWHQ reported kill by 1.15 for antlerless and 1.075 for bulls. For the more controlled Northern Yellowstone late hunt, we multiplied antlerless harvest by 1.1 and bull harvest by 1.05.

Most harvest for the WCWMA elk population occurred in HD 323 and most for the BT-RL WMAs population occurred in HD 324. However, because harvest of these populations also occurred in other Gravelly-Snowcrest hunting districts (Hamlin and Ross 2002) we partitioned harvest within all Gravelly-Snowcrest hunting districts by the percent distribution of WCWMA and BT-RL WMAs female elk during the hunting season (Hamlin and Ross 2002, p. 142, Table 9.2). We then summed harvests attributable to the WCWMA and BT-RL WMAs populations across hunting districts 323, 324, 325, 326, 327, and 330 for the total harvest estimate for each population.

Estimates of Wolf-killed Adult Female Elk

We used estimates provided in Smith *et al.* (2004a) and Becker *et al.* (Chapter 17 by Becker *et al.*, this volume) to estimate total wolf-killed elk as 0.060 elk killed per wolf day during the 181 day (1 November–30 April) winter period and reduced summer kill rates (184 days, 1 May–31 October) to 70% (0.042 elk killed per wolf day) of winter rates (Messier 1994). We used 25% (0.015 adult female elk killed per wolf day in winter and 0.0105 in summer) as the estimate for percent of wolf-kill that was adult females based on averages in reports for the Northern Yellowstone (Smith *et al.* 2004b, 2005, 2006), Gallatin Canyon (Creel *et al.* 2007), and Lower Madison (Hamlin 2005, Garrott unpublished data). Thus, estimated wolf-killed adult female elk annually by area was: $[(\text{Number of wolves}) \times (0.015 \times 181) + (\text{Number of wolves}) \times (0.0105 \times 184)]$.

Wolf Survival/Mortality

Smith *et al.* (2006a) indicated that during the first 9 years of wolf restoration to YNP (including both the NR and Madison headwaters) wolf mortality averaged 18% per year and dispersal averaged 28% per year, totaling 45% annual loss to the population. This total was more than exceeded by production and survival of pups in most years, resulting in increasing populations. Except for the Sheep Mountain pack, wolves associated with YNP were not subject to agency control actions.

We did not have telemetry-determined survival information for wolves on our other areas, but information on human-caused mortality for wolves during 1999–2006 (U.S. Fish and Wildlife Service *et al.* 2000, 2001, 2002, 2003, 2004, 2005, 2006, 2007) in these areas indicated the relative degree of human-caused (agency lethal control, private citizen 10j regulation removal, and other unknown/suspected illegal kill) mortality varied substantially among the populations. Human removal accounted for 34 (48.5%) of 70.17 cumulative wolves associated with the BT-RL WMA during years they were present. Percentages for other areas were: 33.5% (18.5/55.25, Lower Madison), 21.2% (11/52, Yellowstone Valley), 10.9% (10.5/96.5, Gallatin), and 4.3% (27/626, Northern Yellowstone).

Human removal of wolves did not occur within the Madison headwaters elk range. The high human removal rates in addition to unknown natural mortality and dispersal for the small populations associated with BT-RL WMAs, Lower Madison, and Yellowstone Valley likely accounts for their low/negative growth rates compared to the NR, Madison headwaters, and Gallatin where human removal was none to very low.