Elk

Elk (*Cervus elaphus*) belong to the Cervidae family, which also includes deer, moose, caribou, and other ruminants in which the males generally have branching antlers that are shed each year. The *C. elaphus* in North America are much larger than those in Europe, where they are referred to as "red deer." North American elk are also called "wapiti," an American Indian name. Like many other animal species now found in the Western hemisphere, the elk's ancestors arrived from Asia by crossing the Bering land bridge during a glacial period thousands of years ago. Because elk differ from red deer in morphology, ecology, behavior, and mtDNA variation, and they are not connected by interbreeding populations, some taxonomists consider the North American elk a separate species, *C. canadensis* (Baker et al. 2003). However, most authors regard the North American elk as conspecific with the red deer of western Eurasia (O'Gara 2002; Wilson and Reeder 2005). Elk subspecies have been distinguished based on physical attributes such as pelage and antler shape, but the wide geographic distribution of elk has resulted in many variations that may be caused by habitat rather than by genetic separation (O'Gara 2002).

In part because elk from Yellowstone were used to reestablish herds elsewhere in North America during the twentieth century, the elk in Yellowstone today are not considered genetically distinct. Their significance lies in their being by far the most abundant ungulate in greater Yellowstone and therefore having substantial effects on the ecosystem's structure and functioning. Elk grazing and browsing may affect the productivity of plant species and, as prey and carrion, elk provide sustenance to many carnivores and scavengers, as well as socioeconomic value outside the park for sport hunting. However, some elk remain in Yellowstone year-round, which means that, unlike most elk herds, their population dynamics are not affected by hunting.

Distribution and Abundance

In North America. At the time of the first Euro-American settlement, elk range extended across most of temperate North America except the Great Basin and what would become the southeastern United States. By 1900, a combination of uncontrolled harvests, market hunting, and habitat destruction reduced elk distribution to parts of Canada and the Rocky Mountain and west coast states. Various conservation strategies were used to augment depleted elk populations, including state and federal protection, reintroduction of elk, hunting regulations, and acquiring, restoring, and sustaining adequate habitat. These efforts, funded primarily by hunting interests, increased elk numbers ten-fold, to a total North American population of almost 800,000 (Bunnell et al. 2002; Peek 2003). Elk have been restored to most suitable ranges in western North America, with current efforts focused on establishing populations in the mid-continent and eastern states and provinces (Wolfe et al. 2002).

In Yellowstone National Park. An estimated 20,000 elk from at least seven herds mix to some extent on summer ranges in Yellowstone National Park. They are identified as herds by the winter ranges they use: central Yellowstone (or Madison–Firehole), northern Yellowstone, Clarks Fork, North Fork Shoshone, Carter Mountain, Jackson, Sand Creek, and Gallatin. Elk tend to move to areas of less snowpack to minimize energetic costs and access forage more easily during the winter (Skinner 1925; Craighead et al. 1972; Boyce 1989; Hurley 1996). Because of the deep snow that usually accumulates in the park interior, only the central herd and part of the northern herd spend the winter in the park; the other elk migrate to lower elevation ranges beyond the park boundary. Most research on elk in Yellowstone has been on the central and northern herds, both of which have declined in numbers during recent years. Factors such as elk density, habitat condition, nutrition, predation, hunting and other human activities can interact in complex ways, making it difficult to determine the cause of population fluctuations.

Central Yellowstone Herd. The central Yellowstone elk herd occupies 280 km^2 in the upper Madison River drainage, an area with elevation from 2,048 to 2,560 m (Garrott et al. 2003). Snow depths frequently make foraging difficult, but the geothermal features in this part of Yellowstone reduce snow cover in many areas. Because they remain in the park, these elk are not harvested by hunters, but they are preyed upon by grizzly bears and wolves, and the young and the old are especially vulnerable to death by starvation during hard winters. The herd's density remained relatively constant, around 500–550 elk (2 elk/km^2) during 1968–2003 (Garrott et al. 2005). However, wolf packs, which had been absent since the 1920s, reestablished territories in this area of the park in 1997, with multiple packs totaling 30–40 wolves by 2002. Moderate kill rates, combined with high wolf densities and modest elk densities, resulted in an estimated 20% of the elk population being killed during winter and projections for a declining elk population (Garrott et al. 2005). This herd numbered fewer than 100 during winter 2009 (Garrott et al. 2009).

Northern Yellowstone Herd. The northern herd is one of the world's largest migratory elk populations. Winter counts have fluctuated markedly, but have exceeded 10,000 in most years since the late 1970s. When deep snow restricts the area available for feeding on the northern range, elk move to lower elevations (mostly 1,500–2,500 m) inside and outside the park where the climate is warmer and drier (Houston 1982). The number of elk migrating out of the park during winter has been positively correlated with snow water equivalent, which is an index of snow pack and winter severity (National Research Council 2002; White and Garrott 2005a).

Prior to Euro-American settlement, elk winter range included land north of the park now used for agriculture and residential areas. By the 1960s elk congregated on the portion of the northern range inside Yellowstone National Park between Gardiner, Montana, and the upper Lamar Valley. However, during the harsh winter of 1989, which followed the extensive wildfires of 1988, more than 7,000 elk migrated outside the park and more than 3,000 elk traveled north of Dome Mountain (16 km north of the park). This restored migratory pattern was probably a result of high elk densities within the park, acquisition of former agricultural land as elk winter range (Dome Mountain Wildlife Management Area), and changes by the state of Montana in the hunting seasons to allow more elk to move further from the park (Lemke et al. 1998). Having learned the landscape, in subsequent winters more of the northern herd was likely to migrate outside the park where elk may be hunted. In addition, since 1989 Montana Fish, Wildlife and Parks (FWP) has leased property on Dome Mountain that is used to produce alfalfa. Growth after the first cutting is left as forage for wildlife, which has probably provided an inducement for elk to return there during the winter (National Research Council 2002). Thus, the winter range used by the northern herd increased in the 1980s by more than 40% to ~1,500 km^2 (Coughenour and Singer 1996; Lemke et al. 1998). About one third of the northern herd's winter range now lies north of the park on Gallatin National Forest and private land.

Elk density on the winter range has varied between 4 and 16 elk/km^2 since 1969 (Houston 1982; Coughenour and Singer 1996; Lemke et al. 1998). Part of the herd remains on the northern range year-round. Most elk in the herd move to higher-elevation summer ranges along the east-central boundary of the park, north of the park onto Buffalo Plateau, or as far south as Lewis Lake (50 km). They return to the winter range from mid-October to mid-November as snow accumulates at higher elevations (Skinner 1925; Craighead et al. 1972).

Elk counts during 1982–1995 were consistently high and ranged mostly between 15,000–20,000 animals. After wolf reintroduction in 1995–1996, the count decreased to approximately 12,000 elk in 1998 following a substantial winterkill and harvests of >3,300 elk outside the park during the severe winter of 1997. Counts increased to 15,000 elk by 2000, but then decreased to approximately 6,000 elk by 2010. Predation by wolves and bears, sustained harvests of antlerless elk outside the park, and climatic variations (e.g., severe winters, drought) were implicated as factors in the recent elk population decline (Vucetich et al. 2005; White and Garrott 2005). Substantial winterkill occurred in the winters of 1988–1989 and 1996–97 and drought-related effects on pregnancy and survival may have contributed to some extent because severe, sustained drought conditions existed on the northern range during 1998–2007. The number of wolves on the northern range, which decreased from 95 in December 2007 to 37 in December 2010 due to intra-specific strife, food stress, and mange. There are currently four packs of wolves in northern Yellowstone.

Ecology

Habitat

Elk are versatile generalists that use a mixture of habitat types in all seasons (Houston 1982); they feed on grasslands and in open areas but use coniferous forests for shelter. The ecotone between open and dense cover is important because sagebrush and other shrubs or taller herbaceous vegetation is used to hide newborn calves (Peek 2003). Elk are grazers, but also browse in fall and winter, especially in severe winters. Most of their winter diet in Yellowstone is grasses and shrubs; the consumption of forbs increases during spring. The ranges used by both the northern and central herds include large areas where fires, primarily in 1988, have left a mosaic of burned and unburned forests at different states of regrowth.

The central herd. The habitat used by the central elk herd includes wet meadows in the unforested areas along the Firehole, Gibbon, and upper Madison rivers that have standing water or saturated soils and grasses, sedges (*Carex* spp.), and marsh reedgrass (*Calamagrostis* spp). Drier meadows are dominated by grasses (*Festuca idahoensis*, *Poa* spp.) and sagebrush (*Artemisia* spp.). Lodgepole pine (*Pinus contortus*) on the slopes above are interspersed with stands of Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and Douglas-fir (*Pseudotsuga menziesii*).

The central herd makes local shifts in habitat use during the year rather than pronounced seasonal migrations. Snowpack may vary greatly in different parts of the Madison–Firehole area because of the disparity in elevation from the Madison Plateau to the river valleys and the influence of wet sedge meadows and geothermal features. To avoid the energetic costs of traveling through deep snow, the elk largely restrict their movements in winter to the valley bottoms and geothermal areas where less snow accumulates. Geothermal activity and thermal effluent from four geyser basins and many small springs keeps the three major rivers from freezing and enables some plant communities to continue photosynthesis year-round.

Also present in the area used by the central elk herd are two large predator species, grizzly bears and wolves. One other abundant ungulate species, bison, moves into the area from early winter to early spring, sometimes numbering more than 1,500, resulting in a substantial degree of range overlap with elk (Ferrari and Garrott 2002).

The northern herd. The summer ranges used by the northern herd are dominated by coniferous forests of Engelmann spruce, subalpine fir, lodgepole pine, Douglas fir, and whitebark pine (*Pinus albicaulis*). Most of the northern winter range is grassland (*Agropyron spicatum*, *Festuca*, *Poa* spp., *Koeleria macrantha*, *Calamagrostis* spp.) and sagebrush steppe dominated by Idaho fescue (*F. idahoensis*), bluebunch wheat grass (*Elymus spicata*), and big sagebrush (*Artemisia tridentata*). These relatively open areas are interspersed with forests of lodgepole pine and Douglas fir, along with some aspen (*Populus tremuloides*) and willows (*Salix spp*.). Bulls and older cows in the northern herd tend to occupy the more easterly, higher elevation areas within the park while cows with calves and yearlings are more likely to migrate to lower elevation areas inside or outside the park (Houston 1982; Coughenour and Singer 1996; Cook et al. 2004).

The northern elk herd is part of a more diverse ungulate complex than is the central herd; it includes bison as well as bighorn sheep, moose, mountain goats, mule deer, white-tailed deer, and pronghorn. But elk are the primary prey of wolves on the northern range, and also important for mountain lions, of which there were a minimum of 14–23 adults on the northern range during 1987–2004 (Ruth 2004). Elk calves on the northern range are seasonally important in the diet of coyotes (~225), grizzly bears (60–70), and black bears (unknown abundance). Grizzly bears also kill adult elk. While the abundance of mountain lions and grizzly bears has increased on the northern range since the mid-1980s, coyote abundance has decreased since wolf restoration (Crabtree and Sheldon 1999; Ruth 2004; Haroldson and Frey 2005).

A comparison of elk radio locations in 1985–1990 and 2000–2002 indicated that elk habitat selection on the northern range likely changed as a result of the combined effect of wolf restoration, fire-related habitat changes, and climate (Mao et al. 2003). In summer, when wolf activity was centered around dens and rendezvous sites, elk apparently avoided wolves by selecting higher elevations, less open habitat, more burned forest, and, in areas of high wolf density, steeper slopes than before wolf restoration. Elk did not attempt to separate themselves spatially from wolves during winter, but selected more open habitats and relied on other strategies (e.g., grouping behavior) to deter attacks.

Reproduction

For most of the year, bulls remain in bachelor groups or alone, focusing on food intake to maximize body size and antler growth, while cows, calves, and yearlings favor security in groups of fluctuating size that depend at least partly on forage availability (Geist 2002).

During the rut, which may last from September through October, each bull that intends to breed attempts to sequester and maintain control of a group of cows with their calves, sometimes tolerating yearling bulls but not adult bulls. Yearling bulls may be fertile but, depending on the age structure of the herd, they are usually unable to prevail against older, larger bulls until they are at least four years old. The bulls in prime condition, usually six to eight years old, are most likely to succeed in gathering a harem and fending off challengers. Rutting behavior of bulls includes bugling, thrashing, digging, rubbing antlers, wallowing, and sparring.

Elk cows can breed as yearlings, but usually become pregnant for the first time at age two. Decreasing day length in the fall initiates the elk cow's ovarian cycle. If she does not conceive during her first estrus period, she may have up to three more during the rut (Peek 2003). The gestation period is about 8½ months, with cows usually giving birth to a single calf in May or June. Twins are rare. Cook et al. (2004) found that the probability of an elk cow being pregnant in mid- to late winter was related to body fat rather than age, but pregnancy rates decreased markedly at age 14, possibly because the older cow is less able to maintain or recover energy reserves if she had a calf the preceding year or because of normal wearing of the teeth (White and Garrott 2005a).

Data collected on the central elk herd from 1991 to 1998 indicated that reproductive rates remained essentially constant (mean = 0.91) and near their biological maxima (Garrott et al. 2003). Pregnancy rates for the northern herd from 2000 to 2006, when elk densities on the winter range varied from 8–12 elk/km^2, remained consistently high (0.90 for cows age 3–15; 0.50 for cows ≥ 16) and similar to those found from 1950 to 1967 when elk densities were 5–9 elk/km^2 (Houston 1982; Cook et al. 2004; White and Garrott 2005a).

Recruitment

Prior to wolf restoration, the number of young elk that survived to sexual maturity in the central herd was highly variable and influenced by winter severity. Based on their 1991–1998 research, Garrott et al. (2003) found that the most severe conditions resulted in the virtual elimination of a juvenile cohort. Recruitment in the northern elk herd has also varied markedly. In data collected from 1971–1991, Coughenour and Singer (1996) found that calf:cow ratios were correlated positively with winter and summer precipitation two years earlier, and negatively correlated with the previous year's spring precipitation. These correlations are presumably the result of plant growth responses to precipitation and subsequent effects on elk nutritional status (Coughenour and Singer 1996). From 1996–2001, the number of calves per 100 cows in late winter ranged from 22–34; from 2002–2008, it changed to 11–24 calves (Northern Yellowstone Cooperative Wildlife Working Group, unpublished data).

A study of 127 radio-collared elk calves in the northern herd during 1987–1990 by Singer et al. (1997) found that their summer survival (mean = 0.65) was inversely correlated with the estimated size of the elk population the previous winter and positively correlated with their estimated birth weight. Predation (by bears, coyotes, eagle) was the cause of 72% of the summer deaths. Winter survival (mean = 0.72) was inversely correlated with the estimated winter elk population and positively correlated with the mildness of the winter and early calving. Winterkill was the cause of 58% of the winter deaths; predation, 3%. A similar study of 151 newborn elk calves during 2003–2006 found that 69% of the calves died within the first year of life and >90% of the deaths occurred during the first summer (Barber et al. 2005). Grizzly bears and black bears caused 58–60% of the deaths, and wolves and coyotes were each responsible for 14–17%. These results suggested that while summer predation of elk calves had increased since the 1987–1990 study, mortality from winter malnutrition had decreased.

Survival

Male elk have a shorter life span than females because their energy expenditures during the rut predispose them to malnutrition or predation, especially the following winter. Fighting among bulls during the rut can be intense and occasionally results in injuries that are fatal or contribute to death by other causes (Peek 2003). The survivorship of prime-aged females, however, is the major factor in elk population growth and therefore has been a focus of research in Yellowstone. Data collected prior to wolf restoration indicated that adult female survival was high (>0.95) and relatively constant in both the northern (Houston 1982) and central herds (Garrott et al. 2003). The mortality of calves and senescent females increased with snow pack, but prime-aged females were not directly affected except during the most extreme winters (Singer et al. 1997; Coughenour and Singer 1996). In the northern herd, increasing snow pack indirectly influences the survival of prime-aged females by increasing the number of elk wintering at lower elevations outside the park and consequently the number of elk harvested (National Research Council 2002).

Undernourishment can occur during winter even at low population levels because nutrition depends on the quality as well as the quantity of the available forage (Houston 1982). The worn teeth of older elk makes obtaining adequate nutrition especially difficult during winter, and without it they are more vulnerable to both winterkill and wolf predation. The geothermal features in the Madison drainage that create snow-free patches where elk tend to cluster also produce high levels of fluoride in the forage, causing flouride toxicosis in elk that is exacerbated by the abrasive silica in the volcanic soils. A comparison of 25–32 female elk in the Madison drainage that were monitored from 1991–1998 by Garrott et al. (2002) with data compiled by Houston (1982) for elk in the Lamar drainage found that tooth wear in the central herd resulted in the earlier onset of senescence (10–11 years) than in the northern herd (~16 years) and a shorter life span, with no elk surviving more than 16 years, compared to 20–25 years in the northern herd. These differences were reflected in the potential annual population growth rate (Lamar drainage, 11.5%; Madison drainage, 8.7%), and the proportion of the adult population in the senescent age classes (Lamar drainage, 5.8%; Madison drainage, 11.4%). Garrott et al. (2002) noted that these differences would make the central herd less able than the northern herd to compensate demographically for increased predation losses following wolf restoration.

Until the late 1990s, hunter harvest and winterkill of older animals were the primary causes of mortality for adult female elk in the northern herd (Houston 1982; Singer et al. 1997; Coughenour and Singer 1996; Taper and Gogan 2002). From 1969–1975, when hunting harvests were relatively low (<210 elk per year) and wolves were absent, the survival rate for adult females was estimated to be 0.99, compared to 0.83 for females age 1–18 during 2000–2003 (Evans et al.). For the 91 radio-collared adult female elk that were monitored during that period, the primary cause of mortality was hunter harvest (10), wolf predation (9), unknown causes (5), and mountain lion predation (3).

The majority of the northern Yellowstone elk harvested since 1976 were removed during the Gardiner Late Elk Hunt. Since the mid-1980s, the vast majority of permits issued for this hunt were for antlerless to help maintain the number of elk wintering north of the park at a level that is sustainable by winter habitat and will minimize depredation of private pastures and crops. Consequently, most of the harvested elk have been prime-aged females (2005 average = 8.2 years), whereas predation typically has a disproportionate effect on calves and older age classes. Montana FWP maintained the number of antlerless permits at more than 2,600 during 1995–2000 before gradually reducing them to 1,100 in 2005, and 100 in 2008 because of decreased elk abundance and low recruitment. Even conservative estimates of wolf predation of elk indicate that it has exceeded the number of harvested elk since 2003 (White and Garrott 2005a).

Elk have evolved behavior patterns and survival strategies that have enabled them to coexist with predators for millennia. What is not known are the population levels at which these two species will continue to coexist, and whether wolf predation over the long term will be additive to other causes of elk mortality rather than compensatory, i.e., to what extent losses through wolf predation will be offset by reductions in elk mortality from other causes. No consensus on these questions has been reached based on the short-term evidence collected so far. Vucetich et al. (2005) suggested that wolf predation from 1995 to 2004 was almost entirely compensatory because hunting harvest, climate (below average rainfall and above average snowfall), and density dependence appeared to account for 98% of the elk population decline during that period. In contrast, White and Garrott (2005a) countered that it was hard to rationalize how the ~17% of wolf kills that consisted of prime-aged females 3–16 years old from 1995 to 2004 was largely compensatory given that their survival rates were typically high at population levels well below carrying capacity and in the absence of hunting and major predators. Nonetheless, Varley and Boyce (2006) predicted that because both wolf predation and hunting are density-dependent, they would have a "stabilizing influence" that reduces the possibility of severe elk population decline by reducing the magnitude of fluctuations caused by variations in winter severity and forage production.

Natural Regulation

Although natural regulation is often understood to be a management policy in which ecological processes are allowed to function without human interference, it is also an ecological concept in which species abundance is regulated by density dependent feedback loops. Evidence has been found that the elk herds in Yellowstone are regulated by density-dependent mechanisms that change with population size, such as competition for food, and limited by density-independent environmental conditions such as winter severity. For example, evidence has been found that increases in elk density have been followed by declines in pregnancy rates (Houston 1982). Increases in elk density have also been positively correlated with declines in calf survival rates because more calves were born later and at lower weights (Houston 1982; Coughenour and Singer 1996; Singer et al. 1997; Taper and Gogan 2002). Calves are at a competitive disadvantage when population numbers are high because they begin winter with less fat and are more susceptible to mortality as a result of density-independent processes (National Research Council 2002).

Coughenour and Singer (1996) concluded that the density-independent factors important to elk survival in the northern herd were spring precipitation, forage production, and snow depth, and that winter weather, rather than elk density, accounted for 55% of the variation in per capita growth rate in the northern elk herd. Increased energy expenditure and reduced forage intake during harsh winters may reduce the condition of pregnant cows, resulting in calves with low birth weights and poor survivorship (National Research Council 2002).

Density-dependent and density-independent factors may interact in ways that cause large fluctuations rather than stabilization of the population size around an equilibrium point. Researchers have detected significant correlations between precipitation and plant production, elk population responses and precipitation, and elk population responses and elk density that suggest forage availability may limit elk population growth at high densities (Coughenour and Singer 1996; Taper and Gogan 2002). Varley and Boyce (2005) concluded that although both hunting and predation have diminished population fluctuations on the northern range since wolf predation, the stochastic effects of climate still alter carrying capacity from year to year. Elk are also more likely to migrate outside of the park and be harvested during severe winters when ecological carrying capacity is reduced and hunter success is increased (Singer et al. 1997; White and Garrott 2005). In this way, climate may facilitate a density-dependent source of mortality by hunting if the annual number of permits is varied in accordance with elk density (Varley and Boyce 2005).

Trophic Cascades

Ungulate behavior and distribution are among the many variables that influence ecosystem dynamics in the greater Yellowstone area. By defoliating plants, depositing dung and urine, trampling, and dispersing seeds, elk can increase or decrease plant density, height, nutrient content, productivity, and distribution (Frank 1998; National Research Council 2002). The decline in aspen that has occurred over the past century in Yellowstone and other parts of the Rocky Mountains may have been the result of multiple factors of which elk herbivory was central (Kay 1990). By altering elk abundance, behaviour, or distribution, wolves could therefore have "trophic cascade" effects on animal and plant species at lower trophic levels in the food web. Deliberate reductions in the northern elk herd from 1930–1968 to less than half of recent levels resulted in no significant difference in percent leader use of willows and only an 11% increase in heights (Singer et al. 1994). However, some researchers have proposed that the predation risk associated with wolves rather than a reduction in elk abundance is “the primary forcing mechanism for trophic cascades” in Yellowstone (Ripple and Bechsta 2004).

Trade-offs between gaining access to food and minimizing predation risks can influence prey behavior such as the timing, intensity, and habitat used for elk food selection (Fortin et al. 2005). Monitoring has shown that wolves alter elk vigilance, movements, spatial and temporal distribution, and group sizes (Mao 2003; Ripple et al. 2001; Ripple and Bechsta 2004; Creel and Winnie 2005; Fortin et al. 2005). Some research suggests that these behavioral alterations have reduced foraging pressure on deciduous trees and increased willow and aspen height in some areas, but the changes are patchily distributed (Ripple et al 2001; Ripple and Bechsta 2004). The patchiness of the changes could indicate that the wolf predation pressure is unevenly distributed or that the changes have some other cause.

Research on the Gallatin herd on winter range northwest of Yellowstone found that elk behave differently depending on whether wolves are present in the immediate area on a given day and that elk group sizes tend to increase in open habitats when the predation risk is lower (Creel and Winnie 2005). Data from GPS radio collars on 14 elk in the Gallatin herd during a three-month period in late winter of 2002 and 2003 showed that elk moved into wooded areas when wolves were present and reduced their use of preferred grassland foraging habitats that had higher predation risk (Creel et al. 2005). For Creel et al. (2005), these findings demonstrated that elk anti-predator behavior could drive a trophic cascade, but they noted that changes in elk numbers were also likely to have affected elk–plant interactions.

The increased energy expenditure and reduced foraging efficiency that would be the likely costs of anti-predatory responses could lead to lower elk fecundity and survival rates. However, White and Garrott pointed out (2005b) that no cause and effect relationship has been demonstrated between the presence of wolves and observations of woody vegetation release, and given the relatively brief interval since wolf restoration, woody vegetation release is difficult to explain based on reductions in elk abundance alone. Ongoing research is also considering the potential variations in weather, water table levels, winter severity, or other possible environmental factors.

Status and Threats in the Greater Yellowstone Area

The private, state, and federal land in the greater Yellowstone area, which includes two national parks, seven national forests, and the National Elk Refuge, is home to approximately 50,000 elk. For most of the last two decades, the Jackson herd, which currently numbers about 13,000, has been larger than the northern Yellowstone herd. Some ranges and migratory routes overlap, and some interchange occurs among the herds. Summer range in the southern part of Yellowstone National Park is used by part of the Jackson herd as well as by elk from the North Fork Shoshone and northern Yellowstone herds. Because the wildlife responsibilities of the National Park Service, the U.S. Fish and Wildlife Service, the U.S. Forest Service, and state wildlife agencies also coincide, elk management in greater Yellowstone requires substantial coordination among government agencies with different priorities. Although Yellowstone’s central herd and part of the northern herd remain within the park year-round, elk outside the park are managed primarily as big game animals. The state wildlife agencies set population objectives based on the number of elk that can be sustained through the winter and use regulated hunts to control herd sizes. Montana’s objective for the northern Yellowstone herd, which only applies to elk outside the park, is to have 3,000–5,000 elk wintering from the park boundary to Six-Mile Creek, and 2,000–3,000 of those elk north of Dome Mountain (Montana FWP 2004).

Although predation pressure has been a factor in the decline of Yellowstone’s central and northern herds, and in the Gallatin herd which migrates north into Montana during the winter, elk numbers in other areas of Montana subject to wolf predation are stable or increasing (USFWS 2006). Many elk herds throughout the greater Yellowstone area, including all of those adjacent to Yellowstone National Park in Wyoming, have exceeded their population objectives. This is partly because of the increasing amount of private land on which hunting has been prohibited or curtailed, creating elk sanctuaries and property damage problems (Montana FWP 2004).

As migratory routes from summer range to lower elevation winter ranges became blocked by settlement in the Jackson area during the twentieth century, the state of Wyoming sought to maintain its elk herds and limit depredation by establishing winter feedgrounds. In addition to 22 state-run feedgrounds, elk are fed during the winter at the National Elk Refuge. Because of their high densities, elk that use Wyoming feedgrounds have sustained high levels of brucellosis, a contagious bacterial disease that originated in livestock and often causes infected cows to abort their first calves. Transmission of brucellosis from feedground elk, where an average of 30% have tested positive for exposure to the bacteria, was the apparent source of infection in Wyoming cattle in 2004. Several cattle herds had to be slaughtered and the U.S. Department of Agriculture suspended the state’s brucellosis class-free certification, resulting in additional testing requirements for Wyoming cattle until the state is recertified. The majority view of the Wyoming State Brucellosis Coordination Team (2005) was that for the "foreseeable future" some use of feedgrounds would be necessary as a means of keeping elk away from areas used by cattle.

The artificial feeding of elk has long been prohibited in Montana. The Idaho Department of Fish and Game has sought to eliminate all but "emergency" feeding in the eastern part of the state. At the Rainey Creek feedground near the Wyoming boundary, where up to 500 elk have been fed during the winter to help keep them off farms and ranches, elk have been tested since 1998. Females that test seropositive are sent to slaughter; seronegative elk have been relocated in an attempt to establish herds on winter range in other areas (Idaho Fish and Game Commission 2006). When Idaho lost its brucellosis class-free status in 2005, elk using the Rainey Creek feedground were the likely source of the cattle infection.

Although bison in Yellowstone continue to have high seroprevalence rates (~40%) despite the passage of more than 50 years since winter feed was provided on the northern range, the prevalence of brucellosis in Yellowstone elk is similar to that of non-feedground herds in Montana that have little or no range overlap with infected bison. Elk are commonly observed within 100 meters of bison during late winter and spring when brucellosis-induced abortion or calving occurs in Yellowstone. The seroprevalence rate of 100 adult female elk captured on the park's northern range during the winters of 2000 to 2005 was 2%; it was 3% in 130 neonatal elk on the park's northern range during the summers of 2003–2005; and it was 3% in 73 adult female elk captured in the park's Madison–Firehole drainages during winters of 1996–1998 (Ferrari and Garrott 2002; unpublished data).

Elk as well as deer and moose in greater Yellowstone are at risk for exposure to chronic wasting disease (CWD). This contagious, fatal disease for which there is no vaccine or known treatment has spread across Wyoming toward Grand Teton and Yellowstone national parks. In 2004 CWD was detected in mule deer located ~130 miles from Yellowstone's southeast boundary near an area where elk that migrate from the park could mingle with mule deer during winter. Tissue samples from 703 elk that were harvested outside Yellowstone's northwest boundary in 2004 and 2005 tested negative for CWD.

Management in Yellowstone

Historical Management

Despite the establishment of Yellowstone National Park in 1872, elk herds in the area did not escape the widespread slaughter for elk hides that took place throughout the West in the 1870s and early 1880s. Sport and subsistence hunting of elk and other game was not prohibited in Yellowstone until 1883, and widespread poaching persisted until substantial penalties and the means of enforcing them began to have an effect at the turn of the twentieth century. In order to reduce their impact on elk and other game animals, predators were killed, and no wolf packs were left in the park by the time predator control programs ended in the 1930s.

Early elk population estimates in Yellowstone are not considered reliable (Houston 1982), but by 1914 elk seemed numerous enough that it was considered appropriate to begin baiting them into traps and using them to restore herds where elk had been eliminated. Elk were fed on the northern range during the winter with the intention of preventing mass starvation or mass migration out of the park where the animals would be hunted. But by the 1930s, when the northern elk herd numbered about 12,000, research appeared to confirm concerns that elk were having a deleterious effect on vegetation in the park, especially deciduous woody species like aspen, cottonwood, and willow on the northern range. Park managers therefore sought to reduce ungulate populations in the northern part of the park and maintain them at what was thought to be a sustainable level for the winter range. For elk, the population goal fell as low as 5,000. During the next 30 years, more than 13,500 elk were sent to 38 states, Canada, and Mexico; about 13,000 elk were trapped and shot in the park; and 45,000 were killed by hunters north of the park. As a result, elk counts on the northern range had dropped below 4,000 when removals ended in 1968 (Houston 1982).

Mounting public opposition was the principal impetus for ending herd reductions and allowing elk numbers to fluctuate in response to weather, predators, resource limitations, competing land uses, and hunting outside the park. Elk numbers increased rapidly under this "natural regulation" policy and by the mid-1970s the population had rebounded to ~12,000 (Houston 1982). This rapid increase in numbers exacerbated the controversy about overgrazing (Kay 1990) and in 1976 the state of Montana resumed liberal elk harvests, focusing on antlerless elk after 1985 (Lemke et al. 1998; White and Garrott 2005*a*). Despite liberal harvests, the winter count of the northern herd grew to more than 19,000 in 1988.

In 1997, the U.S. Congress directed the National Park Service to initiate a National Academy of Sciences review of all available science related to management of ungulates and the ecological effects of ungulates on the park. In the resulting report, the National Research Council concluded that "the best available scientific evidence does not indicate that ungulate populations are irreversibly damaging the northern range" and recommended that "a comprehensive, integrated program of research and monitoring be established to measure the consequences of current and future changes" (National Research Council 2002).

Current Management

After wolf restoration began in 1995, the major controversy about elk in Yellowstone shifted from whether the elk population was too large to whether it had gotten too small. The potential effect of wolf restoration on big game animals has been a contentious issue with many local hunters, outfitters, and legislators. Opposition escalated in 2002 and 2003 when park biologists estimated that recruitment of elk calves was the lowest since surveys begin in the mid-1960s. Many other factors could have contributed to the low recruitment (e.g., drought, winterkill, and hunting), but some people believed wolves were the primary cause and therefore called for the immediate delisting of the wolf as an endangered species and tight controls on wolf populations by the states.

To evaluate elk demographics, Yellowstone staff have a monitoring program that focuses on the northern and central herds and depends on partnerships with other federal, state, and private organizations. For example, Dr. Robert Garrott of Montana State University has collaborated with park staff to conduct research on the dynamics of the central Yellowstone elk population since 1991. Radio telemetry is used to monitor the following vital signs of elk:

- Annual estimates of cause-specific mortality and survival rates for adult females
- Annual estimates of recruitment
- Annual estimates of population size
- Estimates of age-specific reproductive rates
- Estimates of age structure
- Annual estimates of human harvest
- Influence of weather conditions on vital signs
- Disease surveillance

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