NORTHERN YELLOWSTONE ELK

Resilience and Adaptation to Changes in Management Policies and the Ecosystem

P. J. White, Daniel R. Stahler, Douglas W. Smith, Daniel R. MacNulty, and Robert A. Garrott

Cover photo by Jacob W. Frank, National Park Service.
Female elk rests on travertine below Palette Spring in Yellowstone National Park.

This book is dedicated to Lee Eberhardt, Doug Houston, and Francis Singer—three influential scientists that vastly increased our knowledge of wildlife and ecological processes in Yellowstone. We appreciate their friendship, mentoring, and support in continuing their work.

An adult female (cow) and calf elk walk by the Roosevelt Arch at the north entrance of Yellowstone National Park. Photograph by Jacob W. Frank, National Park Service.

Northern Yellowstone Elk

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Adult male (bull) elk bedded in Yellowstone National Park. Photograph by Jacob W. Frank, National Park Service.

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Technical Editor: Charissa O. Reid

Featuring the photography of National Park Service employees

Library of Congress Control Number: ??????????????
ISBN: ???-0-???-?????-1

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Adult male elk grazing in Yellowstone National Park during winter. Photograph by Neal Herbert, National Park Service.

Preface

Cameron H. Sholly
Superintendent, Yellowstone National Park

Yellowstone is a land of icons. We often refer to several of Yellowstone’s wildlife species as such. The grizzly bear is an icon of wildness. The bison is an American icon. The gray wolf and cutthroat trout are icons of ecosystem restoration and conservation success. But among these cherished species, the elk of Yellowstone prominently stand. The elk is an icon of resiliency; a guardian of biodiversity; key to the structure and function of this dynamic landscape. Their influence touches the far reaches of this vast Yellowstone ecosystem, and spans millennia. The mark of Yellowstone elk is of immense ecological, scientific, and cultural importance.

One could argue our own species and elk share the most unique relationship in the history of Yellowstone human-wildlife dimensions. To some tribal nations, what we now refer to as the Yellowstone River was long known as the Elk River. This reflects Yellowstone’s significance as a vital home to elk, that in turn provided sustenance, clothing, tools, and other ingredients that constitute the rich cultures of native peoples who inhabited these lands. Elk are revered as a symbol of abundance, strength, and spiritual connection. In the late 1880s, when Teddy Roosevelt’s interest in Yellowstone became focused, he united with George Bird Grinnell, founder of the Audubon Society and co-founder of the Boone and Crockett Club, to defend Yellowstone and its wildlife from market hunting, poaching, and commercial development. Yellowstone elk were a main target of their protection, and they delivered. As Yellowstone National Park crystalized as a preserve, it resumed its role as one of the most important sanctuaries and breeding grounds for elk in North America.

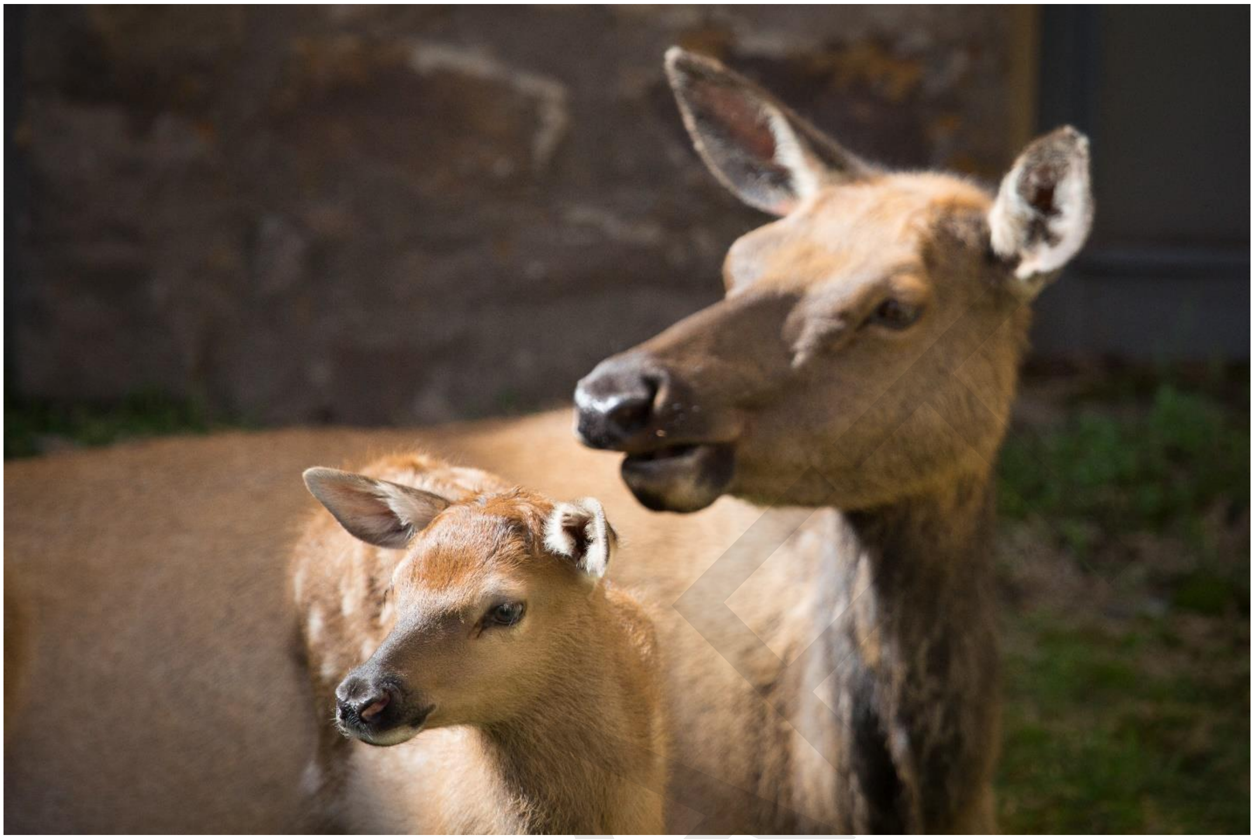
What followed on the heels of this protection expanded an already dynamic history of elk and human relations. It is a path defined by shifting management policies, human values, and maturing ecological understanding of how elk and other wildlife fit into the Yellowstone ecosystem. Today, up to eight distinct elk herds have been described throughout the Greater Yellowstone Ecosystem, with many relying seasonally on the productive habitats encompassed by the park. But one elk herd has been in the spotlight ever since the establishment of the National Park Service in 1916 – the elk of Northern Yellowstone.

The northern herd has long been at the heart of challenging issues in Yellowstone National Park. Concerns throughout the last century over too many elk, or too few, have generated ample debates from regional to national focus, congressional examination, and even reviews by the National Academy of Sciences. For Yellowstone National Park, whose primary mission is to preserve resources in their natural condition, controversies over elk have included human-caused changes in abundance, impacts on range quality, disease spread, competition for food with other wild ungulates or livestock outside the park, and of course, rivalry between hunters and large carnivores over their shared use. Fortunately for us, and for these elk, we have a rich legacy of scientific inquiry and hard-earned lessons from the past that has set a course under which elk continue to thrive in northern Yellowstone.

This book explores the multifaceted importance northern Yellowstone elk play in the park’s history, maintaining its biodiversity, and captivating the minds and hearts of people who care about Yellowstone and wildlife. Throughout these chapters, we learn about the history of northern elk management and research, along with an understanding of their biology and dynamic relationships with other ungulates, predators, scavengers, and the plants they utilize. Northern elk are an ecologically important species influencing plant communities and their succession, while supporting diverse wildlife communities and contributing to the fascinating complexity of the entire ecosystem.

From this book, we also gain a profound appreciation for the significant role humans have played in the story of northern Yellowstone elk. From our own agency's elk feeding, culling, and translocation programs, to their suspension, to the reintroduction the gray wolf simultaneous to the recovery of cougars and grizzly bears, the National Park Service's role is significant. Just across the northern boundary of the park, the state of Montana has also importantly influenced this migratory elk herd through hunting regulations and hunter harvest rates that have varied through time. Moreover, Yellowstone's elk have captured the imagination of visitors for generations. Observing elk in their natural habitat, witnessing their seasonal migrations, the nursing newborn calf, or listening to the bugle of a bull elk during the fall rut, all adds a unique allure to the Yellowstone experience. These elk enhance support for Yellowstone National Park, our local economies, and awareness for their conservation. In fact, we can trace the bugle of the elk across much of North America, and their species' conservation, back to those who originated from Yellowstone generations ago.

Much of our more recent understanding about northern Yellowstone elk comes from a body of research the editors of this book have conducted along with their colleagues, building on the phenomenal efforts of previous biologists. We are fortunate to have this knowledge which stems from the ever-advancing, best available science. Through the dedication and vision of scientists who see value of long-term ecological studies, and support from the commitment and passion of diverse stakeholders, the elk are in good hands. Northern Yellowstone elk continue to inspire our understanding of ecological processes and ensure the preservation of this iconic species and its habitat. It is our mission to do so.

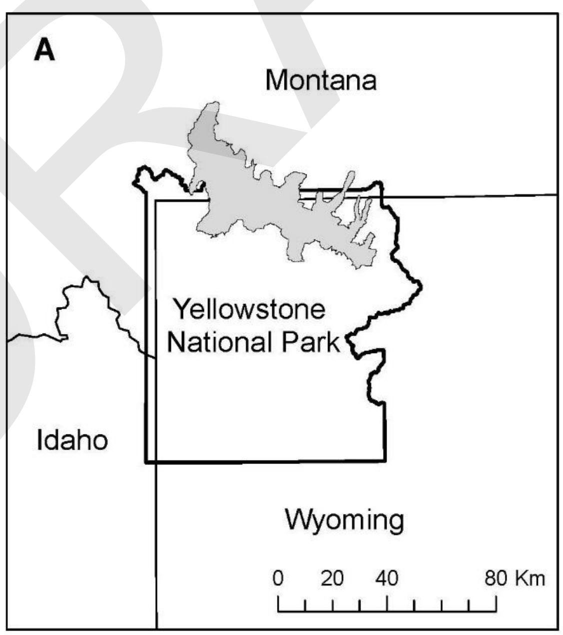


Adult female and calf elk in Yellowstone National Park. Photograph by Neal Herbert, National Park Service.

Introduction

Historically, the Yellowstone area supported a diverse association of wild ungulates (hooved mammals), including bighorn sheep, bison, elk, moose, mule deer, and pronghorn. These plant eaters provided a large prey base for predators such as black bears, cougars (mountain lions), coyotes, grizzly bears, and wolves, as well as carrion for numerous scavengers, such as insects, birds, and smaller meat eaters. However, numbers of these ungulates and predators were decimated by colonization, market hunting, and settlement of the region by European Americans during the late 1800s. Thereafter, this predator-prey association and their role as ecosystem engineers in maintaining or modifying habitats and creating a more diverse environment for plants and other animals was absent for more than a century.

However, the high mountains and plateaus in and near Yellowstone National Park, established in 1872, continued to provide summer range for about 20,000 to 25,000 elk from as many as 6 to 8 populations (or herds) that intermingled to some extent but then migrated to separate winter ranges at lower elevations outside the park. Only part of the relatively large northern population and small, scattered groups in geothermally warmed areas spent winter in the park. Today, the northern population spends winter on more than 580 square miles (1,500 square kilometers) of grasslands, sagebrush steppe, and lodgepole pine forests adjacent to the Yellowstone River and its tributaries. About two-thirds of this winter range is within the northern portion of the park while the remainder is in the State of Montana to the north, primarily on U.S. Forest Service and private lands.



The winter range for northern Yellowstone elk (gray shading) in the northern portion of Yellowstone National Park and Montana (White et al. 2012).

The climate pattern of long, cold winters and shorter, cool summers in the Yellowstone area has a strong influence on elk by affecting forage growth and availability, as well as their energetics and movements. Major snowstorms typically begin in November and continue through March or later. More snow accumulates on the higher-elevation mountains and plateaus (3 to 6 feet; 1 to 2 meters) than in the lower-elevation valleys (1 to 2 feet; 0.3 to 0.6 meter), most of which extend well outside the park. Snowpack melts during April and early May at lower elevations but can persist into June at higher elevations and in forested areas. Rainfall and thunderstorms occur from May through July. Thereafter, the climate is relatively dry until winter storms begin. New growth of grasses and forbs begins in spring following snow melt and progresses from lower elevation valleys and basins upslope to higher-elevation mountains and plateaus. Depending on elevation and precipitation, grasses stop growing in middle to late summer or autumn and become dormant through the winter.

Since the establishment of the National Park Service in 1916, the management of northern elk has been one of the most contentious issues in Yellowstone National Park, triggering regional and national debates, congressional scrutiny, and reviews by the National Academy of Sciences. Concerns focus on the appropriate size of the population (abundance), the effects of ungulate grazing on range conditions (habitat) and crops on private ranches, the spread of diseases (such as brucellosis) to cattle, and what intensity and types of management are appropriate for elk in a national park whose primary mission is to preserve resources in their natural condition. In 1982, park biologist Doug Houston published a book entitled *The Northern Yellowstone Elk Herd* that described their behavior and ecology and chronicled their management, including the controversial culling and harvest of tens of thousands of elk from the park and nearby areas in Montana during the 1920s through the 1960s to limit numbers and maintain desired range conditions. He also described a transition in management approach beginning in the 1970s to reduce human intervention and rely more on the natural regulation of elk numbers through ecological processes, such as competition for food (forage), and environmental conditions, such as summer precipitation, grass production, and snow cover, that limit forage availability. In 1986, Dr. Houston and his colleagues Dr. Don Despain, Dr. Mary Meagher, and Paul Schullery described the preliminary findings from this new management approach in a book entitled *Wildlife in Transition: Man and Nature on Yellowstone's Northern Range* which laid the groundwork for continued research by predicting how increased mortality and decreased reproduction would regulate (control) the number of elk on the winter range as competition for forage increased. At the time, they did not believe predation was necessary to attain this regulation of population size.

In the mid-1990s, park managers reintroduced wolves to Yellowstone National Park and over the next decade a thriving population established in the ecosystem. This restoration coincided with the continued increase and expansion of populations of grizzly bears and cougars in the northern Yellowstone area. As a result, a complete association of native ungulates and large predators again lived in the region by the mid-2000s. This significant achievement led to a proliferation of research that continues to this day. In addition, the region continues to experience substantial ecological change from a growing human influence on the landscape, warming climate, invasive plants and diseases, and other stressors. Human development outside the park continues to fragment wildlife movement corridors, and temperatures have increased significantly since the 1950s, with shorter winters and complex effects on the timing and extent of rainfall, snowpack, and plant production. These changes could cause shifts in the distribution and growth of some plants and animals, contribute to the further spread of invasive plants, and trigger transitions in some ecological communities that affect the amount of forage for ungulates.

This book summarizes the management of northern Yellowstone elk described by Dr. Houston and his colleagues and more recent management and research findings, emphasizing the period after the restoration of a full complement of predators. Chapter 1 provides general information on the behavior and traits of elk, while Chapter 2 outlines the management history and population trends of elk in northern Yellowstone. Chapters 3 through 5 provide information on the demography (reproduction, survival), seasonal movements, and nutritional ecology of these elk. Chapter 6 focuses on predation by bears, cougars, and wolves, and the potential for competition among elk and with other ungulates for food and other resources. Chapter 7 discusses the ecological role and adaptive capabilities of elk, while Chapter 8 focuses on human impacts. Chapter 9 addresses current management and issues, including social and political influences. Information from other nearby populations of elk in the Yellowstone area are compared with findings and trends from the northern Yellowstone population. We hope this information benefits wildlife professionals, students, and the millions of people that visit Yellowstone to observe wildlife or monitor their conservation via the Internet.

Elk grazing in the Gardiner basin of Yellowstone National Park at sunrise. Photograph by Jacob W. Frank, National Park Service.

Chapter 1
Natural History

This chapter provides some general information on the distribution, physical traits, behavior, ecology, and life history of elk in North America. Most of this information originated from the comprehensive book *North American Elk: Ecology and Management* from the Wildlife Management Institute (Toweill and Thomas 2002). More detailed information on northern Yellowstone elk are provided in the remainder of the chapters.

Distribution

Millions of elk once ranged across North America from the present-day provinces of British Columbia, Alberta, Saskatchewan, Manitoba, and Ontario in Canada south to North Carolina and west through the Ohio Valley, Midwest, and Rocky Mountains to northern California, Oregon, and Washington in the United States (Seton 1927, O'Gara and Dundas 2002). Elk provided food for many tribes of indigenous people, as well as colonists and settlers (McCabe 2002). The Shawnee Indians in the central Ohio River valley called elk 'Wapiti," a name many settlers adopted (O'Gara 2002). Settlement and unregulated hunting decimated the large numbers of elk but some populations in the Rocky Mountains recovered after regulated hunting seasons were established in the early 1900s and wildlife managers implemented aggressive restoration efforts involving reintroductions and protection of important winter ranges in low-elevation valleys dominated by agriculture (see Chapter 2). Today, about 1 million elk are found from British Columbia, Alberta, and Saskatchewan south through the Rocky Mountains to New Mexico, west to California, and north through Oregon and Washington (O'Gara and Dundas 2002). There are about 360,000 elk in Idaho, Montana, and Wyoming. There also are several small, reintroduced populations in the eastern provinces and states (O'Gara and Dundas 2002).

Physical Characteristics

The scientific name of elk is *Cervus canadensis*. They belong to the mammalian order *Artiodactyla*, which are descendants of an even-toed ungulate ancestor, the suborder *Ruminantia*, which has ruminant digestion (see below), and the family *Cervidae*, which includes caribou, deer, and moose (O'Gara 2002). Elk are large animals about 4.5 to 5 feet (1.4 to 1.5 meters) tall at the shoulder and 5 to 9 feet long (nose to tail; 1.5 to 2.7 meters), with males being about one-third larger than females (Hudson et al. 2002). They have long legs and hooves made of a hard protein material called keratin that enable them to run up to 30 miles per hour (48 kilometers per hour) and for long distances over rolling, open terrain (Hudson et al. 2002). They are good swimmers and, also, use their front hooves to dig (crater) through snow to expose forage during winter, as well as to confront predators when attacked (Rush 1932, Hudson et al. 2002). Their brown fur has a reddish tint in summer and appears lighter brown or tan in winter. The fur is darker along the neck, and elk have a large, cinnamon brown rump patch. Their fur provides good insulation and makes them quite resistant to cold temperatures (Hudson et al. 2002).

An adult female elk with whitish fur in a group of normal-colored females traveling in the northern portion of Yellowstone National Park. This leucistic or washed-out fur color likely was caused by a lack of melanin production due to a rare recessive genetic trait (Haas 2015). Photo taken by Xanterra employee Stephen Larrabee.

Elk have teeth with highly crowned premolars and molars and a zigzag enamel pattern to break up plant materials for extracting energy and protein (Hudson et al. 2002). They use their tongue to pull vegetation into their mouth where lower incisors push it against a dental pad on the upper part of their mouth to crop (cut) it. Teeth wear with age, so older elk become less efficient at obtaining nutrients and accumulating the fat and protein reserves needed to survive (Hudson et al. 2002). Elk have large eyes set high on the sides of their head and excellent vision in a wide arc for detecting movements of predators and other animals. However, their depth perception is limited (Hudson et al. 2002). They have good hearing across a range like humans and a good sense of smell. Breeding males use a vomeronasal organ in the palate of their mouths to test the urine of females and determine when they are in estrus (sexually receptive; Hudson et al. 2002).

Elk use an array of vocalizations for communication including bugles, grunts, and snorts by males and chirps, mews, and whines by females (Geist 2002). Mature bulls frequently make bugles to attract mates and let other bulls know they will defend their group (harem) of females (Bowyer and Kitchen 1987). Bugles begin with a gradual increase in sound frequency and volume that rises to an extended squeal or whistle that ends abruptly and is often followed by a sequence of grunts or yelps. These sounds are made by changes in the shape of the vocal tract and vibrations in its folds (Feighny et al. 2006). Bugling has been called 'honest advertising' because the distinctive calls may convey information about bull size and potential fighting ability (Geist 2002).

Adult female elk, referred to as cows, can weigh 660 pounds (300 kilograms) or more. Calves weigh about 30 to 40 pounds (14 to 18 kilograms) at birth, with males being slightly heavier (Hudson et al. 2002). They are about 40 inches (102 centimeters) long and 30 inches (76 centimeters) tall at the shoulder. Calves grow rapidly and weigh about 110 pounds (50 kilograms) after 4 to 6 weeks and 310 to 350 pounds (140 to 160 kilograms) by 6 months and the beginning of winter (Hudson et al. 2002, Cook et al. 2013). Adult males, called bulls, can weigh 1,100 pounds (500 kilograms) or more. They have large antlers about 50 to 60 inches (127 to 152 centimeters) long with 6 or 7 tines (points) per side (Geist 2002, Hudson et al. 2002). The first set of antlers is usually a set of spikes each about 16 inches (40 centimeters) long, but antler size and complexity increases over succeeding years with more tines formed until the peak number is reached (Hudson et al. 2002). Antlers begin growing each spring from two outgrowths on the frontal bone of the skull called pedicles. They grow quickly until August by absorbing calcium, phosphorus, protein, and water from the blood and then calcify into hard, dead bone before the autumn breeding season, a process which takes about 150 days in mature bulls (Hudson et al. 2002). Bulls shed (cast) their antlers from mid-February to May and begin the growth process soon thereafter (Hudson et al. 2002). Antler size and shape are influenced by a bull's age, underlying genetics, hormones, and nutritional condition (Cook 2002, O'Gara 2002).

Young calf elk in Yellowstone National Park. Photograph by Ed Austin and Herb Jones, National Park Service.

Social Organization

The basic social organization in elk is matriarchal, with groups primarily consisting of adult females, calves, and yearlings of both sexes (Houston 1982). Group size and composition (sex, age) varies among areas and seasons due to birthing events and calf protection, seasonal changes in food distribution and quality, snow conditions and energetic costs, human disturbances such as hunting, and predation risk and competition (Fryxell 1991, Jędrzejewski et al. 1992, 2006; Gower et al. 2009c). Older, larger females tend to be dominant over younger females during social interactions and displace them from chosen foraging sites (Houston 1982). From mid-May to mid-June, females isolate themselves to give birth and their newborn calves hide in the vegetation for about 2 weeks to avoid detection by predators (Geist 2002, Hudson et al. 2002). After calves are fleet afoot, they join their mothers in nursery groups of 20 or more animals and travel together through summer. Females invest a lot of time and energy in their young (Cook 2002, Geist 2002, Hudson et al. 2002). Calves nurse 4 to 5 times a day for about 6 weeks and are weaned after about 16 weeks, though some continue to nurse sporadically thereafter into mid-winter (Rush 1932, Hudson et al. 2002). Adult males are solitary or in small bachelor groups during this time (Houston 1982).

Elk are polygynous with males 4 years and older attempting to breed multiple females in late summer or early autumn, the September to October rutting period (Hudson et al. 2002). Competition between males is intense as they concentrate females into groups and repel other males using dominance displays or by chasing them away. Occasionally, males spar or fight by clashing with their antlers, which can be dangerous due to the risk of injury or death (Geist 2002). Thus, males typically only breed for a few years, while females breed throughout their adult life, provided they obtain sufficient nutrition to sustain body condition (Cook 2002; see Chapter 5). After the breeding season, females and their young congregate on the winter range from November through March, while mature males segregate by themselves or in small groups (Houston 1982, Geist 2002)

Bull elk sparring during the rut in Yellowstone National Park. Photo by J. Schmidt, National Park Service.

Life History

Populations are aggregations of animals from the same species that interact. The number of animals in a population depends on the number added through births and movements into the population (immigration) minus the number removed through deaths and movements out of the population (dispersal or emigration; Caughley and Sinclair 1994). Whether a population grows depends on whether animals have sufficient resources, such as food, to survive and reproduce; although disease, predation, and severe weather can significantly depress growth in some circumstances (see Chapter 3). Populations of elk with abundant resources tend to grow quickly due to high reproduction and survival. Numbers of elk in a population can increase by as much as 28% in 1 year when forage and other conditions are optimal (Eberhardt et al. 1996). However, population growth slows if the number of animals increases so there are fewer resources for everyone which can cause decreased nutrition, body condition (fat and muscle), reproduction, and survival (Eberhardt 1977, 2002). This concept is referred to as density dependence.

Female elk usually do not begin breeding until about 15 to 17 months old but can breed every year thereafter (Hudson et al. 2002). They become receptive to breeding (estrus) in autumn and may cycle several times if they do not become pregnant initially (Morrison 1960). Females give birth to a reddish-brown calf with white spots during mid-May to mid-June after a gestation period of about 8 to 8.5 months (Hudson et al. 2002). Pregnancy rates are usually high (90%) in prime-aged females more than 3 years of age until they become older and their teeth deteriorate from wear (Cook 2002, Garrott et al. 2003). These older elk can no longer process forage efficiently and, as a result, pregnancy rates decrease quickly due to lower nutrition and body condition which makes it less likely they become pregnant (Cook 2002). Other factors that could lower pregnancy rates include poor forage conditions, an aging population, low numbers of breeding bulls, and diseases such as brucellosis (Noyes et al. 1996, Thorne et al. 2002, Brodie et al. 2013, Cook et al. 2004a, 2013).

Adult female elk generally can live to about 17 to 18 years, while males can live to about 10 to 12 years (Hoy et al. 2020, Smith 2021). Adult males have higher mortality (lower survival) than adult females due to their dangerous and exacting competitions for mates during the rut (Hoy et al. 2020). The survival of prime-aged female elk is generally greater than 95% in areas with good forage and few human harvests or predators (Eberhardt 1977, 2002; Gaillard et al. 2000, Garrott et al. 2003). Snowpack conditions seem to have little effect on prime-aged females except in the most extreme circumstances. However, survival decreases rapidly in older animals as tooth wear reduces foraging efficiency and snowpack conditions worsen (Garrott et al. 2003). The survival of calves is highly variable among years in areas with few predators because severe winters with deep or hard snowpack can kill most calves through malnutrition and starvation (Garrott et al. 2003, Raithel et al. 2007). Mature males expend tremendous amounts of energy during the rut and eat little, losing about 15% of their body weight (Houston 1982). Thus, they enter winter with fewer fat reserves than females and are more likely to die in a severe winter (Cook 2002).

Adult male elk resting near the end of the energetically taxing breeding period (rut) in Yellowstone National Park. Photograph by Neal Herbert, National Park Service.

Seasonal Movements

Elk make some of the longest seasonal round-trip movements (migrations) of any ungulate in the contiguous United States (Kauffman et al. 2018; see Chapter 4). Some elk migrate more than 90 miles (145 kilometers) in spring from winter to summer ranges and return in autumn along the same routes (Vore 1990, White et al. 2010). Other elk migrate shorter distances or do not migrate at all (non-migratory). Populations in which some animals move seasonally between summer and winter ranges while others remain on the same range year-round are called partially migratory (Kaitala et al. 1993). In varied landscapes, migrants typically gain access to more favorable resources like nutritious food or safer areas with fewer predators to raise young (Fryxell et al. 1988). Many ungulates migrate to higher elevations each spring to forage on nutritious plant growth through the summer but return to lower elevations each autumn to avoid deep snowpack that limits food availability and increases energetic costs and predation risk during winter (Fryxell 1991, Mech et al. 2001, 2015; Middleton et al. 2018, Rickbeil et al. 2019). However, migratory individuals also can face additional risks compared to non-migratory residents, such as traversing habitats with increased risk of predation between seasonal areas of use (Fryxell and Sinclair 1988).

Migratory behavior in ungulates likely is transmitted across generations by calves learning from their mothers and social groups (Bracis and Mueller 2017, Jesmer et al. 2018, Merkle et al. 2019). Over many generations, elk and other ungulates occupying diverse landscapes may develop many different migratory strategies to cope with seasonal changes in the resources required to survive and reproduce (Parker et al. 2009, Lowrey et al. 2020, 2021; Zuckerman et al. 2023). This variety of migratory behaviors disperses the population across the landscape. When ungulate populations are reduced to small numbers of animals occupying restricted areas compared to their historic range, much of the cultural knowledge of the broader landscape and movement corridors is lost (Lowrey et al. 2020, 2021; Zuckerman et al. 2023). Restoring these historic migratory behaviors may take many decades or be lost from the population forever.

Habitat Use and Diet

Obtaining adequate energy and nutrients by eating nourishing plants is essential for the survival and reproduction of elk (Cook 2002). Nutrition strongly influences growth and development, pregnancy and lactation, disease resistance, and survival, including their ability to evade predators (Cook 2002, Parker et al. 2009; see Chapter 5). Elk are considered habitat and diet generalists because they use a wide variety of vegetation communities and forages (Christianson and Creel 2007). Elk in the western United States are primarily grazers and consistently select grasses and grass-like plants, such as rushes and sedges, which are collectively called graminoids. Forbs (broad-leaf, non-woody plants) generally comprise a small portion of the diet, but the consumption of browse (parts of woody plants) increases in winter (Christianson and Creel 2007). The depth, hardness, and weight of snowpack during winter limits access to grasses and forbs and determines how much energy elk must use to move it during foraging and travel. Snow density (water content) and crusting or ice layers can substantially reduce forage availability and increase energetic costs (Newman and Watson 2009, Watson et al. 2009). Elk often move to forested areas with less snow during times of deep snow or strong, chilling winds in open areas (Barmore 2003).

Predation and Competition

Potential predators of elk include bears, cougars, coyotes, and wolves. Bears and coyotes often cue in on solitary female elk during the birthing season, searching the area nearby to locate calves in hiding (Gunther and Renkin 1990, Mattson 1997; see Chapter 6). After calves begin traveling with their mothers, cougars are effective at ambushing or stalking them in areas near rugged terrain and tall vegetation (Ruth et al. 2019, Stahler et al. 2020). Wolves kill elk by coursing through areas and searching for vulnerable individuals to attack (Mech et al. 2015, Smith et al. 2020). Predation rates of calves can be quite high in areas with abundant predators and range from 20% to 65%, with abandonment, accidents, birth defects, diseases, drowning, malnutrition, and severe weather accounting for the remainder of deaths (Barber-Meyer et al. 2008). Elk populations in areas with multiple large predators often have lower calf survival than other areas (Griffin et al. 2011, Lukacs et al. 2018).

Competition occurs when individuals use a resource, such as consuming forage, or exclude other individuals from accessing the resource and, in turn, decrease the ability of the other individuals to survive and reproduce (Begon et al. 2005, Garrott et al. 2013). There is the potential for competition among elk for forage or other resources as their numbers and density increase and resources become more limited, which is called intraspecific competition. There also can be competition with other ungulate species that have similar diets, ranges, and timing of the use of resources, which is called interspecific competition (Caughley and Sinclair 1994).

Adult female elk chasing a coyote away from her hidden calf in Yellowstone National Park. Photograph by Jacob W. Frank, National Park Service.

Adaptive Behaviors and Capabilities

Historically, elk in temperate climates have evolved patterns of movement and habitat use to exploit predictable seasonal changes, moving to higher elevations with growing nutritious forage during the warm summer and returning to lower elevations with less snowpack during the cold winter (Craighead et al. 1972, Houston 1982, Rickbeil et al. 2019). The long legs and large body sizes of adults enhance movements in montane environments and reduce the energetic costs of maintaining their body temperatures (thermoregulation) and moving through snow (Gates and Hudson 1979, Robbins 1993, Parker and Robbins 1984, Wickstrom et al. 1984, Hudson et al. 2002). Adult elk also have large reserves of fat and muscle to sustain them through the long period of undernutrition during winter (Cook 2002, Garrott et al. 2003). However, there is considerable random variation in weather among years, and severe winters can still influence their nutrition and body condition (Cook 2002). Calves have a much smaller body size with shorter legs and limited body reserves that makes them more susceptible to starvation during winter (Hudson and White 1985, Cook 2002, Garrott et al. 2003).

Elk have a four-chambered stomach (including a rumen) that contains microorganisms, such as bacteria and protozoa, to break down and ferment plant materials and produce volatile fatty acids that provide them with energy (Robbins 1993, Van Soest 1994). Most plants eaten by elk in temperate climates are dormant and not growing during the winter season. The digestibility and energy and protein content of these dead and dried grasses is low and results in a longer fermentation time in the rumen to extract energy, protein, and nutrients (Robbins 1993, Van Soest 1994). Elk regurgitate and re-chew their food (cud) to break ingested plants into smaller fragments before re-swallowing so more nutrients can be absorbed (Cook 2002). They can also recycle urea to the rumen where microbes convert it into protein for digestion when forage intake is insufficient to meet demands for body maintenance during winter (DelGuidice and Seal 1991, Parker et al. 2009). As a relatively large ruminant, elk are capable of digesting and subsisting on lower quality forage than smaller ruminants, such as deer and pronghorn (Robbins 1993, Van Soest 1994). Having a larger rumen means elk do not have to be as selective for high quality forage as smaller ruminants (Caughley and Sinclair 1994).

Mature male elk bugling in Mammoth Hot Springs, Yellowstone National Park. Photo by Neal Herbert, National Park Service.

Current Management

There are about 1 million elk in North America (O'Gara and Dundas 2002). Most western states and provinces initiated and then increased regulated harvests as elk numbers increased over the last century. The most significant threat to elk populations is the destruction or fragmentation of habitat along movement corridors and in calving and wintering areas (Lyon and Christensen 2002, Berger 2004). Human development and changes in land use almost certainly will continue to degrade these habitats. In addition, a warming climate could affect precipitation and snow melt patterns, as well as the frequencies of droughts and wildfires, and lead to invasive annual plants dominating native vegetation communities and negatively affecting productivity and water, energy, and nutrient cycles (Cole and Yung 2010, Wilmers et al. 2013; see Chapter 8). Emerging wildlife diseases also pose threats for elk populations with links to human management practices that result in aggregations of elk that contribute to disease transmissions (Thorne et al. 2002).

Wildlife agencies need to work together and with local communities and private landowners to conserve elk and their habitats, retain or restore migration pathways, minimize disease transmission risks, and reduce conflicts (Clark 2021). Most low-elevation valleys in the Rocky Mountain region have been converted to agricultural production. These valleys typically were the primary winter ranges for elk migrating out of the mountainous areas. Agriculture, primarily livestock production, can degrade elk habit by radically modifying native plant communities, displacing or prohibiting elk use of private lands, and reducing forage available for elk due to livestock grazing. However, agriculture maintains open spaces used by elk and other wildlife (as opposed to urban/exurban development) and the increasing use of intensive irrigation is creating forage 'hot spots' that are attracting larger numbers of elk on winter ranges throughout the intermountain valleys of the Rocky Mountains (Tilt 2020). As a result, most elk herds depend on low-elevation agricultural valleys for wintering and if these valleys were urbanized or elk were not tolerated by landowners, there would not be nearly as many elk roaming the Rocky Mountains as we have today. It is important to understand just how much migratory wildlife that seasonally spend time in protected areas, such as national parks or forests, also depend on privately owned land surrounding these areas during the remainder of the year.

Relocating elk captured in Yellowstone National Park during January of 1935. Photograph by Francis LaNoue, National Park Service.

Chapter 2
Historical Trends

Distribution

Historical accounts indicate elk were abundant and widespread in the Yellowstone area during the 1800s, including throughout present-day Yellowstone National Park (Figure 1; Houston 1982, Schullery and Whittlesey 1992, Whittlesey and Bone 2020). In 1877, Superintendent Norris declared "in no other portion of the West or of the world was there such an abundance of elk, moose, deer, mountain sheep, and other beautiful and valuable animals, fish and fowl, nor as ignorant, or as fearless of and easily slaughtered by man as in this secluded and unknown park but seven years ago" (Norris 1877). There were no complete or rigorous counts of elk in the area, however, and it is impossible to derive accurate estimates from occasional sightings and reports (Whittlesey et al. 2018). Several observers suggested 25,000 to 40,000 elk spent summer in areas of Yellowstone National Park during the late 1800s, with as many as 75,000 elk in the entire region (Chittenden 1895, First Lieutenant E. Lindsley in Seton 1898, Benson 1910, Rush 1932, Whittlesey and Bone 2020). By 1925, however, a park ranger estimated only 25,000 elk remained in the region due to larger harvests and starvation during a severe winter in 1919 and 1920 (Skinner 1928).

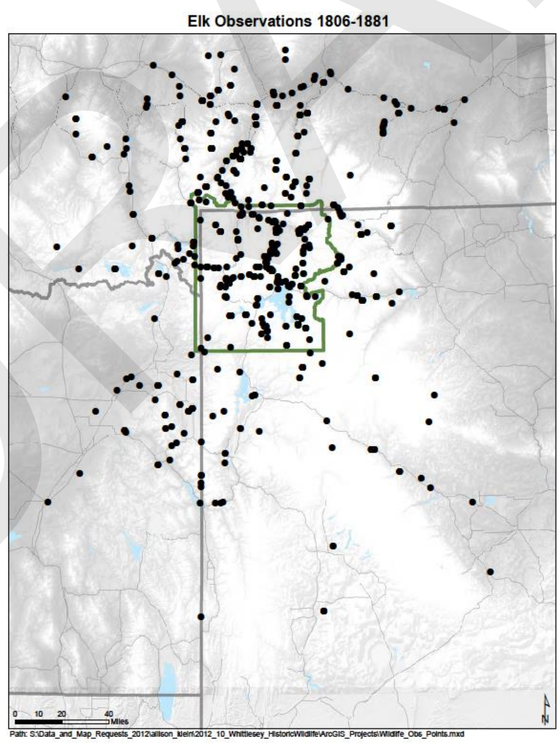


Figure 1. *Elk sightings in and near Yellowstone National Park from 1806 to 1881 (Whittlesey et al. 2018, Whittlesey and Bone 2020). The boundary of the park, established in 1872, is indicated by the green line. Gray lines represent the boundaries of Idaho, Montana, and Wyoming, admitted into the Union in 1889 and 1890. Map created by Allison Klein, National Park Service.*

Many elk in the Yellowstone area during the 1800s and early 1900s apparently made seasonal movements between the mountains in summer and lower-elevation valleys in winter (Benson 1910, Skinner 1928, Rush 1932, Whittlesey and Bone 2020). Elk that spent summer in portions of present-day Yellowstone National Park moved to various winter ranges in and outside the park during autumn (Skinner 1925). Thousands of elk reportedly moved through the Gallatin and Yellowstone River valleys to the north into Montana, through the Madison River valley to the west in Montana, along the North Fork of the Shoshone River and Middle and Soda Butte Creeks to the east in Wyoming, and through the Snake and Lewis River corridors to the south in Wyoming (First Lieutenant E. Lindsley in Seton 1898, Whittlesey and Bone 2020). Some elk also moved south into the Thorofare area of Wyoming. However, as many as 2,000 to 5,000 elk remained at higher elevation areas in the park through winter along the Yellowstone and Lamar River valleys (Yount 1881, First Lieutenant E. Lindsley in Seton 1898, Rush 1932, Houston 1982, Schullery and Whittlesey 1992, Whittlesey and Bone 2020). Other elk spent winter in the geothermally warmed areas in central Yellowstone (Skinner 1925).

Today, elk from several populations with discrete wintering areas outside Yellowstone National Park migrate into portions of the park during summer and intermingle to some extent (Kauffman et al. 2018, Stahler et al. 2022). The Gallatin (Paradise Valley) population spends winter in the Gallatin and northern Paradise valleys north of the park in Montana and some of these elk migrate into the northwest part of the park during summer (Figure 2). The Northern Yellowstone population spends winter in the northern portion of the park and the Gardiner basin and southern Paradise Valley of Montana. Many of these elk migrate throughout the park during summer. The Clarks Fork population spends winter east of the park in the Sunlight and Crandall Creek basins of Wyoming and some elk migrate into the northeastern portion of the park during summer. The Cody population spends winter east of the park in Wyoming along the North Fork of the Shoshone River and some elk migrate into the eastern and southern portions of the park during summer. The Jackson population spends winter in the Gros Vente area south of the park near Jackson, Wyoming, and some elk migrate into the southern portion of the park during summer. The Madison Valley population spends winter west of the park in the Madison Valley of Montana and some elk migrate into the northwestern portion of the park during summer. There is also a small, non-migratory population of elk in the upper Madison River drainage in the park that lives throughout the year along the Madison and Firehole rivers (Garrott et al. 2009a).

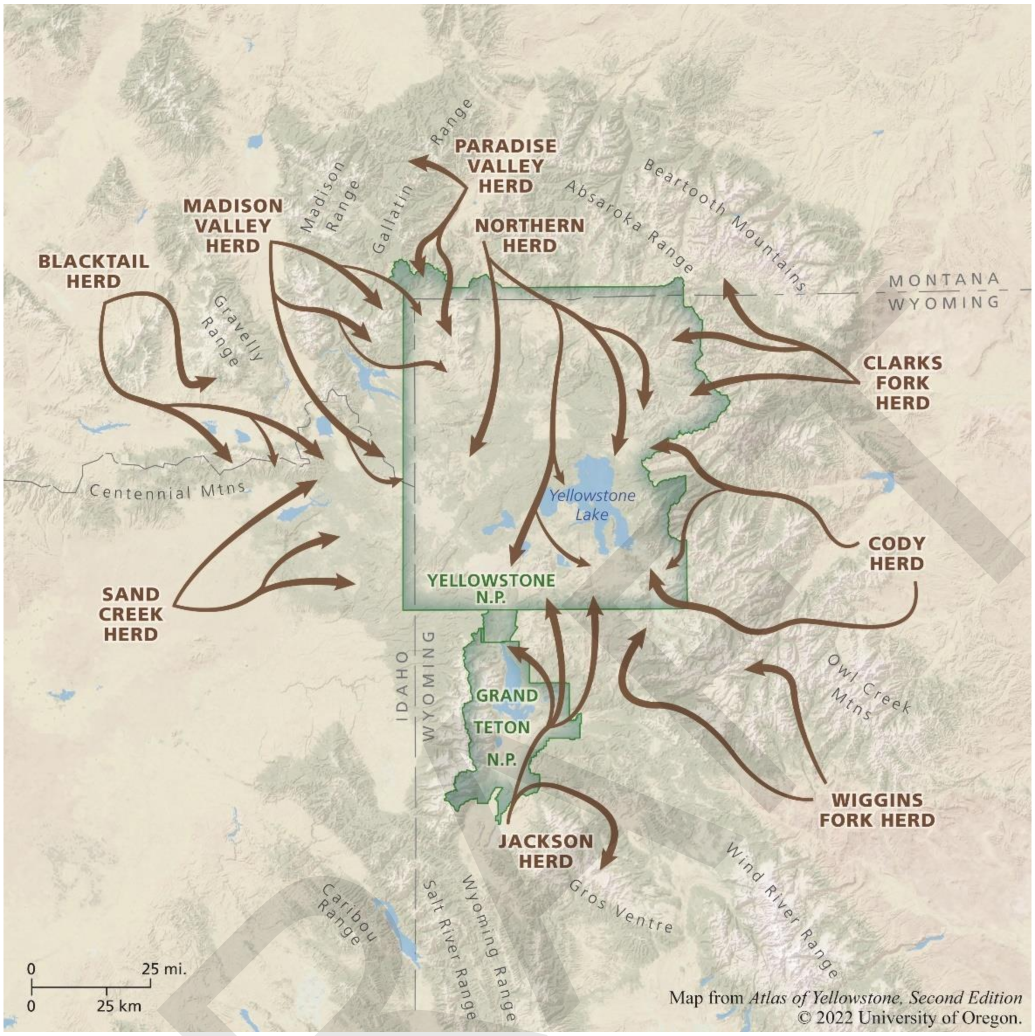


Figure 2. *Elk populations (herds) and general migration patterns in the Yellowstone area. Reprinted with permission from the Atlas of Yellowstone, Second Edition © 2022 University of Oregon (Marcus et al. 2022). Elk data is from the Wyoming Game and Fish Department, Montana Fish, Wildlife and Parks, Idaho Fish and Game Department, National Park Service, U.S. Fish and Wildlife Service, Wildlife Conservation Society, Wyoming Cooperative Fish and Wildlife Research Unit, Iowa State University, and the Yale School of Forestry and Environmental Studies.*

Influence of Native People

Tribes of indigenous people including the Bannock, Blackfeet, Crow, Kootenai, Nez Perce, Salish, and Shoshone lived as part of the natural community in the Greater Yellowstone Area for more than 10,000 years with sustainable fishing, hunting, and gathering practices (Nabokov and Loendorf 2002, Stark et al. 2022). A band of the Mountain Shoshone, called the Sheep Eaters, lived in the area encompassed by present-day Yellowstone National Park year-round and hunted bighorn sheep and other animals for food and clothing (Norris 1881a,b; Nabokov and Loendorf 2002). The Crow tribe resided in the northeastern portion of the Greater Yellowstone Area and used large portions of the present-day park and surrounding national forests (White 2005). The Yellowstone River was known to the Crow as the Elk River due to the large herds of elk in adjacent valleys (Whittlesey and Bone 2020). They hunted bison, elk, and other wildlife and gathered berries, fruits, roots, and seeds for ceremonial, nutritional, and medicinal purposes. Bands from other tribes moved through the Yellowstone area seasonally. The Eastern Shoshone lived in the Green and Wind River areas to the south but traveled seasonally through Yellowstone to access bison further north, fish in Yellowstone Lake, and gather obsidian and other resources (Historical Research Associates 2006b). Bands from the Eastern Shoshone tribe used the Yellowstone area more frequently as bison became scarce following colonization and settlement.

Indian fish trap at Yellowstone Lake in the southeastern portion of Yellowstone National Park. The photograph was taken in 1961 but the photographer is unknown. National Park Service photograph collection.

Elk were an important food source for most if not all tribes living in the Greater Yellowstone Area (Nabokov and Loendorf 2002). Communal hunters sometimes drove elk along drivelines into ambushes, pitfalls, or traps where they were killed with arrows, clubs, spears, or guns. Hunters made game drivelines from brush, poles, or rocks at several sites in the Yellowstone area (Norris 1881a,b). Several tribes hunted elk on horseback, while some used dogs to chase elk (McCabe 2002). Hunting parties lit fires to influence the movements of game and regenerate habitat (Confederated Salish and Kootenai Tribes 2005). Indigenous people dried some meat and mixed it with berries and fat to create pemmican that lasted for many months. They also used hides for clothing, sinew as thread, bladders for containers, hooves for glue and implements, teeth for decorations and exchange, and antlers and bones for tools and weapons (Kuhnlein and Humphries 2017).

Bannock Indians in front of a wickiup during 1871. The location and photographer are unknown. National Park Service photograph collection.

Diseases introduced by colonists, settlement of their lands, slaughter of wildlife populations, and government oppression decimated tribes in the Greater Yellowstone Area by the mid-1870s (Nabokov and Loendorf 2002). Federal treaties limited tribal use of traditional lands and confined them to reservations where they depended on government rations and were urged to adopt farming and ranching lifestyles (Nabokov and Loendorf 2002, Historical Research Associates 2006a,b). When Yellowstone National Park was established in 1872, the eastern portion overlapped the Crow Reservation until Congress removed this land from the Reservation in 1882 (Norris 1881b, Historical Research Associates 2006a). Federal agents relocated the Mountain Shoshone bands living inside the park to reservations in the Idaho and Wyoming territories by 1880 (Historical Research Associates 2006b). Reservation agents and soldiers discouraged indigenous people from using Yellowstone National Park for their traditional hunting and gathering activities (Norris 1881b, Harris 1889, Historical Research Associates 2006a,b). As a result, tribal foraging, hunting, and spiritual activities in and near the park waned during the 1890s (Nabokov and Loendorf 2002, Historical Research Associates 2006a,b; White 2005, Stark et al. 2022). Settlers and park managers suppressed fires which reduced their regenerating effects and allowed conifers to invade some grassland habitats used by elk (Norris 1881a,b; Wear 1885, Harris 1889, Benson 1910, Meagher and Houston 1998).

Effects of European American Settlement

Settlements were sparse and isolated and livestock uncommon in the American West through the 1840s but the discovery of gold in California during 1848 led to a mass western movement of settlers and livestock. There was an influx of prospectors and settlers into the northern portion of the Greater Yellowstone Area during the 1860s and 1870s when gold was discovered in Emigrant Gulch in the Paradise Valley (1864), Bear Gulch near Jardine, Montana (1866), and the headwaters of the Clarks Fork of the Yellowstone River near Cooke City, Montana (1870). The influx of miners led to the building of settlements in the Gardiner basin north of the park boundary and nearby areas including Gardiner (1880), Cinnabar (1883), Horr/Electric (1894), Aldridge (1896), and Jardine (1898; Haines 1974, Keating 2002). A railroad line was built to near the northern boundary of Yellowstone National Park (Cinnabar) in 1883 (Whittlesey 1995). Settlers removed native vegetation along the Yellowstone River valley to create settlements and grow crops. Farmers erected fences to contain livestock and exclude wildlife from cultivated areas. Similar actions occurred in several other river valleys emanating from the park.

Ranchers brought livestock into the Greater Yellowstone Area by 1867, and numerous ranches were established during the 1870s in areas used by elk. There were no restrictions on numbers, seasonal use, or type of livestock (cattle, horses, sheep) grazing within or outside the park, leading to many more fences, habitat degradation from overgrazing, and soil erosion as well as competition for forage with elk during winter (Pitcher 1905, Skinner 1925, 1928; Rush 1932, Houston 1982). These effects increased after 1879 when the completion of the transcontinental railroad led to a substantial increase in livestock numbers and additional pressures on remaining wildlife (Gill 2010). There were about 35 to 40 million cattle in western states by the mid-1880s and about 10 million sheep in Montana and Wyoming from 1885 to 1915 (U.S. Department of Agriculture 2020).

Livestock grazed without any restrictions within the park between Mammoth, Wyoming and Gardiner, Montana (Rush 1932). In 1900, the Superintendent established regulations to impound and dispose of loose livestock found grazing or being herded in Yellowstone National Park (Benson 1910). However, the park and concessionaires grazed as many as 3,000 horses on the Blacktail Deer Plateau until 1916 and 200 to 300 thereafter until sometime in the 1930s (Rush 1932). Smaller bands of sheep and cattle grazed at numerous sites in the park through the 1930s for meat and milk, including near the Buffalo Ranch in the Lamar Valley (Rush 1932, Whittlesey 1994, Meagher and Houston 1998). Also, grazing by cattle in areas outside the park, such as the Yellowstone River valley, continued and combined with cultivation substantially degraded native vegetation communities on the valley floor by the mid-1920s (Rush 1932). Range managers considered all the grasslands on the northern winter range for elk overgrazed by the 1930s, primarily due to heavy use by cattle and horses (Rush 1932, Houston 1982).

In addition, there was a massive slaughter of elk and other wild ungulates and predators in the Greater Yellowstone Area, including in the newly established (1872) Yellowstone National

Park, by market hunters during the 1870s and 1880s (Norris 1881a, Wear 1885, Harris 1889, Picton and Lonner 2008, Whittlesey et al. 2018, Whittlesey and Bone 2020). In 1874, traders shipped 97,600 pounds (44,270 kilograms) of elk hides from Bozeman, Montana which equates to about 7,800 animals (Angler 1883). Philetus Norris, Superintendent of Yellowstone, reported "at least 7,000 of these valuable animals [elk] were slaughtered [in the park] between 1875 and 1877 for their hides, or perhaps for their carcasses, which were stripped and poisoned for bear, wolf, or wolverine bait" (Norris 1881a). A trader in Fort Benton, where many hides from the Yellowstone area were shipped down the Missouri River, purchased 26,800 pounds (12,156 kilograms) of elk hides in 1875 which equates to roughly 2,140 animals (Avant Courier 1875).

While numbers of elk were substantially reduced during the 1870s and 1880s, they apparently rebounded or remained high enough not to elicit substantial concern (Rush 1932). For example, Superintendent Norris reported in 1881 that elk numbers in Yellowstone "have not been seriously diminished" … "and frequent all portions of the park" … "in herds of a hundred or more …" (Norris 1881a). In 1883, a newspaper in Bozeman, Montana, reported a traveler saw (likely estimated) "at least 5,000 elk" between Mammoth Hot Springs, Wyoming, in the northern portion of Yellowstone National Park and Cooke City, Montana, about 50 miles to the east (Avant Courier 1883). As a result, the reporter apparently concluded the elk population was not threatened by hunting (Whittlesey and Bone 2020).

Protection and Conservation

The Secretary of the Interior prohibited hunting in Yellowstone National Park in 1883 and the legislature of the Territory of Wyoming passed an act in 1884 to protect fish and game within the park (Harris 1889). However, poaching continued due to a lack of enforcement so the United States (U.S.) Army sent a detachment of cavalry to the park in 1886 to enforce regulations and prevent poaching (Conger 1882, 1883; Wear 1885, Harris 1889, Houston 1982, Keating 2002, Olliff et al. 2013). The U.S. Army managed the park until 1917 and protected elk and other game species. They also implemented predator control such as poisoning, shooting, and trapping, which was continued until about 1935 (Pitcher 1905, Murie 1940, Keating 2002). In addition, the U.S. Engineer Department erected about 4 miles (6.4 kilometers) of wire fence along the north boundary of the park near Gardiner, Montana, during 1903 to prevent cattle from entering the park and wild ungulates from leaving and being killed (Pitcher 1905, Benson 1910). This fence was not a permanent barrier to movements by elk, however, due to disrepair and other factors (Keating 2002).

The U.S. Army began feeding elk and other ungulates during winter in the northern portion of the park (Cahalane 1944). They began growing hay on about 50 acres (20 hectares) near Gardiner, Montana, in 1904 and, over the next several decades, this operation expanded to about 530 acres (215 hectares) in the Gardiner basin, 575 acres (233 hectares) in the Lamar Valley, and some areas along Slough Creek and in Yancey's Hole (Seone 1904, Pitcher 1905, Goodacre 1933, Toll 1929, Whittlesey 1995, Keating 2002, White et al. 2022b). These areas were cleared of native vegetation and planted with nonnative grasses (Kentucky bluegrass, clover, oats, smooth brome, timothy) to grow hay for bison, elk, pronghorn, and other ungulates (Benson 1910, Rush 1932, Skinner et al. 1942, Whittlesey 1995). This feeding program continued until 1945, with the most hay fed during winters from 1908 to 1937 (Houston 1982). Combined with predator control until 1935, this feeding program contributed to an increase in the numbers of ungulates in northern Yellowstone, with about 13,000 elk counted during the winter of 1927 (Rush 1932, Keating 2002). During the 1920s and 1930s, managers also put out salt for elk and other ungulates at more than a dozen sites across the northern winter range and some areas of the summer range, such as Alum Creek in the Hayden Valley (Rush 1932). The U.S. Forest Service and State of Montana distributed 1,000 pounds (454 kilograms) of salt blocks on the winter range outside the park in 1927 (Rush 1932).

Elk along a feed line of hay during winter near Gardiner, Montana, prior to 1909. Photographer unknown. National Park Service photograph collection.

State and national sporting organizations and wildlife advocates took many actions from the late 1880s to the mid-1900s to conserve wildlife and protect their habitats. Hunters campaigned against poaching, promoted ethical practices, and urged state legislatures to limit harvests (Picton and Lonner 2008, Olliff et al. 2013). Idaho, Montana, and Wyoming passed seasonal restrictions and limits on ungulate harvests by 1874 and subsequently required hunting licenses and hired game wardens. Congress passed the Forest Reserve Act in 1891 and presidential orders over the next 12 years designated more than 6.5 million acres (26,300 square kilometers) surrounding Yellowstone National Park as public forest lands. Congress passed *An Act to Protect the Birds and Animals in Yellowstone National Park, and to Punish Crimes in said Park, and for Other Purposes* (16 U.S. Code [USC] 26) in 1894 to prohibit hunting and the harassment, possession, or removal of wildlife from Yellowstone National Park. These and other efforts preserved remaining wildlife and eventually led to an approach known as the North American Model of

Wildlife Conservation, whereby wildlife are managed for all people based on reliable scientific knowledge (Rocky Mountain Elk Foundation and Conservation Visions 2006).

In addition, biologists began efforts to restore elk populations in some areas where they had been decimated or extirpated. From 1892 to 1907, park rangers captured 34 northern Yellowstone elk and shipped them to Washington, D.C. (National Zoological Park), Nebraska (Omaha City Park), and British Columbia (Vancouver City Park), Canada, for display to boost support for their conservation. Rangers captured another 3,795 elk from 1912 to 1934 and relocated them to Canada, 35 states and the District of Columbia, and 6 national parks (Banff, Glacier, Jasper, Platt [now Chickasaw], Rocky Mountain, Wind Cave) for release (94%) and display or food (6%; Houston 1982, Yellowstone National Park Archives Box N-64).

The National Park Service issued the Graves Nelson Report in 1919 which recommended the acquisition of many private lands between Gardiner, Montana, and Yankee Jim Canyon at the southern end of the Paradise Valley (Whittlesey 1995, Keating 2002). A private corporation called the Game Preservation Company bought thousands of acres of adjacent land north of Yellowstone National Park in the Gardiner basin and operated the Game Ranch during the 1920s to protect the remaining winter range for elk and other ungulates (Whittlesey 1995, Keating 2002). Staff irrigated fields using water from springs and creeks to grow hay and feed elk and other ungulates. Congress authorized the appropriation of this 7,609-acre (3,079-hectare) Game Ranch "to improve and extend the winter feed facilities of the elk, antelope [pronghorn], and other game animals of Yellowstone National Park and the adjacent land" (Seventieth Congress, Session I, Chapter 626, May 18, 1928). The area was formally added to the park and the Absaroka and Gallatin national forests from 1926 to 1932 (Whittlesey 1995, Keating 2002). Park staff removed fences to allow elk and other ungulates to use this area and continued irrigating and producing hay on about 300 acres (121 hectares) to feed ungulates and government horses during winter until about 1934 (Whittlesey 1995). Many of the abandoned fields were infested with cheatgrass, dandelion, foxtail barley, and Kentucky bluegrass (Rush 1932, Houston 1982).

Population Reduction Efforts

The National Park Service was created by Congress in 1916 and assumed management of Yellowstone National Park in 1918. Managers believed overgrazing was adversely affecting vegetation and, in 1923, Congress authorized the Secretary of the Interior to "give surplus elk, buffalo [bison], bear, beaver, and predatory animals inhabiting Yellowstone National Park to Federal, State, county, and municipal authorities for preserves, zoos, zoological gardens, and parks" (16 USC 36). Managers removed about 3,287 elk from northern Yellowstone during 1923 to 1929, primarily by hunting in Montana but also by captures in the park for relocation elsewhere, to reduce numbers and restore other populations (Houston 1982).

Biologists conducted annual ground counts of elk in northern Yellowstone during the 1930s but counts from the 1940s through the mid-1960s were sporadic and sparse (Houston 1982). The reliability of these counts is uncertain because they were conducted over multiple days and at various times each winter. However, there probably were about 10,000 to 15,000 elk in northern Yellowstone by 1930, despite a severe drought that lasted from 1919 to 1936 (Houston 1982). About three-quarters of the elk were counted in the park during most winters, with 3,000 to 5,000 on the upper portions of the winter range, such as Slough Creek, Lamar Valley, and Soda Butte Creek (Houston 1982). Hundreds of hunters began crowding the park boundary, with more than 4,000 to 5,000 hunters in the vicinity of Gardiner, Montana by 1930 (Rush 1932). Evidently, encircling animals and indiscriminate shooting was common.

Concerns about overgrazing and sagebrush degradation led park and state managers to remove about 70,000 elk from the population over the next 38 years to reduce population size and satisfy predominant livestock views regarding range capacity and condition (Kittams 1953, Houston 1982, Huff and Varley 1999). Managers used three methods to reduce elk numbers, including public harvests of elk outside the park in Montana from mid-October through November during the general rifle season, shooting elk within the park, and hazing elk to traps for capture and relocation or onsite slaughter (Kittams 1953, Houston 1982, Despain et al. 1986, Barmore 2003). From 1935 to 1955, biologists primarily (84%) relied on harvests in Montana to reduce elk numbers which disproportionately decreased numbers of migrant elk moving outside the park (Kittams 1953, Craighead et al. 1972, Houston 1982).

Removals in the park increased after 1955 (70% of total removals) with park staff hazing elk into a series of traps erected across the elk winter range in northern Yellowstone (Craighead et al. 1972, Houston 1982). During 1962 to 1967, trapping locations ranged from the Gardiner basin, across the Blacktail Deer Plateau, and east to the Lamar Valley (Craighead et al. 1972). Annual reductions were erratically spaced over time, but biologists removed 25% to 40% of the population during several winters (Houston 1982, Barmore 2003). They used helicopters to drive animals into corrals during the peak of captures in the 1960s when more than 1,000 elk were removed in some years, including about 4,620 in 1962 (Despain et al. 1986, Barmore 2003).

Helicopter hazing elk into a trap near Crystal Creek in Yellowstone National Park during winter in 1968. Photo by Ted Scott, National Park Service.

Biologists conducted 7 aerial counts during winters from 1956 to 1968, mostly from a helicopter during a single day (Houston 1982). These counts were more systematic and rigorous than previous ground surveys but often occurred after intense capture and culling activities that scattered elk and made reliable counting difficult (Houston 1982, Barmore 2003). By the mid-1960s, few elk migrated outside the park to spend winter, except during a very severe winter (Houston 1982, Barmore 2003).

In summary, from 1935 to 1968 hunters in the State of Montana harvested about 43,700 elk, with concentrations (firing lines) of hunters developing along the northern boundary as elk migrated outside the park (Craighead et al. 1972, Houston 1982). Another 15,400 elk were shot or killed at traps in the park by rangers, with most of the meat distributed to American Indian tribes in Montana, Wyoming, Idaho, North Dakota, and South Dakota and relief organizations in Montana and Wyoming (Franke 2005, White 2005, Whittlesey 2013). In some instances, tribal members processed harvested animals in the park for distribution to their families and other tribal members. However, there is no evidence of them being allowed to hunt within the boundaries of the park (Whittlesey 2013). In addition, about 10,828 Yellowstone elk were captured and relocated to 2 countries (Argentina, Mexico), 25 states and the District of Columbia, 2 national forests (Dixie, Gila), and 4 American Indian tribes (Apache, Crow, Sioux, Ute) for release (98%) and display or food (2%; Yellowstone National Park Archives Box N-64). These sustained removals over a period of 40 years caused a substantial decrease in the population size of northern Yellowstone elk, with a count of 3,172 animals in 1968 (Houston 1982). Despite these reductions, intense browsing by elk in the Gardiner basin decreased sagebrush by about 43% from 1957 to 1990 (Singer and Renkin 1995).

Members of the Blackfeet Nation dressing elk shot by rangers in Yellowstone National Park during March 1961. Photo by Hadley, National Park Service.

'Natural Regulation'

In 1963, a special advisory board on wildlife management in national parks recommended allowing natural ecological processes to function with less human influence (Leopold et al. 1963). They suggested the National Park Service emphasize managing wildlife based on its mandate to preserve park resources unharmed and in their natural condition for the benefit and enjoyment of people (16 USC [United States Code] 21, 54 USC 100101 *et seq.*). However, they did not rule out human intervention when deemed necessary. Public outrage and political pressure intensified against the killing of large numbers of elk and the use of helicopters to drive elk for long distances through snow for capture. The reductions were publicized on television and led to a Senate hearing about elk management in Yellowstone during 1967 in which Senator McGee from Wyoming insisted the park stop culling elk, which subsequently occurred (Despain et al. 1986). In addition, some scientists were beginning to question long-term beliefs about elk abundance and range deterioration in Yellowstone based on prevailing range science standards (Cole 1971, Houston 1982, Despain et al. 1986). These questions about artificial (human) versus natural control (regulation) emerged in the 1970s and led to a substantial shift in management approach in national parks and wilderness areas (Boyce 1998, Huff and Varley 1999).

In 1969, managers in Yellowstone began allowing numbers of elk and other ungulates to vary in response to forage availability, harvests outside the park, predation, and weather (Cole 1971, Houston 1982, Despain et al. 1986). In addition, hunter harvest in Montana was reduced to less than 210 elk per year with a moratorium on late season harvests from mid-December through mid-February (Houston 1982, Evans et al. 2006, Wright et al. 2006). There was a transition in management approach within the park over the next several decades to reduce human intervention and rely more on the regulation of elk numbers through environmental conditions, such as summer precipitation, forage production, and snow cover, that limit forage availability and ecological processes, such as competition for food and increased starvation as densities of elk increased on the winter range (Despain et al. 1986, Olliff et al. 2013). Park managers began to intervene less and let the natural world regulate itself, which was referred to as 'natural regulation' (Cole 1971, Despain et al. 1986). They also began planning during the 1980s to reintroduce wolves into the park (Boyce 1990, Boyce 2018).

Since 1968, biologists have conducted winter counts of northern Yellowstone elk from fixed-wing airplanes on 1 or 2 consecutive days (Houston 1982, Barmore 2003, Coughenour and Singer 1996). They counted about 4,305 elk in 1969 but predicted numbers would increase without culling in the park and small harvests in Montana (Houston 1982, Despain et al. 1986). Indeed, elk numbers increased rapidly to a count of about 12,600 elk in 1975, which equates to roughly a 17% growth rate for the population each year (Houston 1982, Eberhardt et al. 2007). Elk began to reoccupy areas used historically and migrate outside the park again, with larger migrations occurring during the late 1970s (Houston 1982, Lemke et al. 1998). Elk counts continued to increase to about 18,900 elk by the late 1980s and more than 19,000 elk by 1994, with population estimates of 20,000 to 25,000 elk (Coughenour and Singer 1996, Taper and Gogan 2002, Eberhardt et al. 2007). In 1976, Montana resumed liberal harvests of elk that migrated outside the park during mid-December through mid-February (Houston 1982, Lemke et al. 1998). These late-season harvests were initially small in some winters but increased to consistently sizeable levels after 1981 and focused on female elk after 1983 to reduce population growth (Vucetich et al. 2005, White and Garrott 2005a, Wright et al. 2006). These harvests were extremely popular, very profitable, and consistently removed about one-quarter of the migrant females each year during 1976 to 2004; mostly prime-aged females 3 to 15 years old (Duffield and Holliman 1988, White and Garrott 2005a, Wright et al. 2006, Eberhardt et al. 2007).

During 1976 to 1990, the distribution of northern Yellowstone elk expanded along the Yellowstone River valley north of the park by about 41%, more than doubling the extent of the winter range north of the park to beyond Dome Mountain in the southern Paradise Valley (Lemke et al. 1998). This expansion into an area previously occupied by few elk likely occurred due to increasing numbers of elk in the park, the acquisition and restoration of more than 8,650 acres (3,500 hectares) of winter range outside the park by the Rocky Mountain Elk Foundation and Montana Fish, Wildlife and Parks, and changes in the timing of hunts in Montana to facilitate elk migration out of the park (Lemke et al. 1998). The range expansion provided additional resources for population growth and about 18,900 elk were counted during winter 1988 (Coughenour and Singer 1996, Eberhardt et al. 2007). Between 3,000 and 5,800 elk starved during the winter of 1989 following an extended drought and major fires in 1988 that burned about 30% of their summer range and 27% of their winter range (Singer et al. 1989, 1997). Another 2,900 elk were harvested in Montana when more than 7,000 northern Yellowstone elk migrated outside the park (Lemke et al. 1998). The effects of the fires and subsequent starvation on the elk population were short-lived, however, and thereafter an average of 5,460 elk (range = 1,500 to 8,625) spent winter north of Yellowstone National Park with 2,000 to 4,500 of those elk north of Dome Mountain (Figure 3; Lemke et al. 1998, Taper and Gogan 2002). Prior to 1989, fewer than 600 elk were counted in this area. In turn, late season harvests increased from about 900 elk each winter during 1980 to 1988 to 1,460 each winter during 1989 to 1997 (Lemke et al. 1998).

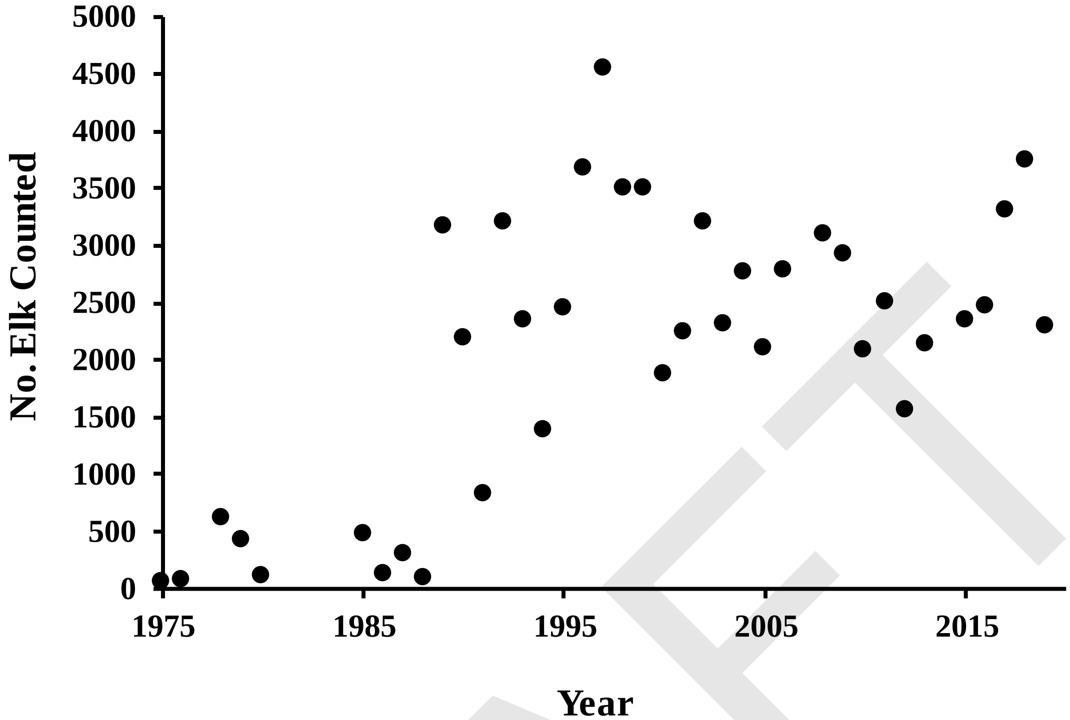


***Figure 3**. Numbers of northern Yellowstone elk counted north of Dome Mountain in the southern Paradise Valley of Montana during winter from 1975 to 2019. A severe winter occurred in 1997. Data is from the Northern Yellowstone Cooperative Wildlife Working Group which includes Montana Fish, Wildlife and Parks, Custer Gallatin National Forest, Northern Rocky Mountain Science Center (U.S. Geological Survey), and Yellowstone National Park.*

The population rebounded from the 1989-1990 decrease and by 1994 biologists counted about 19,045 elk during winter (Taper and Gogan 2002). The actual number of elk probably was quite a bit higher (25,000), as is the case for interpreting any annual count conducted, because observers miss seeing up to 50% of elk during aerial surveys depending on sighting conditions such as group sizes and use of forested habitats (Samuel et al. 1987, Singer and Garton 1994, Coughenour and Singer 1996, Eberhardt et al. 2007, Tallian et al. 2017). Some biologists thought the population was nearing the maximum capacity of forage on the winter range to support elk (Coughenour and Singer 1996, Taper and Gogan 2002). Each elk has fewer resources available to use when the population is near carrying capacity. As a result, calf survival and recruitment decreased (Singer et al. 1997, Taper and Gogan 2002).

The overall increase in elk numbers and range expansion onto agricultural lands in the southern Paradise Valley led to concerns about overgrazing and crop depredation. In 1998, the U.S. House Appropriations Committee directed the National Park Service to initiate a National Academy of Sciences review of the management of ungulates and their ecological effects in the northern region of Yellowstone National Park. In 2002, the National Research Council published its findings in a book entitled *Ecological Dynamics on Yellowstone's Northern Range* which indicated "[t]he best available scientific evidence does not indicate that ungulate populations are irreversibly damaging the northern range … If YNP [Yellowstone National Park] continues to follow a policy that permits the natural range of variation, it will need to monitor ecosystem attributes … The committee recommends that a comprehensive, integrated program of research and monitoring be established to measure the consequences of current and future changes" (National Research Council 2002).

Predator Restoration

Forty-one wolves were released in Yellowstone National Park from 1995 to 1997 and their abundance and distribution rapidly increased with a growth rate of about 20% per year (Eberhardt et al. 2003, 2007; Smith et al. 2020). The count of northern Yellowstone elk was about 17,000 in 1995 but decreased to an estimated 12,000 elk in 1998 following the harvest of about 3,320 elk in the winter of 1996-1997 (Vucetich et al. 2005). There was a mass migration of elk north of the park due to severe snow conditions and hunters harvested about 855 elk during the general (autumn) rifle season and 2,465 elk during the late-season (winter) hunt (Vucetich et al. 2005). There also was substantial starvation of elk, especially calves (Eberhardt et al. 2007). Thus, the beginning of the elk population decrease occurred prior to any substantive effects from reintroduced wolves. Elk counts varied between 11,000 and 15,000 from 1998 to 2002 (Vucetich et al. 2005). Wolf predation had little effect on the population dynamics of elk at this time because wolf numbers were low, elk numbers were high, and wolves selected younger and older elk that produce few calves and are more prone to starvation. In contrast, harvests focused on reproductive-aged elk and removed 1,100 to 3,300 per year, which exceeded wolf predation and accelerated the decrease in elk abundance (Eberhardt et al. 2003, 2007; Vucetich et al. 2005, White and Garrott 2005a, Evans et al. 2006, Wright et al. 2006, MacNulty et al. 2020b, Smith 2021).

By 2003, however, there were 174 wolves living in the park, including 98 in northern Yellowstone (Smith et al. 2004, 2020). Wolves became a primary factor influencing the dynamics of elk and, in combination with recovered populations of bears and cougars, contributed to lower calf recruitment (survival through their first year of life), old adult survival, and overall numbers of elk (White and Garrott 2005a, Eberhardt et al. 2007, Barber-Meyer et al. 2008, Proffitt et al. 2014, MacNulty et al. 2020b, Metz et al. 2020a,b; Stahler et al. 2020, Smith 2021). Wolves killed a substantial number of calves and about 85% of adult, female, elk killed by them during 1995 to 2016 were more than 10 years old (MacNulty et al. 2016, 2020b, Smith 2021). The median age of radio-collared female elk killed by wolves during 2000 to 2016 was 16 years (range = 6 to 24 years) and 55% were older than 14 years (MacNulty et al. 2016, 2020b, Smith 2021).

Counts of northern Yellowstone elk decreased from about 10,000 to 3,915 from 2003 to 2013 as hunters and multiple carnivore species competed for decreasing numbers of elk and continued to influence elk calf recruitment and the age structure and portion of older, less fertile, adult females in the population (Figure 4, Hoy et al. 2020, MacNulty et al. 2020b, Smith 2021). In response, permits for harvesting antlerless elk in Montana were reduced from 2,882 in 2000 to 1,100 in 2004 and 140 in 2006, before being eliminated by 2010 (Evans et al. 2006, Wright et al. 2006, Montana Fish, Wildlife and Parks 2019). Estimates of wolf predation exceeded the number of hunter-harvested elk during this period, even though counts of wolves in northern Yellowstone decreased from 98 to 34 (Eberhardt et al. 2007). However, harvests had a larger impact on the decreasing elk population trend because hunters primarily removed prime-aged elk while wolves mostly killed calves and less-fertile females more than 14 years old (Vucetich et al. 2005, White and Garrott 2005a, Evans et al. 2006, Wright et al. 2006, Eberhardt et al. 2007, Brodie et al. 2013, MacNulty et al. 2016, 2020b; Metz et al. 2020b, Smith 2021).

In hindsight, the rapid decrease in numbers of northern Yellowstone elk during 1995 to 2013 is not surprising given the increase in predation and continuation of liberal human harvests during the first decade after wolf reintroduction (Vucetich et al. 2005, White and Garrott 2005a, Eberhardt et al. 2007, MacNulty et al. 2020b). The level of predation likely approached what the northern population experienced during the early to mid-1850s prior to market hunting and predator reduction efforts in the late 1800s (MacNulty et al. 2016, 2020b). Harvests approached the lower levels of culls in the park and harvests in Montana during the 1950s and 1960s (Houston 1982, Taper and Gogan 2002, Barmore 2003, MacNulty et al. 2016, 2020b). This combination of bears, cougars, and wolves killing large number of calves and older elk, and hunters killing large numbers of prime-aged females, resulted in substantial removals of elk across all ages (Smith et al. 2004, Evans et al. 2006, Wright et al. 2006, MacNulty et al. 2016, 2020b; Smith 2021). As survival and recruitment decreased, the abundance of elk plummeted, and the age structure shifted towards older, less-fertile females (Eberhardt et al. 2007, MacNulty et al. 2016, 2020b; Hoy et al. 2020, Smith 2021).

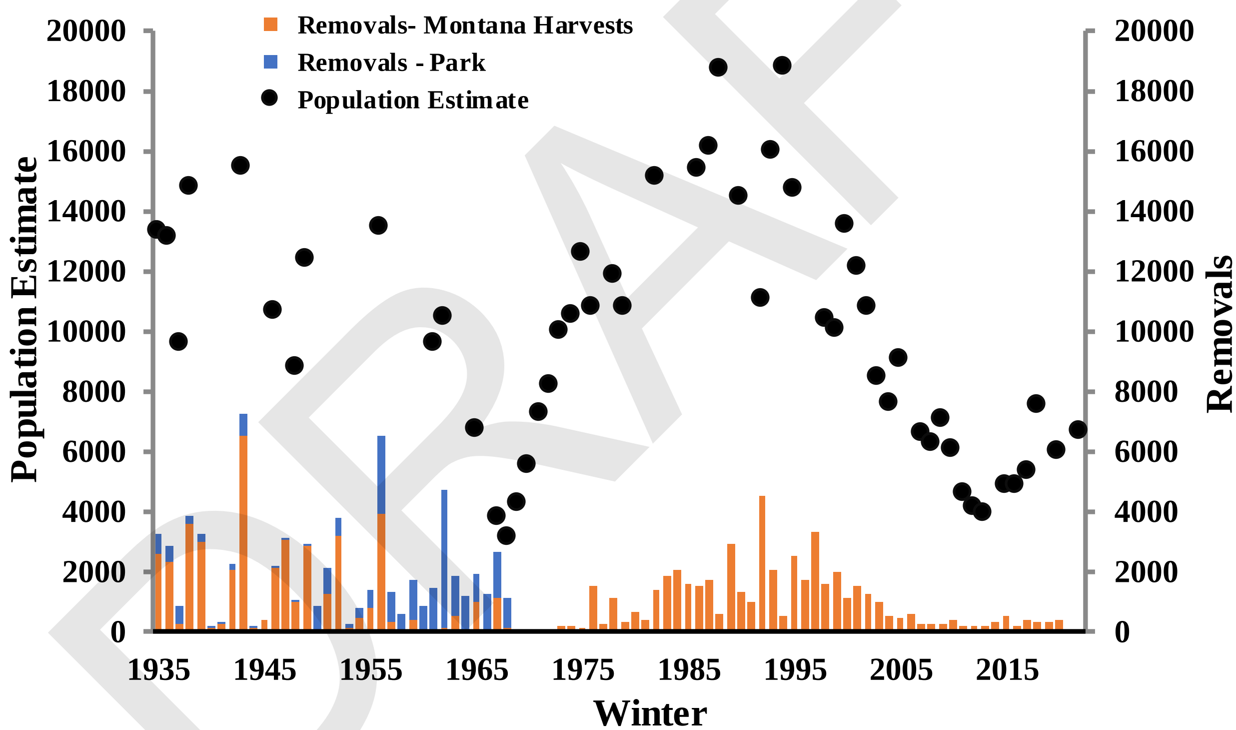


__Figure 4__. Post-hunt population estimates of northern Yellowstone elk (black circles), with numbers removed from the park (blue bars) and harvested in Montana (orange bars) during winters from 1935 to 2020. Population estimates are the count minus late-season harvests thereafter. The general rifle hunting season occurred before the counts. Data from Houston (1982), Lemke et al. (1998), Taper and Gogan (2002), White and Garrott (2005a), and Montana Fish, Wildlife and Parks. These counts are not adjusted for the uncertain detection of elk during surveys, meaning they underestimate true abundances.

Between 2000 and 2020, the proportion of northern Yellowstone elk spending winter inside the park decreased from about 80% to 20% due to the simultaneous occurrence of increased predation on elk using higher elevation, deeper snowpack areas in the park during winter and spring compared to increased survival and recruitment for elk using lower-elevation areas outside the park after the substantial reduction in hunter harvest of antlerless elk between 2004 and 2010 (White et al. 2012, MacNulty et al. 2020b). Prior to 2004, Montana designed harvests of northern Yellowstone elk based on the assumption that a substantial portion of the population (84% during 1971 to 2004) remained in the park and was not subject to harvest. By 2012, lower calf recruitment, combined with an increase in the number of bulls harvested in Montana, contributed to a decrease in brow-tined bulls in the population. State-licensed hunters have harvested fewer than 60 antlerless elk during each autumn hunting season since 2012 (Montana Fish, Wildlife and Parks 2019). Tribal hunters that largely come to hunt bison through treaty-reserved hunting rights near Gardiner, Montana, also take elk of both sexes, but in unknown quantities due to inconsistent reporting.

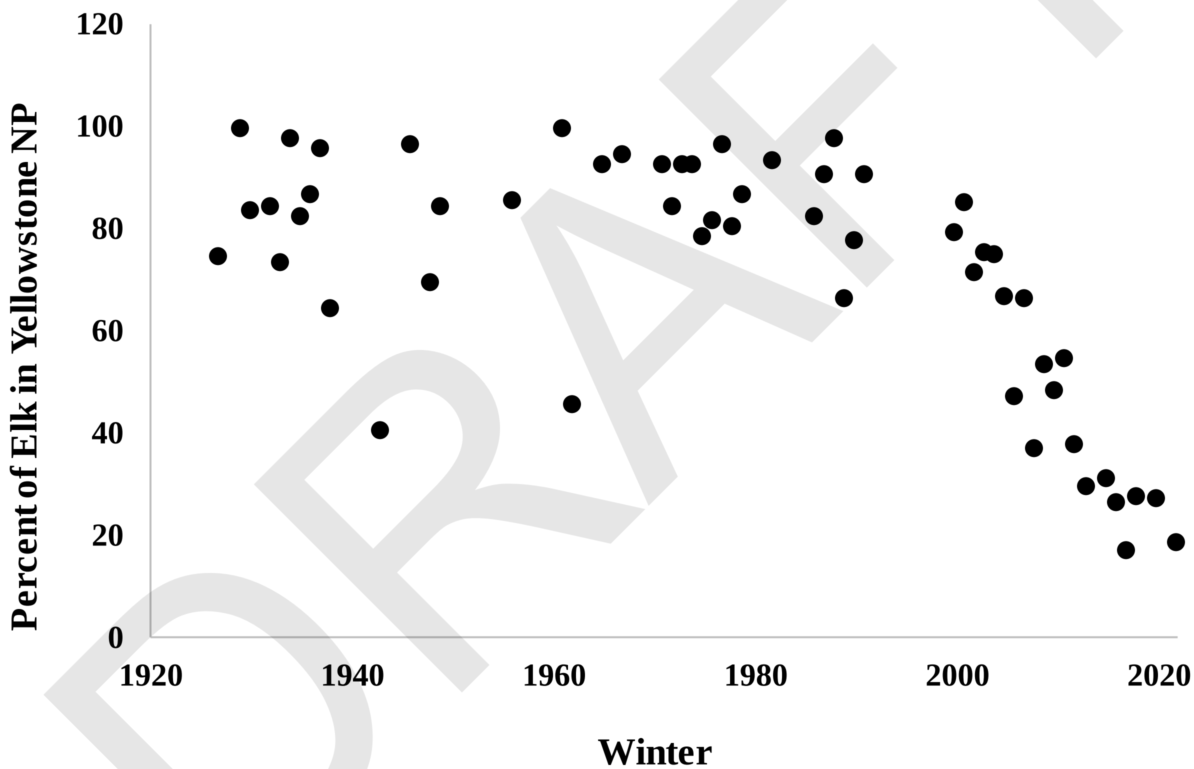


Figure 5*. The portion of northern Yellowstone elk observed in the park during winter counts from 1971 to 2020. Data are from Houston (1982), Coughenour and Singer (1996), and the Northern Yellowstone Cooperative Wildlife Working Group.*

Counts of northern Yellowstone elk ranged between 4,800 and 5,400 from 2015 to 2017. In 2016, Montana Fish, Wildlife and Parks shortened the rifle season for brow-tined bulls to 3 weeks on a regular license, followed by a 50-tag, limited-draw, permit-only opportunity during the last 2 weeks of the season. The northern Yellowstone elk population is currently at or above the objective of 3,000 to 5,000 elk in Montana hunting district 313 north of the park with about

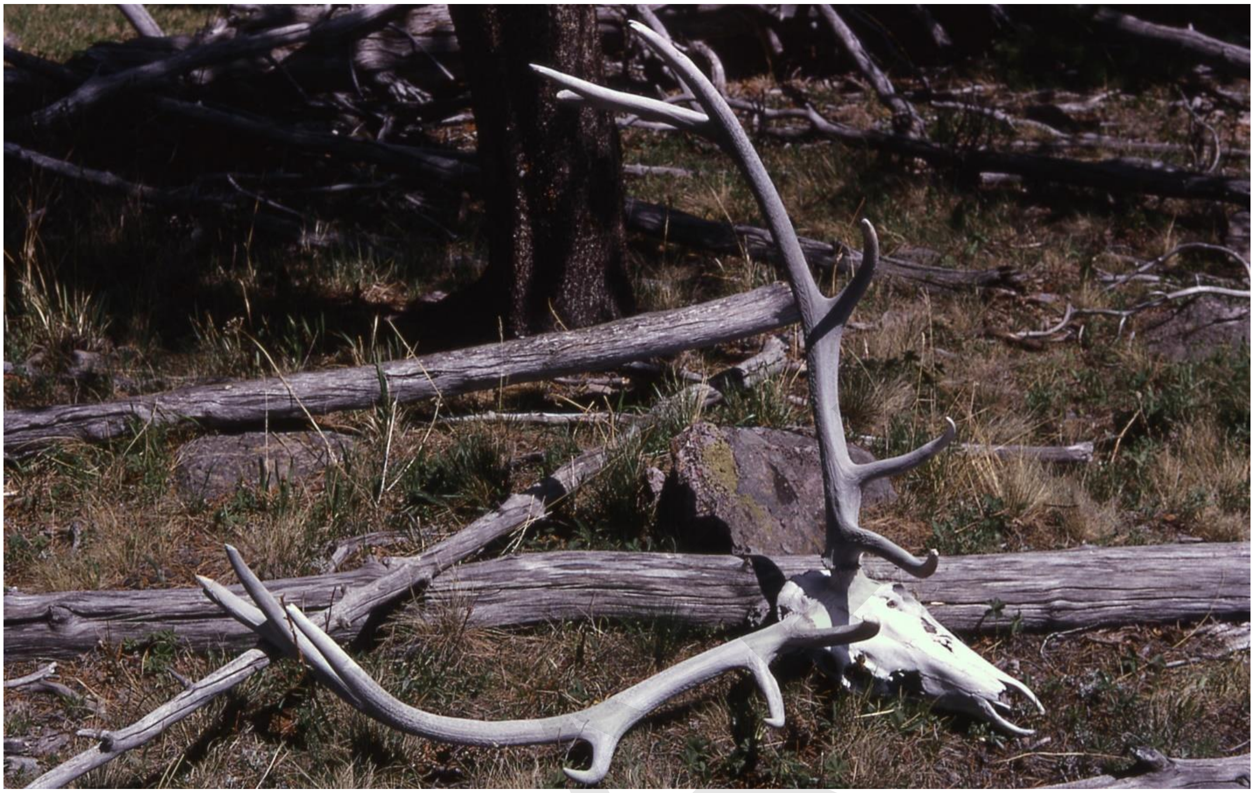
4,600 elk observed during March 2021 and 5,475 during March 2022 (Montana Fish, Wildlife and Parks 2019, 2021c; Northern Yellowstone Cooperative Wildlife Working Group 2022).

Conclusions

Scientists did not fully realize the importance of large predators in the Yellowstone ecosystem when 'natural regulation' began being implemented in the park in the 1970s (Despain et al. 1986, White and Garrott 2013). Wolves were extirpated by 1930, cougars nearly so, and bear numbers decreased further during the 1970s due to removals following the closing of garbage dumps in and near the park (White et al. 2017, Ruth et al. 2019, Smith et al. 2020). Human culls and harvests had predominantly influenced trends in the northern elk population since the establishment of Yellowstone National Park in 1872 (Houston 1982, Eberhardt et al. 2003, 2007). Predation, in combination with liberal harvests in Montana and occasional severe weather, rapidly decreased numbers of elk after the recovery of the most abundant and diverse predator community in the conterminous United States during the 2000s (Vucetich et al. 2005, White and Garrott 2005a, Proffitt et al. 2014, MacNulty et al. 2020b, Smith 2021). As a result, it was necessary for Montana Fish, Wildlife and Parks to eliminate the late season harvest of antlerless elk to increase adult female survival and reproduction and offset consistently lower recruitment due to predation (White and Garrott 2005a, Evans et al. 2006, Wright et al. 2006, Eberhardt et al. 2007, Brodie et al. 2013, Montana Fish, Wildlife and Parks 2019, MacNulty et al. 2020b).

The number of wolves in northern Yellowstone, which peaked at 98 wolves in 8 packs during 2003 has averaged 45 wolves in 4 packs since 2008 (Smith et al. 2004, 2020). Numbers of wolves living in Yellowstone decreased as elk numbers decreased, even though numbers of bison increased concurrently (Cubaynes et al. 2014; see Chapter 6 for wolf prey selection information). In addition, the survival and reproductive success of wolves decreased as their numbers and density increased (density dependence; Smith et al. 2020). As a result, wolf numbers decreased and, in response, numbers of northern Yellowstone elk increased to between 5,000 and 7,500 elk after a low count of 3,915 in 2013 (MacNulty et al. 2020b). Elk numbers may stabilize or increase somewhat in future years if conservative harvests of females are sustained, and carnivore numbers remain depressed outside the park (MacNulty et al. 2016, 2020b, Boyce 2018, Metz et al. 2020a, Smith 2021). However, there is still substantial uncertainty about the long-term dynamics of northern Yellowstone elk in this multi-predator system.

The concept of allowing the natural world in protected areas like Yellowstone National Park to regulate itself through ecological processes, such as competition, dispersal, migration, natural disturbances, predation, and vegetation phenology, is enticing because it most closely reflects the National Park Service's mission of conserving resources in park units unimpaired (unharmed) for the benefit and enjoyment of people (16 USC 21 *et seq*., 17 Stat. 32; Boyce 1998, 2018; National Park Service 2006, White et al. 2013a, White 2016). In modern society, however, the term 'natural regulation' is not an accurate description of all the forces that control the dynamics of natural resources because it excludes the important role played by humans, both historically and currently (Cole and Yung 2010, White et al. 2013b). For example, the dynamics of the northern Yellowstone elk population have been primarily influenced by human harvests and culls over the past 150 years, while their habitat has been fragmented and degraded by human development and climate warming with invasions of exotic plants (Houston 1982, Eberhardt et al. 2007, White et al. 2013b). Instead, contemporary management policies for parks direct managers to try and minimize human dominance and intervention in parks to the extent feasible, which includes engaging experts to anticipate adverse effects, analyzing alternatives, and encouraging management practices on adjacent lands compatible with the Service's mission and goals (National Park Service 2006, Jarvis 2012). Park managers also are encouraged to maintain ecological processes and disturbance regimes, restore native species and functioning ecosystems, sustain biodiversity and connectivity for migration and dispersal, and support system integrity and resilience (National Park Service 2006, Smith and Peterson 2021).



Adult male skull and antlers in Yellowstone National Park. Photograph taken in 1966 by an unknown photographer. National Park Service photograph collection.

Chapter 3
Status of the Population

Introduction

Whether an elk population increases, or decreases, depends on factors influenced by the number of animals in an area, such as reproduction and survival, and other factors not related to density, such as climate and year-to-year variations in weather (Caughley and Sinclair 1994). Prime-aged females usually have high and relatively constant survival and reproduction, but calf survival can be highly variable from year-to-year due to factors that affect food availability, growth, and energetic costs (Eberhardt 1977, 2002; Gaillard et al. 1998, 2000; Garrott et al. 2003, Raithel et al. 2007). Population growth slows if the density of animals increases and there is a sustained period of fewer resources for everyone, especially young animals (Caughley and Sinclair 1994). Lower nutrition and body condition initially contributes to lower survival of young, followed by reproduction beginning at an older age, and then lower adult reproduction and survival (Eberhardt 1977, 2002; Cook 2002).

Environmental factors not related to density, such as severe droughts and winters, can exacerbate these demographic responses by affecting food availability, energetic costs and, in turn, reproduction and survival; especially for calves and older adults (Garrott et al. 2003, Lachish et al. 2020). For example, deep wet snow increases energy expenditures and cycles of icing and thawing increase the hardness of the snowpack and make it more difficult to access forage (Robbins 1993, Garrott et al. 2003, Wilmers et al. 2013). Decreased forage intake by pregnant females can contribute to lower birth weights and survival of their calves which enter winter with lower fat reserves and are more susceptible to starvation (Thorne et al. 1976, Houston 1982, Cook 2002, Cook et al. 2004a). Deep snow conditions also increase the susceptibility of elk to predation and the number of elk that migrate outside the park where they are vulnerable to harvest (White and Garrott 2005a, Brodie et al. 2013, Wilmers et al. 2020). In combination, these factors can result in substantial mortality and low recruitment during some winters that affects population trends (Sæther 1997, Coulson et al. 2001, Garrott et al. 2003, 2009b,c).

This chapter summarizes information about the status of the northern Yellowstone elk population, including estimates of abundance, age and sex composition, births, deaths, and recruitment.

Counts and Classifications

The Northern Yellowstone Cooperative Wildlife Working Group uses 2 or 3 airplanes to count elk each winter during December through March. This group is comprised of biologists from Montana Fish, Wildlife and Parks, Yellowstone National Park, Custer Gallatin National Forest, and the Northern Rocky Mountain Science Center (U.S. Geological Survey). Biologists conduct the count when most elk are aggregated on the relatively open, snow-covered winter range. The count typically is completed during a single morning with each plane covering a segment of the winter range (Coughenour and Singer 1996). Observers search for groups of elk and record the number in each group and a rough approximation of their location (since the plane is usually not directly over the group) using a Global Positioning System (GPS).

These counts underestimate the actual (true) number of elk because observers miss seeing up to 50% of elk during aerial surveys depending on sighting conditions such as vegetation cover, group sizes, and elk behavior (Samuel et al. 1987, Singer and Garton 1994, Coughenour and Singer 1996, Eberhardt et al. 2007). Scientists have attempted to resolve this problem by applying statistical tools to correct elk counts for the number of elk missed due to some of these factors (Samuel et al. 1987, Singer and Garton 1994, Tallian et al. 2017, Smith et al. 2022). For example, the probability of sighting groups of elk is higher for larger groups which are more obvious to observers than individual elk or small groups (Tallian et al. 2017). This relationship can be estimated from count data by evaluating whether observers sighted groups of various sizes containing radio-collared elk (Singer and Garton 1994). Logistic regression models can then be developed to predict the probability of sighting elk by dividing the size of each counted group by its predicted sightability and adding these values to obtain a corrected population estimate for each survey (Figure 6; Tallian et al. 2017).

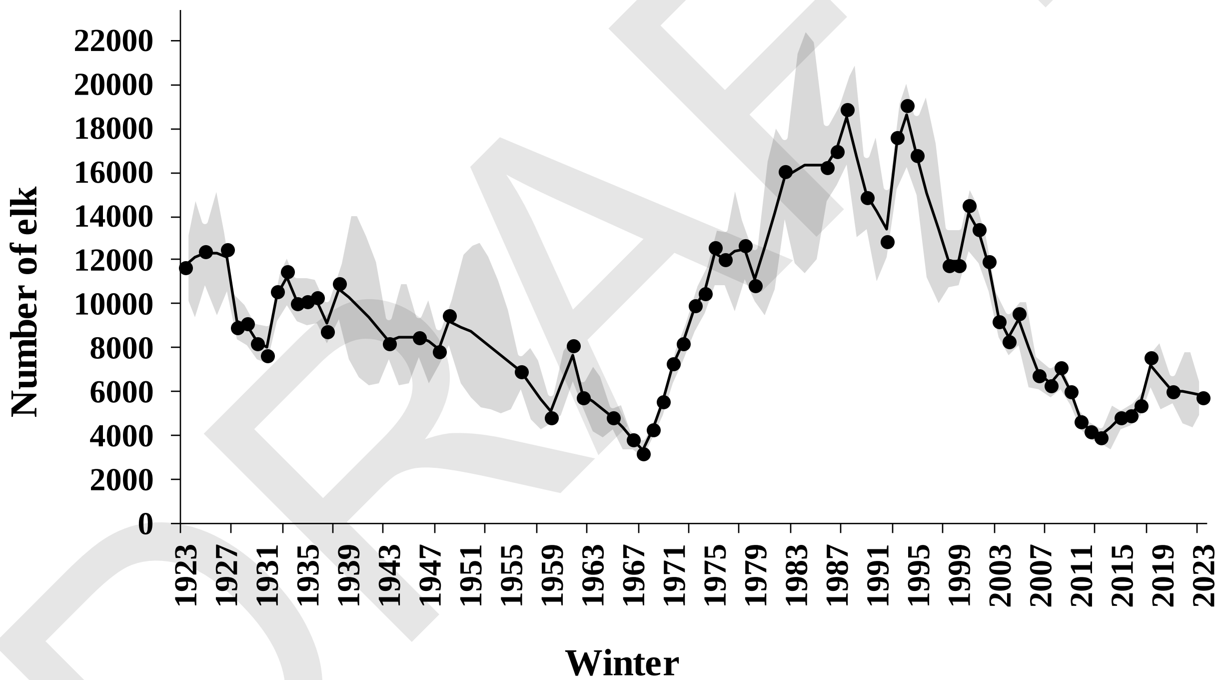


***Figure 6**. Counts (circles) and a fitted trend line estimating the abundance of northern Yellowstone elk during 1923 to 2023. The shaded area indicates the amount of uncertainty for the trend line due to imperfect sightability during each count. Data was provided by the Northern Yellowstone Cooperative Wildlife Working Group and the figure was revised from MacNulty et al. (2020b).*

In addition, biologists use a helicopter to estimate the relative age and sex composition of the northern Yellowstone elk population during late winter (March). Calves are elk less than 1-year-old, cows are yearling and adult female elk, spikes are yearling males, and branch-antlered (or brow-tined) bulls are adult males. These estimates provide indices of calf survival and recruitment, as well as the portion of adult and yearling males in the population. Elk locations are categorized as being in either the upper, middle, or lower sectors of the winter range corresponding to river watersheds with varying elevations and snowpacks (Figure 7; Coughenour and Singer 1996, White et al. 2012). The upper sector includes portions of the Lamar River watershed where elevations range from 6,200 to 8,500 feet (1,890 to 2,590 meters) and snow depths average 2 to 2.3 feet (0.6 to 0.7 meter; Figure 8). The middle sector includes the Yellowstone River watershed from the confluence of the Lamar and Yellowstone rivers near Tower Falls and Junction Butte through the Blacktail Deer Plateau where elevations range from 6,200 feet to 7,790 feet (1,890 to 2,375 meters) and snow depths average 1.6 feet (0.5 meter). The lower sector inside the park includes the Gardner River watershed between Gardners Hole and Mount Everts near Mammoth, Wyoming, and north to Reese Creek at the northern park boundary near Gardiner, Montana, where elevations range from 5,300 to 7,595 feet (1,615 to 2,315 meters) and snow depths are less than 1 foot (0.3 meter). The lower sector outside the park includes mostly Custer Gallatin National Forest and private lands in the Yellowstone River watershed from the park boundary north to Dailey Lake in the southern Paradise Valley of Montana. Elevations in this sector range from 5,300 to 8,500 feet (1,615 to 2,590 meters) and snow depths are less than 1 foot (0.3 meter).

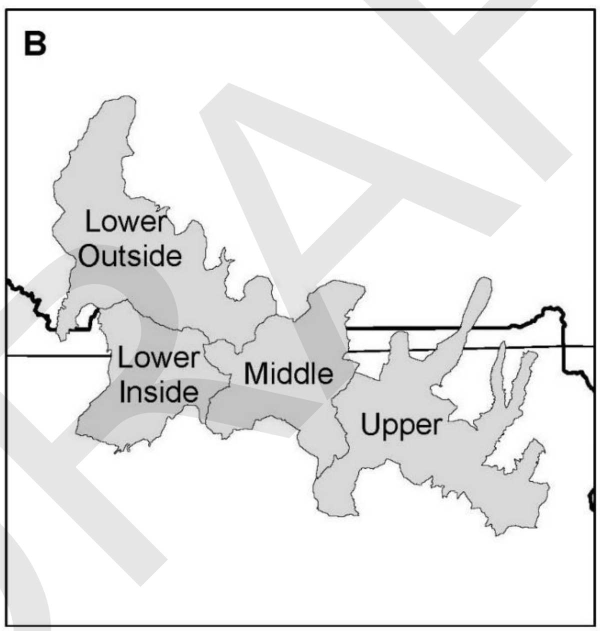


***Figure 7**. Biologists divided the winter range for northern Yellowstone elk into four sectors for counts and classifications. The upper, middle, and lower inside sectors are mostly within Yellowstone National Park, the boundary of which is depicted by the thick black line. The lower outside sector encompasses public and private lands in southwest Montana (Coughenour and Singer 1996, White et al. 2012).*

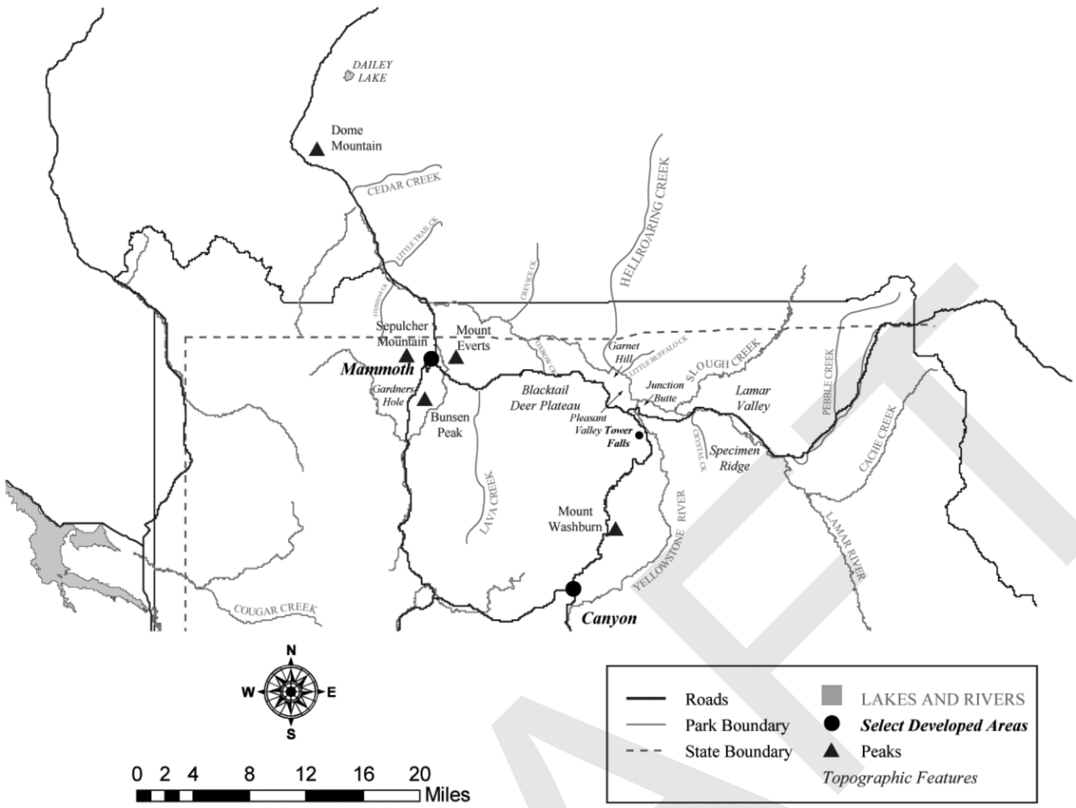


***Figure 8**. Names of places in the northern portion of Yellowstone National Park and nearby areas of Montana.*

Minimum counts of northern Yellowstone elk increased by 440% from 1969 to 1995 when there were minimal harvests and predation and relatively mild winters through the 1980s (Coughenour and Singer 1996, Lemke et al. 1998, Eberhardt et al. 2003, MacNulty et al. 2020b). However, counts decreased to about 10,000 elk in 1999 following the severe winter of 1997 with substantial starvation and harvests of more than 3,300 elk migrating into Montana (White and Garrott 2005a). Counts increased to 14,000 elk by 2000 but decreased rapidly to about 3,900 elk by 2013. Thereafter, counts increased to about 7,600 elk by 2018 (Northern Yellowstone Cooperative Wildlife Working Group 2022).

As the number of northern Yellowstone elk decreased in the 2000s, biologists observed fewer elk spending winter in the upper elevations of the Lamar River watershed (White et al. 2012). Conversely, the number of elk spending winter in the lower-elevation Gardiner basin and southern Paradise Valley increased (White et al. 2012). The change in numbers of elk wintering in and out of the park was the result of the simultaneous action of contrasting demographic forces acting on different segments of the population (White et al. 2012, MacNulty et al. 2020b). There was increased wolf and cougar predation on elk using higher elevation, deeper snowpack areas in the park during winter and increased bear predation during calving in spring (Barber-Meyer et al. 2008, Metz et al. 2020a,b; Stahler et al. 2020). In addition, persistent nutritional limitations during a sustained drought from 1999 to 2007 lowered pregnancy rates for lactating elk and contributed to lower recruitment to replace these animals (Cook et al. 2004b, Middleton et al. 2013b, 2018).

In contrast, elk using lower-elevation areas with less snowpack outside the park had increased survival and recruitment following the substantial reduction in hunter harvest after the elimination of the late-season hunt by 2009-2010 (White et al. 2012, MacNulty et al. 2020b). The elimination of this hunt, which primarily focused on antlerless elk, allowed more elk to move north of the park and contributed to a sustained increase in numbers spending winter in that area (White et al. 2012, MacNulty et al. 2020b). In addition, there are fewer predators in this area due to human harvests and intolerance, and irrigated alfalfa fields provide nutritious forage (Middleton et al. 2013b, 2018; Garroutte et al. 2016, Tilt 2020, Montana Fish, Wildlife and Parks 2022, Sholly 2022a,b). During the 2000s, there was a transition in the ownership of many ranches in the Paradise Valley, with many new owners being more interested in wildlife viewing than livestock production (Haggerty and Travis 2006). Some of these new landowners discouraged hunting and began irrigating and cultivating hay to attract and feed elk. During 2007 to 2015, the number of acres of alfalfa in Montana counties in the Greater Yellowstone Area increased by about 290%; within elk winter ranges it increased by about 350% (Haggerty et al. 2018). High-quality forage was up to 200% more abundant at peak green-up in irrigated pastures outside the park than in grasslands therein (Garroutte et al. 2016), which increased the nutrition, body condition, and demographic rates of elk (Cook et al. 2013, Middleton et al. 2018).

There was a tendency for more females with calves and yearlings to migrate to lower elevations in and outside the park, where snowpack was lower and predators fewer, while a higher proportion of older females and bulls remained at higher elevations (Coughenour and Singer 1996, Cook et al. 2004b, White et al. 2010, 2012; MacNulty et al. 2020b). The age structure of adult females in the population became skewed towards older animals during the 1990s and 2000s because the age classes of adult elk removed by wolves and hunters were quite different (Eberhardt et al. 2007, Hoy et al. 2020, MacNulty et al. 2020b, Smith 2021). Wolves primarily killed older adult elk (average = 14 years old; median = 12 years), while hunters harvested more younger and prime-aged elk (average = 7 years; median = 9 years; Evans et al. 2006, Wright et al. 2006, Metz et al. 2012, 2020b).

The ratio of adult elk was about 50 males per 100 adult females during the 1960s following decades of intense reduction efforts biased towards groups of female elk (Houston 1982, Barmore 2003). This ratio remained relatively high at an average of 34 bulls per 100 adult females (range = 14 to 65) from the late 1980s to early 2000s (Coughenour and Singer 1996, Taper and Gogan 2002, Montana Fish, Wildlife and Parks 2019). Following the restoration of large predators, however, the ratio decreased rapidly to an average of 18 bulls per 100 adult females (range = 12 to 20) from 2003 to 2021 (Montana Fish, Wildlife and Parks 2019, 2021c). Many factors affect bull numbers, including predation, environmental conditions, and hunter harvests in Montana. The extent of predation by wolves varies from year-to-year depending on environmental conditions that affect the body condition and vulnerability of elk (Mech et al. 2001, Metz et al. 2012, 2020b; MacNulty et al. 2020b). During the 2000s, below average summer precipitation and persistent drought conditions resulted in less and poorer quality forage for elk (Cook et al. 2004a,b; Middleton et al. 2013b, 2018). Mature bulls entered the autumn breeding period in relatively poor condition and finished this energetically taxing period in worse condition (Metz et al. 2020b, Wilmers et al. 2020). Mature bulls tend to use higher-elevation habitats with deeper snow during winter, which reduces competition for forage but also can contribute to higher mortality during severe winters (Houston 1982, Coughenour and Singer 1996). Wolves killed more mature bulls in early winter during the period of prolonged drought.

After the drought ended, mature bulls returned to being less vulnerable to predation (Metz et al. 2020b, Wilmers et al. 2020).

Most of the decrease in observed numbers of mature bulls during classification surveys occurred on the portion of the winter range outside the park in Montana. During 1995 to 2021, ratios of brow-tined bulls in Montana averaged about 10 per 100 adult females (range = 1 to 60) compared to an average of 30 (range = 13 to 87) in the park (Montana Fish, Wildlife and Parks 2018a, 2019, 2021). Since 2009, mature bull ratios in Montana have averaged about 3 per 100 adult females (range = 1 to 5) compared to about 17 per 100 adult females (range = 13 to 24) in the park (Montana Fish, Wildlife and Parks 2018a, 2019, 2021c). These changes in ratios are difficult to interpret because they not only reflect changes in bull numbers in and outside the park, but also an increasing number of antlerless elk (females and calves) in the population spending winter outside the park, which would lower the ratios since the mid- to late 2000s. While lower recruitment of elk due to predation has contributed to fewer bulls overall (Proffitt et al. 2014), the differences in bull ratios over time suggest other factors besides predation, including hunting outside the park, may have contributed to fewer mature bulls. The 10-year average of brow-tined bulls harvested in elk hunting district 313 during 2010 to 2019 was 235 compared to 173 during 1999 to 2009 (Montana Fish, Wildlife and Parks 2019). In other words, harvests of mature bulls increased following the restoration of wolves and other large predators.

A scarcity of mature males could eventually result in less synchronous breeding and delayed parturition which, in turn, could reduce calf survival (Noyes et al. 1996, Cook et al. 2004a). Calves born near the peak birth date in Yellowstone National Park from 2003 to 2005 had higher survival, perhaps because of numerous females being vigilant for predators at the same time and abundant newborns diluting the probability of a particular individual being killed (Barber-Meyer et al. 2008). Bears were less likely to kill a calf born near the peak birth date compared to those born pre- and post-peak (Barber-Meyer et al. 2008). However, there is no evidence the apparent decrease in numbers and ratios of mature bulls has decreased reproductive rates in northern Yellowstone elk.

Telemetry

Efforts to monitor wildlife populations in the park were revolutionized in the 1960s when biologists fit telemetry collars on elk and grizzly bears. This technique enabled them to collect important information for management, including activity patterns, cause-specific mortality, dispersal, migration, population estimation, range use, recruitment, resource selection, and survival (White and Garrott 1990). There was a tremendous advancement in scientific knowledge that led to better-informed decisions and benefits to the scientific community and visitors. However, telemetry is intrusive because it requires capturing animals and attaching a device to them, such as a radio collar or an ear tag transmitter (Mech and Barber 2002). Scientists try to minimize these effects because an underlying assumption is that animals with devices behave like other animals (White and Garrott 1990). Biologists and engineers have developed lighter-weight, less visible, and less bulky attachment devices, timed detachment devices, longer battery life, and GPS or satellite collars (Mech and Barber 2002). They also use less invasive sampling methods, such as noninvasive genetic sampling, remote cameras, and stable isotope analysis, to gather information when possible. During 2000 to 2023, biologists captured and fit more than 380 adult female elk and 150 calves in Yellowstone with telemetry devices to monitor their behavior, demographics, movements, reproduction, resource selection, and survival (Barber-Meyer et al. 2008, Smith 2021).

Reproduction

The annual cycle of reproduction for northern Yellowstone elk begins when females ovulate and become receptive to mating in late summer (Hudson et al. 2002). Breeding occurs in autumn (September, October) when elk are in peak body condition from feeding on nutritious forage through the summer and replenishing muscle mass and fat (Cook 2002, Hudson et al. 2002). Gestation lasts about 8 to 8.5 months through winter (Hudson et al. 2002). Fetal mortality is rare, accounting for less than 1% of pregnancy losses (Greer 1966, Houston 1982, Barmore 2003, Cook et al. 2013). Calves are born in spring (mid-May to mid-June; peak about June 1) when grasses are initiating new growth, which provides mothers and their calves with nutritious forage to support nursing, restoration of nutritional condition, and growth prior to winter (Johnson 1951, Barber-Meyer et al. 2008, Cook et al. 2013, Middleton et al. 2013a).

Northern Yellowstone elk generally give birth to a single calf; twins are extremely rare (less than 0.3%; Johnson 1951, Kittams 1953, Greer 1966, Houston 1982). Calves in utero and at birth are about 50% females and 50% males (Johnson 1951, Kittams 1953, Houston 1982, Barmore 2003, Barber-Meyer et al. 2008, Cunningham et al. 2008). Historically, biologists determined the pregnancy status of Yellowstone elk by examining harvested and culled elk. Today, they use ultrasonography or measure hormone levels in blood samples from captured females. Biologists report pregnancy rates as the proportion (0.90) or percentage (90%) of females pregnant (Caughley and Sinclair 1994). Only about 3% of yearling females killed during winter reductions in the park from 1935 to 1951 were pregnant, compared to about 85% of older females (Kittams 1953, Houston 1982). Pregnancy rates of 2-year-old females varied between 73% in 1949-1950 and 95% in 1951 (Kittams 1953). Pregnancy rates of prime-aged females 3 to 15 years old were high (0.91) and relatively constant from 1950 to 1967, but much lower in older elk (Houston 1982, Barmore 2003). Pregnancy rates decreased in younger and older elk as density increased following the cessation of culling and liberal harvests in the late 1960s (Houston 1982, Barmore 2003). However, increased density had little effect on the pregnancy rates of 3- to 9-year-old females (Houston 1982).

Recently born elk calf hiding in Yellowstone National Park. Photograph by William Dunmire, National Park Service.

After the restoration of wolves, pregnancy rates remained high (90%) in prime-aged female elk and continued to be lower (40% to 60%) in elk older than 16 years (Figure 9; Cook et al. 2004b, White and Garrott 2005a, Proffitt et al. 2014, MacNulty et al. 2016, 2020b). Yearling pregnancy rates were relatively low (less than 22%) like pre-wolf rates (Proffitt et al. 2014). Pregnancy rates of yearlings were lower after they survived a severe winter as a calf and decreased as elk density on the winter range increased (Proffitt et al. 2014). Adult pregnancy rates were unaffected by elk density but varied among years, possibly due to persistent drought conditions from the late 1980s to the mid-2000s (Cook et al. 2004b).

In animals with polygynous mating systems, such as elk, adult males compete for breeding opportunities and successful bulls can produce many offspring. Thus, some scientists predicted females would produce more male offspring when forage was good and maternal body condition high (Trivers and Willard 1973). However, female elk in northern Yellowstone produced more female offspring under these circumstances. At higher elk densities, there were similar portions of female and male offspring (Cunningham et al. 2009). With more female offspring, population growth should increase because females have higher survival rates than males and often begin successfully breeding in their second year (Cunningham et al. 2009). In contrast, males usually do not successfully breed until 4 years or older and their survival is much lower due to their larger body size and higher resource requirements, as well as the energetic and physical costs of fighting for breeding opportunities. While breeding males produce many young, less males survive to reproduce (Cunningham et al. 2009).

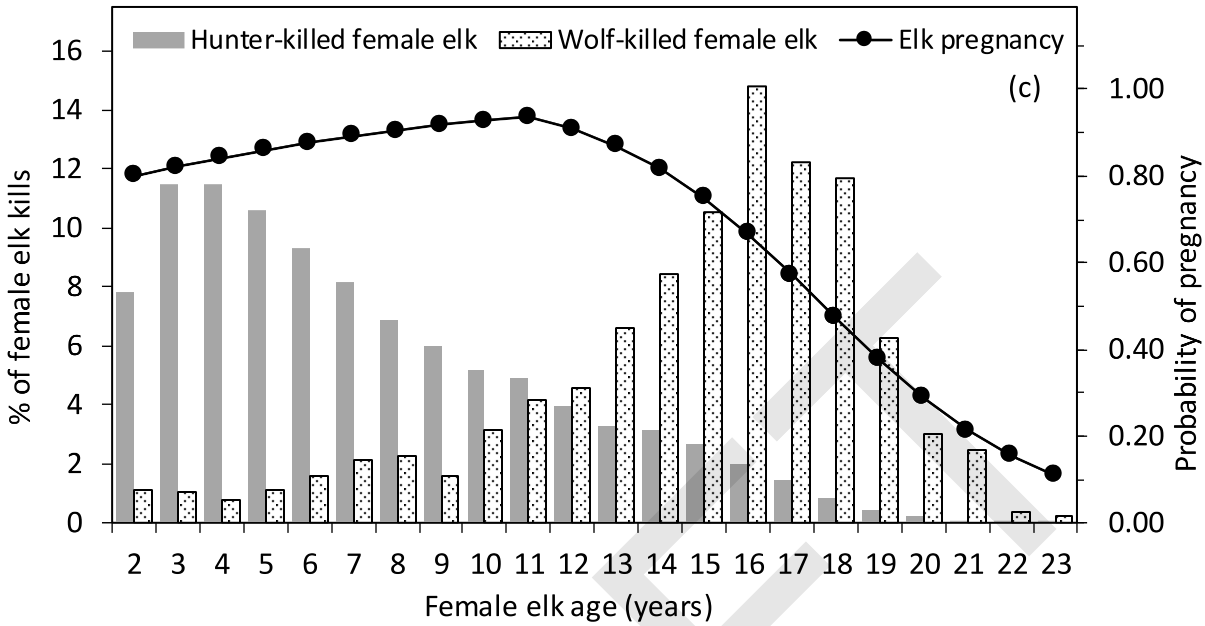


Figure 9. *Age distribution of 892 adult female elk killed by wolves during 1995 to 2016 and 6,869 adult female elk killed by humans during the late season hunt, 1996-2009 (left vertical axis) in relation to average age-specific pregnancy probability derived using mixed effects logistic regression of data from 301 adult females during 2000 to 2018 (right vertical axis). Harvest data are from Wright et al. (2006) and Montana Fish, Wildlife and Parks and wolf-killed elk and pregnancy data from the National Park Service.*

Causes of Death

Mortality of 112 radio-collared, adult, female elk in the northern Yellowstone area from 2000 to 2016 was due to predation (primarily by wolves; 61%), harvest (19%), starvation (6%), and unknown causes (14%; Smith 2021).

Predation—Multiple large predators killed a substantial number of elk, primarily calves and older adults. Black and grizzly bears were the main cause of death for newborn calves, primarily during the first 2 weeks after birth when calves were in their hiding phase (Barber-Meyer et al. 2008, Griffin et al. 2011). Bear predation then decreased to almost zero in another 2 weeks as females and calves congregated into mobile groups (Singer et al. 1997, Barber-Meyer et al. 2008). Cougars and wolves also took some newborn calves but increased predation through the summer and winter (Ruth et al. 2019, Stahler et al. 2020). As a result, the survival of elk calves decreased and varied less among years after wolf recovery, indicating predation limited recruitment and contributed to regulating population size (White and Garrott 2005a, Proffitt et al. 2014, MacNulty et al. 2020b, Smith 2021). In addition, estimates of survival rates (83%) of prime-aged adult female elk 1 to 15 years old during 1996 to 2002 were much lower than the rate of 99% during 1969 to 1975 when there were much lower harvests of antlerless elk and fewer predators (Houston 1982, Evans et al. 2006, Wright et al. 2006, Eberhardt et al. 2007). Estimates of wolf predation were greater than 1,000 elk and surpassed harvests by 2003 (White and Garrott 2005a, Eberhardt et al. 2007).

Harvest—The proportion of the northern Yellowstone elk population harvested in Montana each year during late-season hunts was strongly influenced by weather because more elk migrated outside the park as snowpack increased at higher elevations (Vucetich et al. 2005, White and Garrott 2005a). Thus, harvests were proportional to the number of elk spending winter north of the park (White and Garrott 2005a). Late-season hunters selected adult female elk, primarily prime-aged females (50% to 64% from 1996 to 2001) instead of calves (11% to 13%) or yearlings (5% to 14%) due to the larger amount of meat (Figure 9; Wright et al. 2006). The number of female elk harvested during the late-season hunt remained high (1,300 each winter) after wolf reintroduction (1996 to 2004) like harvests (1,150 each winter) before wolves (1987 to 1995; White and Garrott 2005a, Evans et al. 2006). These consistent and efficient harvests increased the mortality of prime-aged females and contributed to about a 6% decrease in elk abundance per year during 1995 to 2004 (White and Garrott 2005a, Evans et al. 2006, Wright et al. 2006). Montana Fish, Wildlife and Parks reduced the number of hunting permits for adult female elk by 72% from 1997 to 2004 and eliminated this harvest by 2010 to curtail this decrease (Evans et al. 2006, Wright et al. 2006, Montana Fish, Wildlife and Parks 2019).

Starvation—Environmental factors, such as unpredictable variations in weather conditions, rarely affect prime-aged adults but can have a strong influence on calves and older elk (Houston 1982, Sæther 1997, Merrill and Boyce 1991, Garrott et al. 2003). During winter, deep snowpack at higher elevations restricts the foraging area for elk and increases the energetics costs of obtaining forage (Houston 1982, Robbins 1993). These effects intensify when elk density is high and there is more competition for limited food (Houston 1982, Coughenour and Singer 1996, Singer et al. 1997). Such conditions frequently occurred in the Madison headwaters area in west-central Yellowstone, with most calves starving during winters with severe snowpack (Garrott et al. 2003, 2009b). Such conditions also occurred in northern Yellowstone during the winter of 1997, which contributed to significant mortality of calves and older adults via starvation and increased predation (Eberhardt et al. 2003, White and Garrott 2005a).

During 1988, precipitation in northern Yellowstone during winter and summer was about 30% of normal, which contributed to 50% less grass production and earlier drying (senescence) of this forage (Singer et al. 1989). Large fires burned about 39% of the area and killed 1% of the elk population (about 250 animals) from smoke inhalation (Singer et al. 1989). Surviving elk moved to winter ranges about 4 to 6 weeks early, with 54% of the population migrating outside the park (Singer et al. 1989). The severe drought and winter conditions contributed to about 25% of the population starving and 15% being harvested. For comparison, less than 5% of the population starved during the two preceding winters (Singer et al. 1989). Carcasses consisted of about 46% calves, 33% adult females, and 21% adult males (Lemke and Singer 1989, Coughenour and Singer 1996). Biologists estimated 83% of calves, 60% of adult males, and 14% of adult females died during the winter (Lemke and Singer 1989, Coughenour and Singer 1996). Elk surviving the winter were in poor condition which resulted in calves born later in spring, at lighter weights (-3.7 pounds; -1.7 kilograms), and with 50% lower survival (Singer et al. 1989, 1997). Even under high predator abundance, environmental conditions still result in the starvation of elk each winter (Garrott et al. 2003, 2009c).

Diseases—In the late 1800s and early 1900s, some elk in Yellowstone had a scab disease on their skin, possibly brought into the region by domestic sheep. This disease was likely psoroptic scabies, or mange, which is caused from infestation by a parasitic skin mite and spreads by direct contact from one elk to another (Seton 1898, 1927; Skinner 1928). Infestations are usually mild but severe cases can result in fur loss across large portions of the body. This disease is still observed in northern Yellowstone elk and severe infestations sometimes contribute to deaths during winter, primarily in older animals or those in poor nutritional condition (Houston 1982). In addition, sampling of adult females during 2000 to 2005 detected antibodies for bovine-viral-diarrhea type 1 and bovine parainfluenza-3 in 24% and 70% of animals, respectively (Barber-Meyer et al. 2007). Bovine-viral-diarrhea virus can cause intestinal, reproductive, and respiratory illnesses in cattle, while parainfluenza can cause pneumonia in severe cases. Fifty-eight percent of sampled elk calves had antibodies for infectious-bovine rhinotrachetis, which is highly contagious and results in inflamed respiratory passages (Barber-Meyer et al. 2008). However, biologists did not observe any physical signs of these diseases in the elk population.

Adult male elk with mange in Yellowstone National Park. Photograph by John Good, National Park Service.

Chronic wasting disease (CWD) is a contagious, fatal disease of deer, elk, and moose. It has spread north across the State of Wyoming and into Montana during the past 20 years. The disease is in deer populations east and north of the park and some animals from these populations migrate into the park during summer. CWD is a prion disease, like mad cow disease in cattle, scrapie in goats and sheep, and Creutzfeldt-Jakob disease in humans (Williams et al. 2002). It appears to be caused by the accumulation of misfolded variants of prion, a protein in mammals, which over time causes degeneration of the nervous system and ultimately death (Williams et al. 2002). CWD is transmitted when animals contact infected blood, saliva, or particles in carcasses, soil, or vegetation (Johnson et al. 2006, Mathiason et al. 2006, Tamgüney et al. 2009). Animals become infectious within a few months and can remain alive for almost 2 years (Miller et al. 2008). Infected animals appear normal initially, but as infection progresses, they lose weight, drink and urinate more frequently, drool excessively, and exhibit a wide-based stance with lowered head and ears and a blank facial expression (Williams et al. 2002). These signs are not specific to CWD, however, and a conclusive diagnosis requires laboratory testing of brain or lymph nodes from dead animals or obtaining a biopsy of tonsil or rectal tissue from anesthetized, live animals (Spraker et al. 2002, Wolfe et al. 2002).

There is no vaccine or known treatment for CWD and, as a result, no strategy has successfully eradicated the disease from a large area (Williams et al. 2002). Epidemics last decades and their effects on ungulate populations are still being investigated. Deer populations with a high prevalence of CWD (greater than 20%) in females experienced short-term decreases in abundance due to decreased adult female survival (Miller et al. 2008). However, high prevalence did not spread across larger, regional areas (Monello et al. 2014, Geremia et al. 2015a). If CWD causes widespread reductions in deer and elk abundance in the Greater Yellowstone Area, it could adversely affect ecosystem processes, predators and scavengers, and the regional economy based on recreation and tourism (Treanor et al. 2021). Some research suggests predators have the potential to reduce prevalence of CWD by selectively removing diseased individuals (Krumm et al. 2010, Wild et al. 2011). However, this effect is believed to be dependent on predators' selection for prey age and disease severity, which has yet to be demonstrated (Brandell et al. 2022).

Survival

The probability an elk is still alive at some future time, such as 1 year later, is called the survival rate which, historically, biologists reported as a proportion or percentage of animals surviving (Caughley and Sinclair 1994). More recently, survival is usually modeled and described as a probability in a way that controls for bias caused by unknown fates (Skalski et al. 2005). The likelihood of survival from year-to-year depends on an elk's age. It is relatively low from birth through the first year of life but quickly increases to a maximum when animals reach adult body size; survival then remains high through prime age after which it decreases (Eberhardt 2002, MacNulty et al. 2020b, Smith 2021). Biologists estimated the survival rates of northern Yellowstone elk by fitting newborn calves with ear tag transmitters and adult females with either very high frequency (VHF) or GPS radio collars. Adult males were not collared due to the substantial swelling of their necks during the autumn breeding period and, also, because females are considered the most important component of the population given the polygynous breeding system. Biologists tracked elk with VHF collars from the air or ground several times per month, while GPS collars collected locations at 1- to 6-hour intervals. The tags and collars contained sensors that changed the pattern of the transmitted radio signal when they were immobile for 6 to 8 hours, suggesting the animal had died. Biologists located dead animals and examined the remains to determine the causes of death. They also estimated the ages of elk based on incisor irruption patterns, tooth wear, or extracting a vestigial canine and counting the annual rings of cementum in the root like annual growth rings in a tree (Hamlin et al. 2000). In addition, hunters returned collars from harvested elk.

The maximum lifespan of adult elk in northern Yellowstone was 26 years old for adult females and 14 years old for adult males (Hoy et al. 2020, Smith 2021). Prior to predator recovery, the probability of an elk in Yellowstone dying primarily was related to its age, body condition, and snowpack (Houston 1982, Barmore 2003, Garrott et al. 2003, 2009b, 2020). The primary cause of death was starvation, and younger and older elk were more likely to die than elk in the prime of their life (Houston 1982, Coughenour and Singer 1996, Barmore 2003, Garrott et al. 2003, 2009b, 2020). This mortality increased as elk density and competition for forage increased (Houston 1982, Barmore 2003, Coughenour and Singer 1996, Singer et al. 1997). Predation on some early newborn calves was followed by a period of relatively high survival until some starved during late winter (Houston 1982, Singer et al. 1997). Thereafter, survival remained high (greater than 90%) for females until they reached about 15 years of age, and their worn teeth could no longer crop and break apart forage efficiently (Houston 1982, Coughenour and Singer 1996, Garrott et al. 2003, Eberhardt et al. 2007). Females then experienced progressive nutritional deprivation and eventually succumbed to starvation. A life table constructed from males removed from the population during 1951 to 1967 indicated high survivorship from 1 to 5 years with increased mortality from 6 to 10 years and a rapid decrease in survivorship thereafter (Houston 1982). Few males lived longer than 10 to 12 years (Houston 1982).

The resumption of intense harvests of female elk during the 1980s to 2000s was a primary driver of elk population trends by substantially increasing the mortality of prime-aged elk 2 to 14 years old (Eberhardt et al. 2003, 2007; Vucetich et al. 2005, White and Garrott 2005a, Wright et al. 2006, Brodie et al. 2013, MacNulty et al. 2016, 2020b; Smith 2021). Differences in annual snowpack and migrations outside the park led to variations in the extent of harvests and adult female mortality among years and accounted for about one-half of the variation in the growth rate of the elk population (Vucetich et al. 2005, White and Garrott 2005a). These harvests were gradually curtailed between 2000 and 2008 following a precipitous decrease in elk counts from 1995 to 2004 (White and Garrott 2005a, Eberhardt et al 2007).

Following wolf reintroduction, the survival rates of adult female elk decreased from about 99% to between 82% and 92% due to a combination of predation and intense hunter harvest of prime-aged females during the late-season hunt in Montana (White and Garrott 2005a, Evans et al. 2006, Wright et al. 2006). Survival rates from 1996 to 2004 were quite constant for elk aged 3 to 16 years old but decreased rapidly at older ages (White and Garrott 2005a, Evans et al. 2006, Wright et al. 2006). Most deaths occurred from December through March and annual mortality rates were about equal for predation and harvests (Evans et al. 2006). In combination, hunting and predation removed about 20% of the adult females from the population each year (Evans et al. 2006). After 2004, survival rates were very high (95% to 100%) in adult female elk 2 to 9 years old, remained high in females 10 to 14 years old (95% to 80%), and decreased rapidly to between 65% and 25% in older females (Figure 10; MacNulty et al. 2016, 2020b, Smith 2021). Despite decreasing survival rates with increasing age, some individuals' stories demonstrate the resiliency of this species in Yellowstone. For example, one female elk that was radio-collared in 2011 at the age of 16 survived until she was 25½ years old. This female was born in the summer of 1994, one year prior to wolf reintroduction, and survived a quarter century of carnivore recovery and predation risk in northern Yellowstone. Eventually, wolves killed her in the winter of 2020.

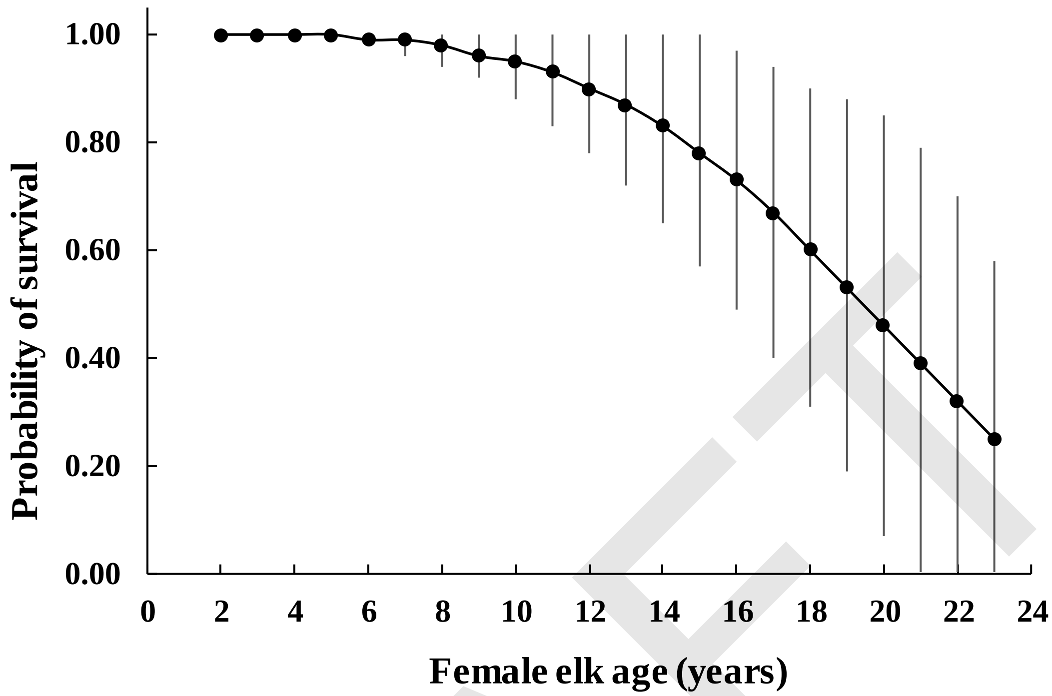


Figure 10. *Average age-specific probability of survival from one age to the next of 281 radio-collared adult female elk during 2000 to 2016. Data from Smith (2021).*

Annual survival rates of calves were similar during summer (72%) and winter (65%) from 1987 to 1990 (Singer et al. 1997). Predation by bears and coyotes during summer was the largest cause of mortality (44%), followed by malnutrition and starvation (23%) during winter (Singer et al. 1997). Other causes of death included stillbirths, starvation, drowning in swift rivers, accidents, and avian predators (Singer et al. 1997). The limited amount of predation reduced elk numbers but was not sufficient to regulate the size of the population (Singer et al. 1997, Barber-Meyer et al. 2008). Both summer and winter survival of calves and, in turn, recruitment decreased as the number of elk in the population and competition for food resources increased (Houston 1982, Barmore 2003, Coughenour and Singer 1996, Singer et al. 1997, Taper and Gogan 2002). Limited food resources reduced the body condition of pregnant females and contributed to smaller calves susceptible to increased predation and malnutrition (Houston 1982, Singer et al. 1997, Cook et al. 2004a). In addition, occasional severe weather conditions, such as the severe drought in 1988 and snowpack in 1997, limited forage availability and substantially reduced calf survival as many died of starvation (Coughenour and Singer 1996, Singer et al. 1997, White and Garrott 2005a). Biologists detected similar results in the Madison headwaters population where extended winters with deep snows killed most calves by starvation (Garrott et al. 2003, 2009b).

Only about 30% of elk calves survived through summer in northern Yellowstone from 2003 to 2005 compared to 65% from 1987 to 1990 prior to the restoration of bears, cougars, and wolves (Singer et al. 1997, Barber-Meyer et al. 2008). The percentage of calves with transmitters that were killed by any predator were 63% during 2003 to 2005 compared to 22% from 1987 to 1990 (Singer et al. 1997, Barber-Meyer et al. 2008). The survival of newborn elk to 3 months of age increased following higher spring precipitation with nutritious grass growth during the lactation period (Griffin et al. 2011). Conversely, survival decreased following drought conditions the previous summer that decreased the body condition of mothers (Griffin et al. 2011).

Recruitment

The number of calves that are produced and survive has a big influence on elk population trends (Raithel et al. 2007). The annual birth pulse adds a few thousand calves to the northern elk population each spring which would rapidly increase abundance if most survived. However, calves are extremely vulnerable to predation and unpredictable weather conditions, such as deep snowpack (Coughenour and Singer 1996, Singer et al. 1997, Garrott et al. 2003, 2009b). As a result, a large portion of calves die during their first year if conditions are not favorable or elk density is high with more competition for forage (Coughenour and Singer 1996). Calves that survive until their first birthday are considered ‘recruited’ into the adult population, which biologists report as a ratio such as 30 calves per 100 adult females or 0.30 calves per adult female (Caughley and Sinclair 1994). Ratios are not ideal for assessing recruitment because they reflect four different processes: adult female survival; pregnancy; birth; and calf survival (MacNulty et al. 2016). However, ratios can be a decent index of recruitment when adult female survival and pregnancy rates remain high and relatively constant (Lukacs et al. 2018).

During population reduction efforts from 1930 to 1967, prime-aged adult female elk in northern Yellowstone had high pregnancy (91%) and survival (99%; Kittams 1953, Houston 1982, Barmore 2003). Most females produced a single calf each year and there were about 90 calves per 100 adult females at birth (Kittams 1953, Houston 1982, Barmore 2003). However, this ratio decreased to an average of 32 calves per 100 adult females (range = 16 to 49) after 6 to 9 months due to predation in summer and starvation in winter (Houston 1982). After the cessation of culling in the park and with low harvests in Montana, recruitment increased to an average of about 37 calves per 100 adult females (range = 25 to 47) from 1968 to 1975 (Houston 1982). When the late-season hunt resumed in 1976 and focused on antlerless elk after 1983, recruitment decreased to an average of 25 calves per 100 adult females (range = 6 to 44) until 1995 (Houston 1982, Coughenour and Singer 1996, Taper and Gogan 2002). There was a decreasing trend in recruitment as elk density on the winter range increased (Figure 11; Houston 1982, Coughenour and Singer 1996, Taper and Gogan 2002, Proffitt et al. 2014, MacNulty et al. 2016, 2020b). In addition, there was high variability in recruitment among years due to weather, primarily summer precipitation and winter snowpack (Houston 1982, Coughenour and Singer 1996, White and Garrott 2005a, Proffitt et al. 2014). When forage conditions were favorable and winters mild, recruitment was relatively high and contributed to rapid population growth. Conversely, when severe winter conditions limited forage availability, recruitment was poor and elk abundance decreased (Houston 1982, Coughenour and Singer 1996, White and Garrott 2005a). During the winter of 1989, after a severe drought and large fires, only about 6 calves per 100 adult females survived (Singer et al. 1989, Coughenour and Singer 1996, White and Garrott 2005a).

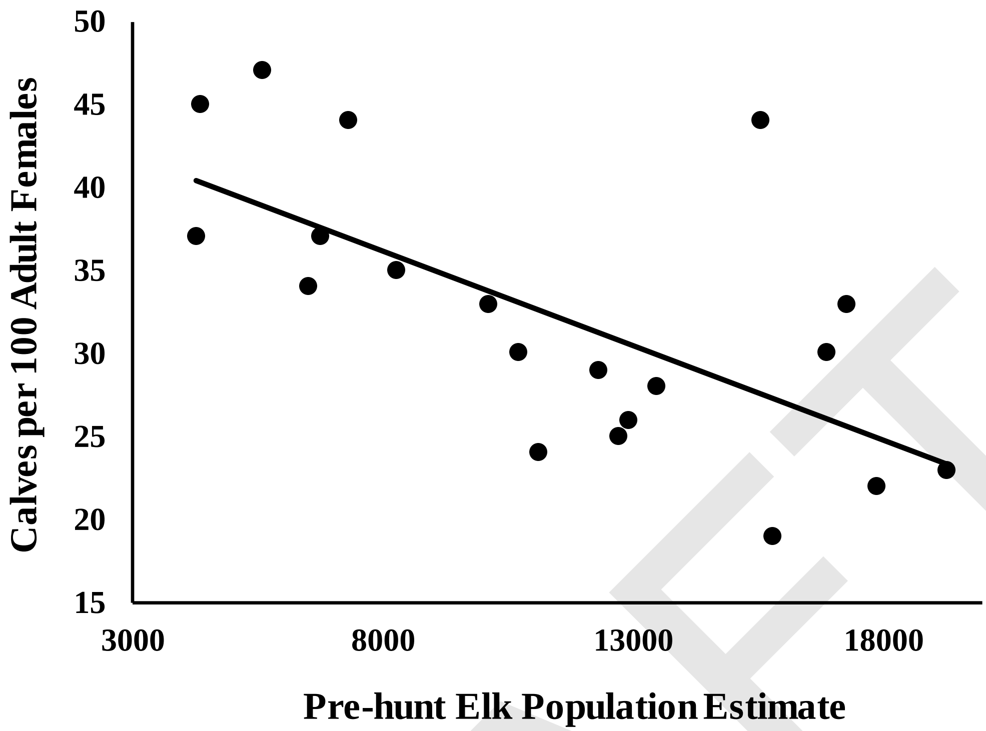


Figure 11. *Decreasing trend in the recruitment of northern Yellowstone elk from 1956 to 1995 as the number of elk on the winter range increased. Data are from Houston (1982), Coughenour and Singer (1996), Singer et al. (1997), Taper and Gogan (2002), and the Northern Yellowstone Cooperative Wildlife Working Group.*

After predator restoration, prime-aged adult female elk retained high pregnancy (90%) and relatively high survival rates (85%; White and Garrott 2005a, Evans et al. 2006, Wright et al. 2006, Eberhardt et al. 2007, MacNulty et al. 2016, 2020b). The calf to adult female ratio at birth likely was somewhere around 77 calves per 100 adult females. By the end of winter, however, this ratio decreased to an average of 20 calves per 100 adult females (range = 11 to 34) from 1996 to 2009 (Figure 12; Montana Fish, Wildlife and Parks 2019). This trend continued from 2010 to 2021 with an average of 19 calves per 100 adult females (range = 11 to 27; Montana Fish, Wildlife and Parks 2019, 2021c). Recruitment was significantly lower and less variable among years due to the consistent harvests of prime-aged females during the late 1990s and killing of calves by multiple large predators (White and Garrott 2005a, Evans et al. 2006, Wright et al. 2006, Middleton et al. 2013b, Proffitt et al. 2014, Garrott et al. 2020, MacNulty et al. 2020b, Smith 2021). Recruitment decreased as numbers of bears, cougars, and wolves increased (Hamlin et al. 2009, Proffitt et al. 2014).

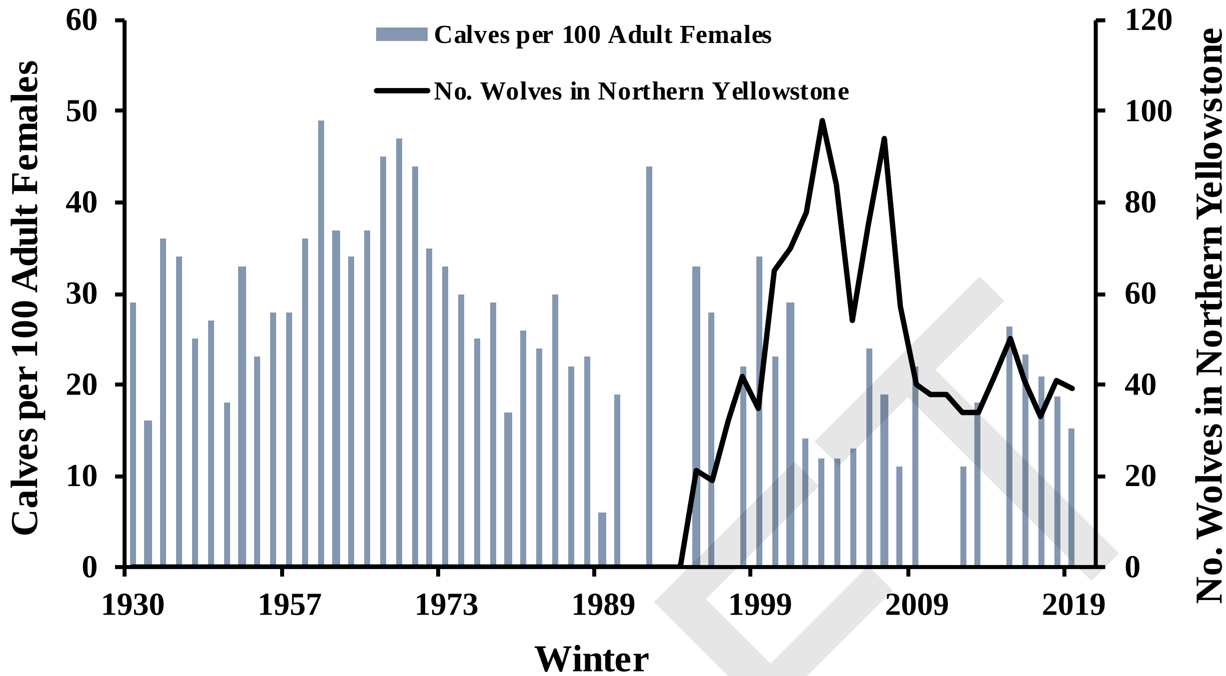


Figure 12. *The number of wolves in northern Yellowstone and calves per 100 adult female elk (index of recruitment) on the northern winter range in Yellowstone National Park and nearby areas of Montana from 1930 to 2020.*

Age Distribution

The average age of adult female elk harvested from the northern Yellowstone population during late-season hunts in Montana was 6 to 7.5 years during 1985 to 1995 but increased to 7 to 9 years during 1996 to 2009 (Montana Fish, Wildlife and Parks 1996-2009; Wright et al. 2006, Proffitt et al. 2014). Likewise, the portion of elk more than 14 years old in the population increased from about 5% in 1997, after wolves were reintroduced, to about 20% in 2007 (Montana Fish, Wildlife and Parks 1996-2009; Figure 13). An increase in the average age of adults, or the portion of older adults, could decrease average pregnancy rates and increase the impact of wolf predation on population growth, thereby contributing to a decreasing trend in elk abundance (Proffitt et al. 2014, Hoy et al. 2020, MacNulty et al. 2020b, Smith 2021).

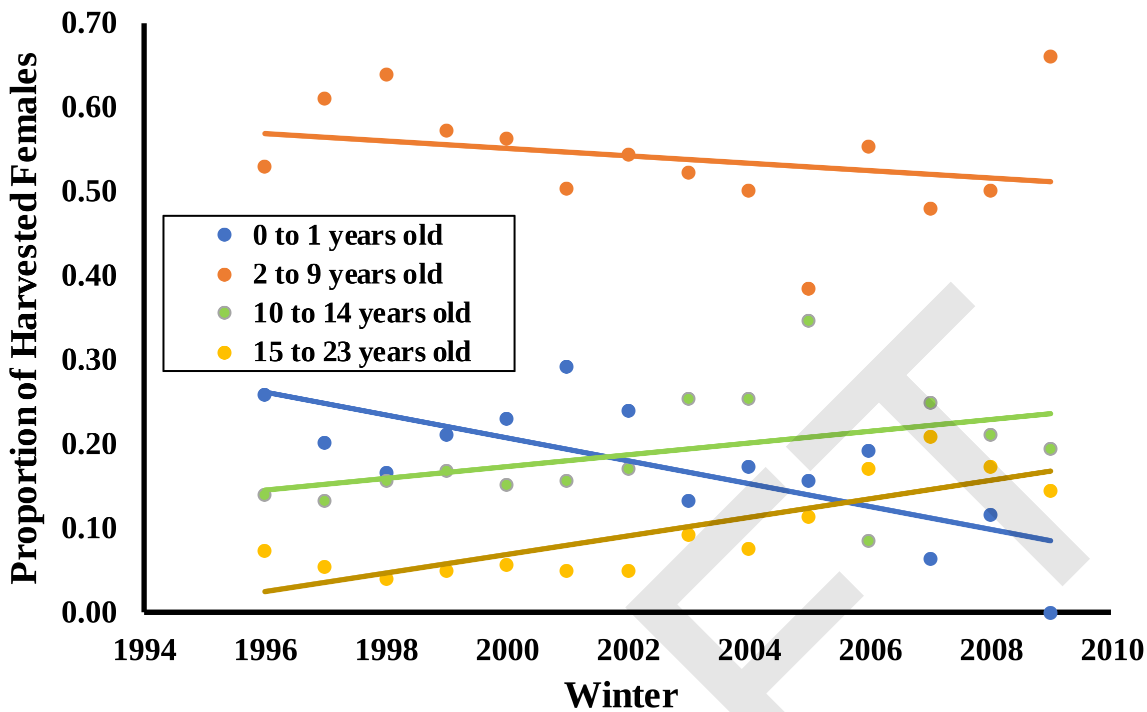


Figure 13. *Age distributions of 8,698 adult female elk harvested from the northern Yellowstone population during the late-season hunt from January to mid-February 1996 to 2009. The harvest trends show a significant decrease in the portion of immature females (blue line), a high and relatively constant portion (50% to 65%) of young females (red line), and a significant increase in the portion of older females (green and brown lines) in the harvest. Data is from Tom Lemke (retired), Montana Fish, Wildlife and Parks, 1996-2009.*

Emigration and Immigration

Most animals born into a population remain within the range used by their parents (Stenseth and Lidicker 1992). As the density of animals increases, however, there are fewer resources such as food available for each animal (Caughley and Sinclair 1994). This situation eventually contributes to lower nutrition, body condition, reproduction, and survival unless animals disperse or expand their range (Stenseth and Lidicker 1992). As a result, some individuals, usually beginning with adult male elk in northern Yellowstone, leave their natal range and move to a different area, after which they are followed by females with calves (Houston 1982). This behavior, called emigration or dispersal, occurs when an animal moves from one area to another without returning (Caughley and Sinclair 1994). Dispersal can contribute to range expansion for the population or gene flow to a neighboring population.

Dispersal occurs in the northern Yellowstone elk population as animals intermingle with groups of elk from other populations on summer ranges within the park and then accompany them to separate winter ranges outside the park. However, it appears to be relatively infrequent (Houston 1982). About 3% of elk tagged on the northern winter range from the 1920s to the 1970s subsequently dispersed to winter ranges used by the Cody, Clarks Fork, Gallatin, Madison, and Jackson populations in later years (Kittams 1963 as cited in Houston 1982; Craighead et al. 1972). Likewise, 1% of calves born in northern Yellowstone and fitted with ear tag transmitters during 2003 to 2005 dispersed as yearlings to winter ranges used by the Clarks Fork, Gallatin, and Jackson populations (Barber-Meyer et al. 2008).

Conclusions

Liberal harvests of prime-aged female elk, with high recruitment when environmental conditions were favorable, were the predominant factors influencing population trends from 1985 through the 1990s (Eberhardt et al. 2003, 2007; Vucetich et al. 2005, White and Garrott 2005a, MacNulty et al. 2020b, Smith 2021). The resumption of liberal late-season hunts with a focus on antlerless elk decreased adult female survival (White and Garrott 2005a, Evans et al. 2006, Wright et al. 2006). As predator numbers and predation increased, state managers eventually reduced and then eliminated most late-season harvest permits to offset the increase in predation and increase elk recruitment (Evans et al. 2006, Wright et al 2006, Montana Fish, Wildlife and Parks 2019). This substantial decrease in the mortality of prime-aged females stemmed the precipitous decrease in elk abundance and led to an increase in population growth from 2011 to 2016 (MacNulty et al. 2020b, Smith 2021).

The main effects of wolves and other predators in decreasing numbers of northern Yellowstone elk were a consistent reduction in recruitment and predation on older adults which comprised an increasing portion of the population during the 1990s and 2000s (Eberhardt et al. 2007, Raithel et al. 2007, Griffin et al. 2011, Proffitt et al. 2014, MacNulty et al. 2016, 2020b; Lukacs et al. 2018, Hoy et al. 2020, Smith 2021). About one-half of the elk killed by wolves were calves and the substantial reduction in recruitment contributed to an older age structure with reduced productivity and more vulnerability to predation (Smith et al. 2004, Wright et al. 2006, Metz et al. 2012, 2020a,b; Proffitt et al. 2014, MacNulty et al. 2016, 2020b; Hoy et al. 2020, Smith 2021). The interacting effects of severe weather, such as drought and deep snowpack, made individuals even more susceptible to predation, especially in the 10- to 15-year-old range (Brodie et al. 2013, Smith 2021). The pregnancy rate of some older elk (14- to 18-year-olds) was likely high enough (50% to 80%) for these individuals to have contributed to population growth had they not been killed by wolves (Smith 2021).

Adult male beginning growth of a new set of antlers during spring in Yellowstone National Park. Photograph by Neal Herbert, National Park Service.

Chapter 4
Seasonal Distributions and Movements

Introduction

The temperate, montane climate of Yellowstone is characterized by short, cool summers and long, cold winters (Houston 1982). Snowpack up to 10 feet (3 meters) deep can accumulate in the mountains and on high-elevation plateaus (Newman and Watson 2009, Watson et al. 2009). Elk adapted to this predictable climate pattern by migrating seasonally, with most animals moving to lower-elevation winter ranges in autumn (November) to avoid deep snowpack and returning to higher-elevation ranges in early summer (May-June) following snow melt to obtain emerging, nutritious forage (Skinner 1925, 1928; Rush 1932, Craighead et al. 1972, Middleton et al. 2018, Rickbeil et al. 2019). These movements enhanced reproduction and survival by increasing access to nutritious foods to support lactation and restore body condition during summer and reducing energetic costs and increasing the survival of their smaller calves during winter (Merrill and Boyce 1991, Singer et al. 1997, Cook et al. 2004b, Middleton et al. 2013b, 2018). In addition, migration increased the survival of newborn elk by increasing the condition of their mothers during late pregnancy and lactation, which resulted in larger calves at birth and higher growth rates (Cook et al. 2004a, 2013; Parker et al. 2009).

Historically, the winter range for northern Yellowstone elk extended perhaps 30 miles (48 kilometers) north of the boundary of Yellowstone National Park into the Paradise Valley of Montana (Rush 1932, Cahalane 1941, Craighead et al. 1972, Houston 1982). By the late 1800s, however, the valleys and foothills north of the park were occupied by ranches and settlements with fences and intense hunting impeding migratory movements by elk out of the park and into these areas (Skinner 1925, 1928; Rush 1932; see Chapter 2). Though migration outside the park increased again by the 1920s, liberal harvests (firing lines) along the park boundary during the 1910s to the 1950s, followed by intense management culls in the park through the 1960s, led to most elk spending winter in the park (Skinner 1928, Rush 1932, Houston 1982, Barmore 2003). Elk occupied a winter range of about 300 to 350 square miles (78,000 to 90,000 hectares) from the upper Lamar Valley in Wyoming to the Gardiner basin in Montana (Rush 1932, Houston 1982, Barmore 2003). When numbers of elk were kept below 10,000 only about 15% to 30% of the population migrated outside the park into the Gardiner basin and surrounding mountains, ranging from 10% in mild winters to 60% in severe winters (Houston 1982, Barmore 2003, Coughenour and Singer 1996).

Northern Yellowstone elk moving across a mountain pass in Yellowstone National Park. Photograph by Jacob W. Frank, National Park Service.

Another consequence of the park's elk reduction program from the 1930s through the 1960s was the elimination several migration routes. At least 8,000 elk reportedly migrated from winter ranges in northern Yellowstone through Dunraven Pass near Mount Washburn to summer ranges in the Hayden and Pelican valleys of central Yellowstone and further south during the early 1900s (Skinner 1925, Craighead et al. 1972). Culls during the early 1960s removed large numbers of elk that used this route, though biologists subsequently detected an increase in numbers migrating along this route after culling ceased (Craighead et al. 1972). In addition, a segment of the northern population migrating up Slough Creek to the Buffalo Plateau was nearly eliminated by reductions in the early 1960s (Craighead et al. 1972). Reductions also may have removed another segment of the elk herd that moved from the Blacktail Deer Plateau north out of the park during winter (Craighead et al. 1972).

When managers ceased culling elk in the park by the 1970s, they anticipated elk would reestablish their traditional migratory routes north of the park (Houston 1982, Taper and Gogan 2002). To identify migration pathways and strategies and inform protection and restoration actions, biologists assessed the movement patterns of northern Yellowstone elk from the 1960s to present by fitting thousands of adult females with collars and tracking their seasonal movements (Craighead et al. 1972, Houston 1982). This chapter summarizes what was learned regarding the extent of migration within the northern elk population and some of the implications of that behavior.

Distribution and Spatial Structuring

During the intense population reduction efforts in the 1960s, park rangers captured many thousands of elk in corral traps at various locations in the Yellowstone and Lamar River valleys of northern Yellowstone (Craighead et al. 1972). Biologists fit about 1,450 of these elk with individually identifiable collars (not radio collars) and released them (Craighead et al. 1972). They recorded subsequent observations of these elk from the ground or in airplanes and helicopters to identify their summer distributions and learn about their migratory movements (Craighead et al. 1972). Major winter ranges in the park were below 7,500 feet (2,285 meters) elevation and, from lower elevations in the west to higher elevations in the east, included the Stephens Creek area near the northern boundary in the Gardiner basin, Blacktail Deer Plateau, Cottonwood Creek to Hellroaring Creek, Little Buffalo Creek to Slough Creek, Crystal Creek, and the Lamar Valley to Cache Creek (Craighead et al. 1972, Houston 1982, Barmore 2003).

During early summer, elk in the northern Yellowstone population migrated to areas above 7,500 feet throughout the park (Rush 1932, Craighead et al. 1972, Houston 1982). Elk that spent winter at lower elevations in the Yellowstone River valley (Gardiner basin) tended to spend summer in the western part of the park (Craighead et al. 1972). About 90% of these elk were sighted in the Joseph Peak and Mount Holmes areas in the northwestern portions of the park (Figure 14). Almost all elk that spent winter at higher elevations in the Lamar River valley moved to summer ranges in the eastern two-thirds of the park (Craighead et al. 1972). These elk used three principal migration routes to reach their summer ranges: 1) from the Blacktail Deer Plateau across the Washburn Range to the Hayden and Pelican valleys; 2) from the Tower Junction and Specimen Ridge areas across Dunraven Pass near Mount Washburn to Canyon and the Hayden Valley; and 3) from Slough Creek and the Lamar Valley across Specimen Ridge and the Mirror Plateau to the Pelican Valley (Craighead et al. 1972). Some elk continued south from the Hayden and Pelican valleys along the east side of Yellowstone Lake to the Mount Stevenson and Two Ocean Plateau areas in the southern part of the park (Craighead et al. 1972).

Elk respond to local snow conditions by occupying areas with lower snow depths or water content. However, they necessarily use areas with more snowpack as snow accumulates during severe winters (Messer et al. 2009). Elk also respond to higher densities of elk on the winter range by moving across larger areas to access forage (Anderson et al. 2005). Elk began to reestablish migration routes north of the park during 1976 to 1986 following the cessation of intense culling in the park and harvests in nearby areas of Montana (Houston 1982, Vore 1990, Lemke et al. 1998, MacNulty et al. 2020b). Some of these migrations extended more than 19 miles (30 kilometers) north of the present park boundary into the southern Paradise Valley, which biologists had not observed since the 1930s (Kittams 1953, Vore 1990, Lemke et al. 1998). Elk eventually occupied a winter range of about 590 square miles (153,000 hectares), with about 35% of the range north of the park (Lemke et al. 1998). This expansion likely facilitated an increase in the size of the population due to access to more resources (Coughenour and Singer 1996, Eberhardt et al. 2003, 2007).

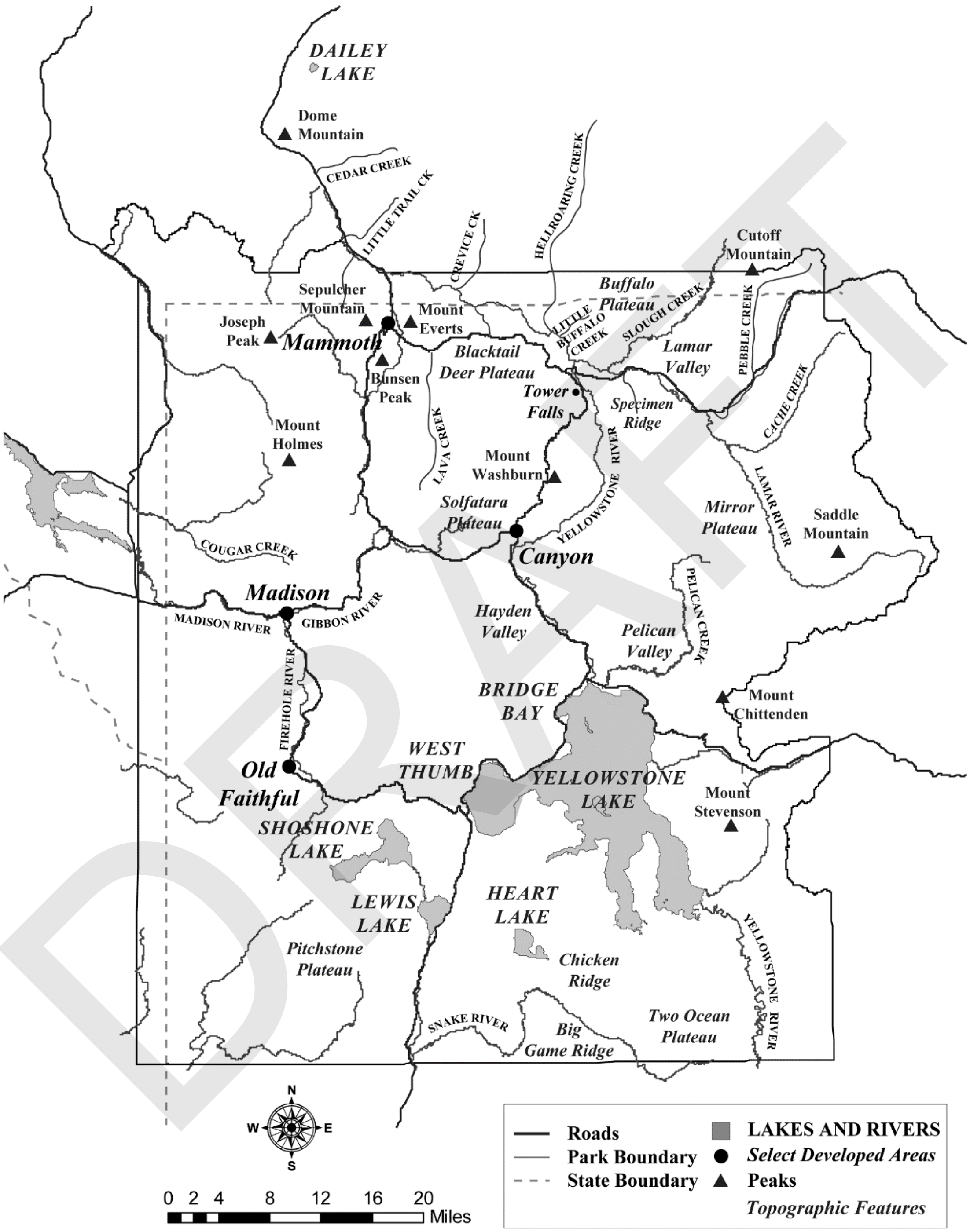


Figure 14. *A map of Yellowstone National Park and nearby areas of Montana with geographic features and names of places used by northern Yellowstone elk during summer and winter (White et al. 2010).*

Migration Patterns

Northern Yellowstone elk are partially migratory with most animals moving seasonally between summer and winter ranges and others remaining on the same range year-round (Craighead et al. 1972, Houston 1982, Vore 1990, White et al. 2010). Snow melt occurs earlier at lower elevations, so there are earlier foraging opportunities on new grass growth with less energetic costs while higher-elevation summer ranges are still covered with snow (Thein et al. 2009). Spring migrations by 140 radio-collared female elk in northern Yellowstone during 2000 to 2008 generally began in late April to mid-May but varied among years based on the severity and duration of the previous winter which, in turn, affected snow melt and the growth of new forage (White et al. 2010). Migration was delayed by several weeks following winters with high snowpack but commenced sooner with earlier melt-out and vegetation green-up (White et al. 2010). New grass growth begins about 100 days earlier in the lower-elevation valleys than in the highest-elevation mountains (Thein et al. 2009, Wilmers et al. 2013). Thus, elk that spent winter north of the park in the Gardiner basin and southern Paradise Valley initiated their migrations and began tracking grass green-up about 1 to 2 weeks earlier than elk at higher elevations on the winter range inside the park (White et al. 2010).

Elk initially followed the green-up of vegetation, called the green wave, as snow progressively melted at higher elevations, but many elk then quickly moved long distances across snow-covered areas to their traditional summer ranges in the park interior, apparently using their spatial memory and experience to anticipate the forthcoming nutritious grass growth in those areas (White et al. 2010, Merkle et al. 2016, 2019; Jesmer et al. 2018, Middleton et al. 2018, Merkle et al. 2019, Rickbeil et al. 2019). Peak growth of grass occurs about 70 days after the onset of growth at lower elevations and 40 days after onset at higher elevations (Thein et al. 2009). Elk selected areas with high plant diversity, including areas burned during the 1988 fires that lacked canopy cover and often contained a variety of grasses and forbs with high forage quality (Boyce et al. 2003, Mao et al. 2005, Barker et al. 2019a,b).

Migrating elk moved between 6 and 93 miles (10 and 150 kilometers; straight-line distance) along the primary migration pathways used during the 1960s to a dozen different summer ranges throughout the park (Vore 1990, White et al. 2010). About 40% of radio-collared elk moved to the eastern portion of the park between Cut-off and Saddle mountains, on the Mirror Plateau and in the Pelican Valley, east of Yellowstone Lake, and south to the Two Ocean Plateau and Big Game Ridge areas (White et al. 2010). Another 40% of the elk moved to the western portion of the park between Joseph Peak and Mount Holmes, on Mount Everts and the Blacktail Deer Plateau, from Cougar Creek to Shoshone Lake, and south to the Pitchstone Plateau (White et al. 2010). Ten percent of the elk moved to Mount Washburn, the Solfatara Plateau, and Hayden Valley in central Yellowstone and another 10% moved north of the park to the Buffalo Plateau (White et al. 2010).

Almost all radio-collared elk that spent winter in the higher-elevation Lamar River valley migrated to summer ranges in the eastern (51%), northern (31%), and central (14%) portions of the park (White et al. 2010). Conversely, most elk that spent winters in the lower-elevation Yellowstone River valley migrated to the western (56%) portion of the park, though others migrated to areas through the entire park (Vore 1990, White et al. 2010). The portion of elk that spent summer in the eastern portion of the park decreased between the 1960s and the mid-1980s, while the portion in the west increased (Craighead et al. 1972, Vore 1990). This trend remained consistent during the 2000s (White et al. 2010).

Fall migration began in late September to mid-October following snow accumulation, with two-thirds of movements starting within 72 hours of a major snowstorm on the summer range

(Houston 1982, White et al. 2010). Elk traveling to winter ranges either in or outside Yellowstone departed at similar times (White et al. 2010). For elk migrating to winter ranges inside the park, the autumn migration lasted about 7 days (White et al. 2010). For elk migrating to winter ranges outside the park, migrations lasted about 43 days (White et al. 2010). Many younger elk with calves moved to lower elevations in and outside the park where snowpack was lower and there was a mix of grassland and shrub steppe habitats interspersed with forests (White et al. 2010, 2012). Similar to the 1960s, elk spent winter in two semi-distinct herd segments (Craighead et al. 1972, White et al. 2010). This spatial segregation, with differences in mortality and recruitment between the herd segments, eventually contributed to a higher portion of the elk population spending winter outside the northwestern portion of the park and summering in the western portion of the park (White et al. 2010, 2012).

Philopatry and Behavioral Flexibility

Elk migration is characterized by fidelity (philopatry) to migration pathways and seasonal ranges with flexibility in the timing of migration to respond to environmental variations, such as weather, and human intrusions, such as hunting (Kittams 1963, Craighead et al. 1972, Houston 1982, Vore 1990, White et al. 2010, Rickbeil et al. 2019). Almost all radio-collared elk monitored during 2000 to 2008 returned to the same summer range each year using the same routes (White et al. 2010). About 60% of these elk used the same winter range each year, but others changed the portion of the northern range they used by 5 to 35 miles (8 to 55 kilometers) between winters (White et al. 2010). Most of these elk moved to lower elevations as winters progressed and snowpack increased, though two elk moved to entirely different winter ranges closer to their summer ranges (White et al. 2010). This flexibility enabled elk to respond to increasing severe winter conditions and forage limitations (White et al. 2010, Rickbeil et al. 2019).

These migration patterns result in northern Yellowstone elk spending fall and winter in areas of variable risk, with hunting in some areas but not others (White et al. 2010, 2012). Northern Yellowstone elk traveling to winter ranges north of the park appeared to delay movements out of the park for several weeks to avoid hunting risk (White et al. 2010). Conversely, elk from the Madison Valley elk population west of the park that spent summer on national forests where hunting seasons occur in autumn began their migrations earlier than animals that spent summer and autumn in protected areas such as the park (Proffitt et al. 2010). Most of these elk spent winter on private lands in the valley that limited or restricted hunting (Proffitt et al. 2010, 2013). These results suggest elk modify their migration timing to reduce hunting risk by varying either the timing of autumn migrations or timing of arrivals onto winter range (Rickbeil et al. 2019).

Few radio-collared females in Yellowstone died during migration or on summer ranges regardless of migration distance and summering area (White et al. 2010). Elk did not appear to modify their migration timing, routes, or use areas after wolf restoration (White et al. 2010). Remaining on familiar terrain enhances forage acquisition, reproduction, and survival, and these benefits likely outweighed the risk of being attacked by wolves, which is negligible for younger adults (MacNulty et al. 2020b). Migration to higher-elevation summer ranges throughout the park distanced elk from the most concentrated area of wolf activity centered around dens on the northern winter range (Fryxell et al. 1988, Mao et al. 2005, Hebblewhite and Merrill 2007, Middleton et al. 2013b, 2018). Migration also lessened, or diluted, individual risk for elk and their calves because on their larger summer ranges they mixed with elk from several other populations that spend winter in different areas outside the park (White et al. 2010, Hebblewhite and Merrill 2007). Similarly, nonmigratory elk in the Madison headwaters area of west-central

Yellowstone did not change their habitat selection during or after wolf colonization (White et al. 2009c).

Changing Migration Strategies

Recent work on elk herds throughout the Greater Yellowstone Ecosystem, including elk from the northern Yellowstone herd, found diversity in migratory tactics ranging from non-migratory, short- and long-distance migrants, and elevational migrants (Zuckerman et al. 2023). On average, about 23% of individual elk changed movement tactics from one year to the next, which may enable greater resiliency to continuously changing environmental and anthropogenic conditions (Zuckerman et al. 2023).

Prior to wolf restoration, as many as 8,000 to 10,000 northern Yellowstone elk spent winter in the park, including 2,500 to 3,500 elk in the upper portions of the Yellowstone and Lamar River valleys (Houston 1982). One segment of the elk population occupied middle to upper elevations in the park, while another occupied lower elevations in and outside the park (Craighead et al. 1972, White et al. 2010). This distribution exposed elk to different risks of mortality after wolf restoration (see Chapter 3; Evans et al. 2006, Wright et al. 2006, Hamlin et al. 2009, White et al. 2012). Wolves encountered and killed elk that spent winters at higher elevations at a higher rate, while elk that spent winters at lower elevations outside the park avoided high densities of wolves but were exposed to hunter harvest (White et al. 2012, Middleton et al. 2013b, 2018; Cusack et al. 2020). After substantial reductions in the harvest of antlerless elk in Montana during the 2000s, elk spending winter outside the park had higher survival rates and recruitment compared to elk spending winter inside the park where predator densities were much higher (Evans et al. 2006, Hamlin et al. 2009, White et al. 2012, Kohl 2019, MacNulty et al. 2020b). As a result, numbers of elk spending winter in upper elevations of the park decreased by about 80 percent, like the decreases observed in portions of the nonmigratory Madison headwaters elk population that inhabited deep-snow areas in the west-central portion of the park (Garrott et al. 2009c, White et al. 2009c, 2012). These differences resulted in a higher portion of the northern Yellowstone and Clarks Fork elk populations spending winter outside the park (White et al. 2012, Middleton et al. 2013b, 2018; MacNulty et al. 2020b).

Two potential benefits of migration for elk in temperate, montane environments are acquiring nutritious vegetation growth during summer and reducing predation risk to themselves and their calves (Fryxell and Sinclair 1988, Fryxell et al. 1988, Middleton et al. 2018). Following the restoration of large predators in Yellowstone, and reductions in antlerless elk harvests outside the park, biologists noted a change in migration tendencies by elk in the northern populations towards fewer migrants into the park and more residents in larger groups outside the park (White et al. 2012, Middleton et al. 2013b, 2018). Higher predation and persistent drought conditions in the park during the 2000s compared to fewer predators near high human activity, irrigated alfalfa pastures, and private land refuges with less hunting outside the park likely reduced the benefits of migration and exacerbated these changes (White et al. 2012, Middleton et al. 2013a,b; 2018; MacNulty et al. 2020b). Migration behaviors in ungulates likely are learned as young animals follow their mothers or other members of their social group and learn the locations of important resources and efficient pathways to travel from one area to the next (Bracis and Mueller 2017, Merkle et al. 2019). Thus, the trend of less migration could be intensified in future years if higher adult female survival and recruitment continues outside the park (White et al. 2012, Middleton et al. 2013b, 2018).

Biologists documented a similar situation in the Clarks Fork elk population, which spends winter east of Yellowstone in Wyoming and partially migrates 25 to 37 miles (40 to 60 kilometers into the northeastern portion of the park during summer where they mingle with northern Yellowstone elk using the same range (Middleton et al. 2013a,b; 2018). During 1979 and 1980, about 80% of the Clarks Fork elk migrated into the park during summer (Rudd et al. 1983). From 1989 to 2009, however, migrants experienced a shorter duration of vegetation green-up due to a persistent drought, while non-migratory residents obtained nutritious forage from irrigated pastures outside the park (Middleton et al. 2013b, 2018). Migrants also experienced higher predation risk in the park compared to residents which had a much lower risk due to human intolerance for wolves outside the park (Middleton et al. 2013a,b; 2018). There was a 19% decrease in pregnancy rates and a 70% reduction in recruitment by migrants due to sporadic reproduction by young and lactating females (Middleton et al. 2013b, 2018). Over time, the age structure of the migrant segment of the population became older which contributed to reduced pregnancy rates (Middleton et al. 2013b). In contrast, resident elk sustained high rates of pregnancy and recruitment (Middleton et al. 2013b). As a result, only 48% of the elk migrated into the park during 2005 to 2009 because changes from predator restoration, land use outside the park, and climate warming reduced the benefits of migration and altered migratory tendencies (Middleton et al. 2013b). Biologists observed similar changes in a partially migratory population of elk in and near Banff National Park in Alberta, Canada (Hebblewhite et al. 2006, Hebblewhite and Merrill 2007, 2009, 2011).

Conclusions

Wildlife managers in Yellowstone are tasked with preserving natural resources unharmed for the benefit and enjoyment of people. They accomplish this by conserving and restoring native species and the ecological processes that sustain them, while attempting to minimize human intervention (White et al. 2013b). However, the park is not large enough by itself to preserve processes such as long-distance migration because it does not include many of the lower-elevation valleys historically used by elk and other ungulates to sustain themselves during winter (Hobbs et al. 2010). As animals move out of the park, they pass into jurisdictions with different mandates such as hunting and multiple uses of renewable resources. Fortunately, there is tremendous overlap between these various management approaches that focus on conserving habitats and sustaining viable populations of wildlife for the benefit of present and future generations (Clark 2021). The extensive habitats on public lands within the region and a strong ethic of wildlife conservation by many private landowners provide opportunities to sustain migration corridors in the Yellowstone area. In addition, numerous non-governmental organizations are restoring habitat and migration corridors with national support due to a growing tourism economy in the region (White et al. 2013c, 2022).

In 2018, the Secretary of the Interior tasked federal agencies with restoring habitat for ungulates along migration pathways and on winter ranges in the western United States. The Secretary emphasized working with the states to advance shared conservation goals, reduce local conflicts, enhance enjoyment by people, and avoid deleterious impacts. In response, agencies have increased efforts to coordinate management and research, share data and expertise, and collaborate with willing landowners and conservation organizations to enhance the movements of animals across highways and through or around developments. They are also working with private landowners and local communities to address social and economic concerns by promptly managing human-wildlife conflicts and providing adequate funding and staff for these efforts. (Kauffman et al. 2018, Middleton et al. 2019)

Elk have tremendous cultural, ecological, and economic value in the Greater Yellowstone Area. They have provided sustenance to predators and scavengers, including humans, for thousands of years and, more recently, indirectly contributed hundreds of millions of dollars to the area's economy due tourism, wildlife watching, and big game hunting (Southwick Associates 2017). The successful conservation of long-distance migratory behavior requires detailed assessments of pathways and seasonal uses areas, close coordination between various agencies with jurisdiction, early and continuous involvement of private landowners, and meaningful engagement with local communities (Berger and Cain 2014, Kauffman et al. 2018, Middleton et al. 2019). By focusing on common interests, these partnerships can work across jurisdictional boundaries to restore and sustain wildlife habitat, migration corridors, and viable populations of wildlife (Clark 2021).

Adult male elk feeding in Yellowstone National Park. Photograph by Jim Peaco, National Park Service.

Chapter 5
Resource Selection, Nutrition, and Condition

Introduction

Winter is a period of prolonged undernutrition for elk in the mountainous Yellowstone area because grasses are cured, dormant, and low in digestibility, energy, and nutrients, while snowpack reduces access to forage and increases energy expenditures (Houston 1982, Parker and Robbins 1984). The body condition of elk decreases with inadequate nourishment for maintenance which triggers the break-down (metabolization) of fat reserves and protein for energy (Torbit et al. 1985, DelGuidice and Seal 1991). This progression leads to animals losing about 3% to 25% of their body weight over the course of the winter depending on the severity of conditions (Parker et al. 2009). Some animals experience severe malnutrition and starvation once their fat reserves become depleted and too much muscle is metabolized for energy (Torbit et al. 1985, DelGuidice and Seal 1991). It is essential for elk that survive to increase their energy and nutrient intake (nutrition) and replenish their body condition during the relatively short summer by feeding on nutritious vegetation (Cook 2002, Parker et al. 2009). In most years, snowpack and spring rains increase soil moisture and stimulate the production of abundant forbs and grasses which provide nutrition for supporting lactation, replenishing body condition, and producing a healthy calf the following spring (Parker et al. 2009, Lukacs et al. 2018).

Elk adapted to these predictable seasonal changes by developing a general foraging strategy to meet their energetic needs through the year. In winter, they minimize energy costs and protein losses and reduce activity and daily food intake (Parker et al. 2009). In spring, females give birth and provide milk to calves by eating newly emerging forage high in digestible energy and protein (Parker et al. 2009). In summer, they maximize the intake of high-energy, high-protein forage to replenish their body condition, enable pregnancy during autumn, and support gestation through winter (Parker et al. 2009, Cook et al. 2016). Their intake of digestible energy and protein is 4 to 10 times higher than during winter, and lactating animals may consume twice as much forage as non-lactating animals (Cook et al. 2004a, 2016; Parker et al. 1999, 2009). In autumn, females continue high forage intake to replenish fat reserves and protein stores during breeding in preparation for prolonged undernutrition through winter (Parker et al. 2009, Cook et al. 2016). In contrast, mature males eat little during the autumn breeding season which is energetically and physically draining. These bulls increase forage intake after breeding but often cannot replenish their fat and protein reserves completely before winter (Parker et al. 2009). Calves are more susceptible to starvation during severe winters due to their smaller body size with limited fat and protein reserves (Parker et al. 2009). Thus, high-protein milk and forage is critical for them to attain larger sizes with more reserves before the onset of winter (Parker et al. 2009).

Nutrient intake by elk occurs in a hierarchic decision-making manner (Parker et al. 2009). Based on learning and experience, animals choose a seasonal range with habitats that can satisfy their dietary needs and lessen their energetic costs and risk of predation (Gregory et al. 2009, White et al. 2009a,b). Prior to feeding, elk select a vegetation community with a sufficient amount and quality of forage at an acceptable energetic cost, while also considering factors such as weather, snowpack, and predation risk (White et al. 2009a,b). While feeding, elk choose among plants of different types or adjacent plants of the same type (Parker et al. 1996). They also decide what size of bite to take from each plant or plant part, and how often to take bites (White et al. 2009a,b). In making these choices, elk attempt to maximize the intake and quality of forage in their diets while decreasing energetic costs (Stephens and Krebs 1986). However, individual elk often select habitats and forages differently yet achieve the same level of nutrition and body condition (Hobbs et al. 1983, Pulliam 1989). In addition, different strategies may be favored under different environmental conditions or by different sex or age groups (Pulliam 1989, Parker et al. 2009).

This chapter summarizes information on resource selection by northern Yellowstone elk and the effects of diet, nutrition, and energetics on their body condition, reproduction, and survival.

Adult male elk moving snow with his hoof to access forage underneath in Yellowstone National Park. Photograph by Jacob W. Frank, National Park Service.

Habitat Use and Energetics

Elk in Yellowstone use a wide variety of habitats, including xeric (dry) and mesic (wet) grasslands, sedge-grass meadows, sagebrush steppe, aspen and riparian (cottonwood, willow) communities, coniferous forests, old agricultural fields, thermal areas, and rivers (Barmore 2003). Snow constrains the amount of forage available to elk and exponentially increases the energetic costs of travel 3 to 6 times depending on the depth the animal sinks in the snow (Robbins 1993, Parker et al. 2009). Almost all elk in northern Yellowstone during winters in the late 1960s fed in areas with less than 2 feet (0.6 meter) of snow; none fed in snow deeper than

2.5 feet (0.8 meter; Barmore 2003). Similarly, elk in the Madison headwaters area in west-central Yellowstone usually fed in areas with less than 2 feet of snow (Messer et al. 2009).

During the 1960s, most elk on the northern winter range fed in open areas with level to moderate slopes during October through January, primarily in sagebrush grasslands, mesic grasslands, and sedge-grass meadows (Houston 1982, Barmore 2003). As snowpack increased, elk fed in more patches along forest edges or within conifer forests where snowpack was lower. They also selected more sagebrush, xeric grasslands, and old agricultural fields at lower elevations (Barmore 2003). As snow melt and vegetation green-up progressed, elk fed in xeric and then mesic grasslands as they moved upslope (Barmore 2003).

Energy demands are higher for mature males than females, with their highest costs occurring in autumn during the breeding season (Parker et al. 2009, Lachish et al. 2020). Breeding bulls begin autumn in their best condition but lose as much as 20% of their body fat and protein during the rut and more during the subsequent winter when protein in many forage plants is low (Parker et al. 2009). Adult males can survive on lower quality diets because their larger stomachs enable them to retain forage longer and extract more nutrients (Singer and Norland 1994, Parker et al. 2009). However, they are in their poorest condition by late winter (Parker et al. 2009).

In contrast, females are in their best condition entering winter (Parker et al. 2009). Their peak energy and protein demands occur during late pregnancy in spring and lactation through mid-summer (Lachish et al. 2020). More than 90% of energy costs during gestation are in the last trimester when most fetus growth occurs (Pekins et al. 1998, Parker et al. 2009). These costs can double during the first month of nursing when calves grow fast, and their protein needs are high (Parker et al. 2009). Thus, females are in their poorest condition during the month after parturition, with about 50% less fat than non-lactating females (Cook et al. 2004a,b; Parker et al. 2009). Pregnant and nursing females feed longer in winter and summer to maximize energy intake to meet these energy and protein demands (Parker et al. 2009). If summer forage is abundant and nutritious, lactating females can replenish this deficit by autumn; otherwise, their ability to become pregnant is jeopardized (Cook et al. 2004a,b; 2016; Parker et al. 2009).

Adult female elk chewing forage in Yellowstone National Park. Photograph by J. Schmidt, National Park Service.

Diets and Nutrition

The heterogeneous landscape of Yellowstone provides a variety of forages for elk with different energy, protein, and toxin characteristics. Biologists estimate the composition of forage (diet) selected by elk through direct observation, analysis of rumen contents, microscopic analysis of plant fragments in feces, or sequencing plant DNA (deoxyribonucleic acid) from fecal samples (Sparks and Malachek 1968, Greer et al. 1970, Singer and Norland 1994, White et al. 2009a,b; Kartzinel et al. 2015). In the early 1930s, stomach contents of harvested elk contained about 95% grass and 5% browse (Rush 1932). During the intense reduction efforts in the late 1950s and 1960s, biologists found graminoids (grasses, rushes, sedges) comprised 60% of rumen contents in autumn and 80% to 90% in winter, spring, and summer. Forbs, such as pussytoes, horsetail, lupine, and phlox, comprised about 7% of diets in spring but increased through summer to 30% by September before decreasing to 3% during winter (Greer et al. 1970). Dormant grasses have low digestibility and low protein content in winter (Robbins 1993, Van Soest 1994). Browse, such as aspen, conifer (lodgepole pine, Douglas fir, Engelmann spruce), and sagebrush, comprised about 5% to 10% of diets in mild to moderate winters, but increased to about 30% or higher during some severe winters, especially with higher elk densities (Greer et al. 1970). Browse often is higher in protein, but sometimes contains chemicals called secondary compounds or toxins that deter feeding and decrease digestibility (Robbins 1993, Van Soest 1994). Young and adult elk used the same amounts and types of forage seasonally except during severe winters when rumens from adults contained more grass and those from young had more browse (Greer et al. 1970). There was substantial individual variation in diet selection, however, with animals from the same groups have varying types and amounts of forage in their rumens (Greer et al. 1970).

Similarly, graminoids comprised 86% of plant fragments in feces from northern Yellowstone elk during winters from 1985 to 1988, with forbs comprising 3% and browse about 11% (Singer and Norland 1994). Elk in the Madison headwaters population also primarily grazed, with grasses dominating diets during autumn (68%) and spring (80%) but decreasing to 40% during winter (White et al. 2009a,b). As the difference in protein content between browse and grass increased during October through January, elk ate less grass and more browse (40% to 50%) with its higher protein content (7%; White et al. 2009a,b). As a result, the protein content in their diets did not decrease (Hobbs et al. 1981). This trend reversed in April when the nutritional quality of grasses and grass-like plants increased (White et al. 2009a,b). Higher protein is needed by rumen microbes during winter to sustain adequate fermentation rates given the low digestibility (30 to 40%) of their diets (Mertens 1973).

Body Condition

Elk calves in Yellowstone weigh about 32 to 37 pounds (15 to 17 kilograms) at birth, with males about 2 to 4 pounds (1 to 2 kilograms) heavier than females (Rush 1932, Johnson 1951, Houston 1982, Singer et al. 1997, Barber-Meyer et al. 2008). Summer nutrition from milk and forage has a strong influence on calf growth, with larger newborns growing faster through early summer than smaller newborns (Cook et al. 2004a). During their first 2 months, growth is dependent on nursing milk from their mother, which is generally high in protein, but the level depends on the mother's condition (Cook et al. 2004a). Calves begin eating forage about 3 to 6 weeks after birth, but regular nursing continues for about 16 weeks and sporadically until mid-December (Rush 1932, Johnson 1951, Cook et al. 2004a). Females grow to about 225 pounds (102 kilograms) by January when males weigh about 254 pounds (115 kilograms; Greer and Howe 1964, Houston 1982). However, calves have low fat reserves through the year because they are using high fat and protein intake from milk and forage to generate muscle mass (Cook 2002, Cook et al. 2013).

Adult female elk weigh between 420 and 605 pounds (190 and 275 kilograms) during winter (Cook et al. 2004a,b). Body condition has a major influence on the likelihood of pregnancy, overwinter survival, calf survival, and susceptibility to predation (Cook 2002, Cook et al. 2004a). The nutritional demands of lactating females and their calves are higher during summer and autumn than winter (Cook 2002, Cook et al. 2004a, 2016). Thus, moderate decreases in nutrition during this period can decrease pregnancy and survival and hinder calf growth (Cook et al. 2004a,b; 2016). Sexual maturity in elk depends on attaining a minimum level of body condition (Cook 2002). More 2-year-olds were pregnant when elk densities were low due to faster growth from better nutrition (Greer and Howe 1964, Greer 1968, Houston 1982). No yearling females weighing less than 335 pounds (152 kilograms) were pregnant during the 1960s compared to 25% pregnancy when they weighed more than 359 pounds (163 kilograms; Greer and Howe 1964, Greer 1968). After reaching maturity, female elk need to attain at least 6% body fat by mid-autumn to begin estrus, breed, and sustain a pregnancy (Cook et al. 2004a,b). However, pregnancy rates begin to decrease below 9% body fat and breeding can be delayed in females with less than 13% body fat (Cook et al. 2004a,b). Females with higher levels of body fat tend to breed earlier (Cook et al. 2004a, Parker et al. 2009).

Body fat is a key indicator of reproduction and survival in montane ungulates (Cook et al. 2004a,b; Parker et al. 2009, Middleton et al. 2018). Abundant, nutritious forage during summer should enable lactating females to replenish their body condition with more than 15% body fat by autumn (Cook et al. 2004a,b). However, lactating females may have lower fat reserves than non-lactating females if nutrition is marginal and they cannot replenish their reserves (Cook et al. 2004a,b; Middleton et al. 2018). This may contribute to lower pregnancy rates or breeding in alternate years (Cook 2002, Cook et al. 2004a,b; Middleton et al. 2018). Lower pregnancy rates in females older than 15 years indicate they often are unable to attain this level of condition regardless of elk density (Cook et al. 2004a,b). In addition, undernourished females often give birth to smaller calves that have a slower growth rate and poor survival due to lower milk production by their mother (Cook et al. 2004a, Parker et al. 2009). Calves with high summer nutrition have a much higher probability of becoming pregnant as yearlings (Cook et al. 2004a). Migratory elk in northern Yellowstone often lost their calves to predation after the restoration of bears, cougars, and wolves (Barber-Meyer et al. 2008). Without the burden of lactation, these elk became fatter than resident, non-migratory elk that remained outside the park from the Clarks Fork population (Parker et al. 2009, Middleton et al. 2013a,b; 2018). During winter, when migratory and resident elk were on the same range outside the park, all elk lost an average of about 8% body fat (Middleton et al. 2013a).

Adult female elk feeding on sedges and rushes in Yellowstone National Park. Photograph by John Good, National Park Service.

The mid-winter body fat levels of female northern Yellowstone elk 4 to 9 years old was high (10%) during intense culling from 1962 to 1968 (Greer 1968). Pregnancy rates also were high (90%) in these young females (Greer 1968). The mid-winter body fat levels for older adult female elk were lower (7%), as were pregnancy rates (64%; Greer 1968). About 60% of sampled elk had more than 8% body fat, suggesting an 80% probability of them being pregnant (Cook et al. 2004b, White et al. 2011). About 23% had less than 5% body fat, suggesting a less than 50% probability of pregnancy (Cook et al. 2004b, White et al. 2011). Two-thirds of these latter elk were yearlings or more than 15 years old. After wolf restoration, the mid-winter body fat levels of adult female elk 4 to 9 years old remained high (9%) from 2000 to 2006 (White et al. 2011). About 70% of sampled elk had more than 8% body fat, while only 14% had less than 5% body fat (White et al. 2011). Fat levels in older adult female elk were slightly lower (8%) as were their pregnancy rates (78%; White et al. 2011). Lactating females had 50% less fat than non-lactating females, suggesting summer nutrition was not sufficient to support both lactation and the replenishment of fat reserves during a persistent drought (Cook et al. 2004b, Parker et al. 2009). Similarly, lactating adult females from the migratory portion of the Clarks Fork population had lower pregnancy rates (21%) than non-lactating females (87%) during this drought (Middleton et al. 2013b, 2018). These migrant elk spent summer in the northeastern portion of the park and mingled with elk from the northern Yellowstone population (Middleton et al. 2013b).

Body fat levels at the onset of winter largely determine whether elk survive and produce a viable calf (Cook et al. 2004a,b; Parker et al. 2009). Survival is greater when adult female elk have more than 15% body fat but decreases at levels less than 10% (Cook et al. 2004a,b). Females entering winter with less than 7% body fat are unlikely to survive (Cook et al. 2004a). Males have low fat reserves after the rut which makes them more susceptible to starvation during severe winters, predation during early winter, and parasitic infection or disease due to a compromised immune response (Houston 1982, Parker et al. 2009). However, elk with more than 5% body fat by late winter should survive provided winter is not prolonged (Cook et al. 2004a,b). During the 1960s, males older than 7 years and females more than 10 years old had lower fat reserves in early winter than younger adults (Houston 1982). Thus, these animals had higher mortality. However, the body condition of female elk captured from 2000 to 2002 during a severe drought was generally good (10% fat) during mid-winter and only 4% had less than 2% body fat which indicates a high probability of starvation (Cook et al. 2004a,b).

Calf elk nursing in Yellowstone National Park. Photograph by John Good, National Park Service.

Calf survival and recruitment depend on their mother's condition during late gestation and lactation, risk of predation, and nutrition and growth attained through the summer (Thorne et al. 1976, Cook 2002, Parker et al. 2009, Lukacs et al. 2018). Pregnant females in poor body condition tend to give birth to smaller calves later in the spring, which contributes to lower calf survival due to increased predation and malnutrition (Singer et al. 1997, Cook et al. 2004a, Lukacs et al. 2018). These calves may be easier for predators to capture or receive less attention and nutrition from their mothers (Singer et al. 1997, Barber-Meyer et al. 2008). Summer survival was higher for calves that weighed more and were born earlier in the summer from 1968 to 1992 (Houston 1982, Singer et al. 1997). In addition, the survival of calves is higher if their body size is larger at the beginning of winter, which is driven by summer nutrition in terms of milk and forage production (Cook et al. 2004a). Smaller calves are more susceptible to starvation because, with less fat, they break-down more body protein for energy (Cook et al. 2004a). Smaller calves also are more susceptible to predation during winter because it is more difficult to compete for food and maneuver through snow (Cook et al. 2004a). In turn, calf survival is highly sensitive to severe weather conditions, such as drought and deep snowpack, that reduce nutrition and condition and increase vulnerability to predation and starvation (Singer et al. 1997, Lukacs et al. 2018). Calves born following mild winters weighed more than calves born after severe winters, and predators killed more calves born lighter and later (Singer et al. 1997).

Conclusions

During the late 1900s, high densities of elk on the winter range increased competition for forage and led to decreased recruitment, especially during severe winters (Houston 1982, Singer et al. 1997, Taper and Gogan 2002). High densities resulted in less forage for each female which accelerated decreases in body condition, resulted in the birth of smaller calves, reduced calf growth rates, and contributed to higher predation and starvation (Thorne et al. 1976, Singer et al. 1997, Cook et al. 2004a,b). Migrant elk benefitted by moving to higher-elevation summer ranges with access to more nutritious forage to attain higher body condition and, in turn, higher pregnancy rates and recruitment than non-migratory residents that remained on the winter range year-round (Middleton et al. 2013a,b; 2018).

More recently, there is evidence of nutritional limitations on some migrant summer ranges, especially during persistent droughts, such as from 1999 to 2007 (Cook et al. 2004a,b; Middleton et al. 2013b, 2018). Northern Yellowstone elk captured during 2000 to 2002 were, on average, in relatively good condition for middle to late winter with 85% having more than 5% body fat that indicated good to excellent survival probability through the rest of winter; however, non-lactating females had twice as much fat as lactating females (Cook et al. 2004a,b). This suggested nutrition on summer ranges during this period of drought was not sufficient to support both lactation and replenishing fat reserves (Cook et al. 2004a,b; Middleton et al. 2013a,b; 2018). A warming climate and persistent droughts have caused earlier peaks in the growing season followed by earlier senescence of vegetation on higher-elevation grasslands, which can result in poorer nutrition for migrant elk during late summer and autumn (Wilmers et al. 2013, Barker et al. 2019a,b). Nutritional limitation in summer can result in reduced calf growth and make elk more vulnerable to predation (Cook et al. 2004a,b; Parker et al. 2009).

Adult male elk traveling through deep snow near Obsidian Creek in Yellowstone National Park. Photograph by Jim Peaco, National Park Service.

Chapter 6
Competition and Predation

Competition

Competition occurs when one animal (or species) consumes a resource, such as forage, or excludes a second animal from accessing the resource and, in turn, decreases the second animal's ability to survive and reproduce (Begon et al. 2005, Garrott et al. 2013). If the removal of a resource by many animals degrades the habitat by affecting its regeneration, such as through overgrazing, then this depletion may affect other animals for a longer period. Overgrazing (or over-browsing) occurs when widespread, repeated foraging removes so much leaf tissue that plant productivity and regrowth decrease considerably, and soils become compacted and unproductive with fewer available nutrients (Crawley et al. 2021). Most grasses are adapted to grazing as the growing portion (apical meristem) of the plant is at the base, whereas in woody vegetation it is at the tip causing the response to consumption to be different. Grazing can stimulate growth (stem regrows at point of consumption) and browsing may suppress growth (stem must begin anew at another point) and this is what was mostly observed on the northern range during the mid-1900s (Singer 1995, Singer et al. 1998).

Excessively grazed areas are vulnerable to erosion and invasion by nonnative plants due to less plant litter and more bare ground. Signs of overgrazing include changes in the variety (composition) of plants, the spread of nonnative plants, and poor body condition and lower productivity and survival in ungulates (Crawley et al. 2021). Signs of over-browsing are suppressed growth and limited distribution of trees and shrubs, stream incision, and lowered biodiversity due to less plant structure and cover for invertebrates (Peterson et al. 2020).

Grasses and browse are an important part of the diets of most ungulates in Yellowstone National Park, including bighorn sheep, bison, elk, mule deer, and pronghorn (Singer and Norland 1994). Thus, there is the potential for competition, especially on shared winter ranges which are smaller and have higher densities of ungulates than the larger summer ranges (Coughenour and Singer 1996). Since 1911, many scientists have expressed concerns about northern Yellowstone elk removing too much vegetation, including grasses and browse such as aspen, cottonwoods, sagebrush, and willows; especially as elk numbers increased to about 19,000 in by the late 1980s (Rush 1932, Kittams 1953, Wagner 2006, Mosley et al. 2018). In Chapter 3, we discussed how the mortality of calves increased as elk density and competition for forage increased, which is an example of intraspecific (within a species) competition. In addition, most scientists agree abundant elk in the absence of wolves contributed to substantial reductions in the abundance and stature of aspen, cottonwood, sagebrush, and willow in the northern portion of the park during the twentieth century, which were replaced by grasses and herbaceous flowering plants in many areas (Hobbs and Cooper 2013, Peterson et al. 2020, Hobbs et al. 2023; see the *Trophic Cascades* section in Chapter 7). This over-browsing by elk affected other species, such as pronghorn (see below), which is an example of interspecific (between species) competition (White et al. 2022c).

Calves begin winter with lower energy reserves than adults due to their lower body size and are subordinate to adult elk when feeding in groups (Houston 1982, Coughenour and Singer 1996). Mature bulls also enter the winter with lower energy reserves than adult females due to expenditures during the rut (Houston 1982, Coughenour and Singer 1996). Bulls tend to use higher-elevation habitats with deeper snow during winter, while females with young elk tend to migrate to lower areas with less snow (Houston 1982, Coughenour and Singer 1996). The lower-elevation winter range is substantially smaller than the summer range and, as a result, available forage is reduced and competition for this limited resource may increase (Houston 1982, Coughenour and Singer 1996). Bulls at higher elevations have less competition for available food even though foraging is more difficult (Coughenour and Singer 1996). During the 1980s and 1990s, prior to the recovery of large predators, there was evidence of competition for food among elk at high densities on the winter range that limited their abundance in the northern population by decreasing calf survival and recruitment (Coughenour and Singer 1996, Singer et al. 1997, Taper and Gogan 2002). In addition, severe winters contributed to substantial starvation and poor recruitment (Coughenour and Singer 1996, Singer et al. 1997). As a result, the population grew more slowly (Coughenour and Singer 1996, Taper and Gogan 2002).

Adult male elk in the Lamar Valley of Yellowstone National Park. Photograph by Stan Canter, National Park Service.

Competition between different species of wild ungulates is difficult to detect because mere overlap in habitat use or diets does not equate to a decrease in demographic rates (Begon et al. 2005). Thus, it is not surprising there was little evidence of competition among elk, bighorn sheep, bison, mule deer, and pronghorn in northern Yellowstone as elk abundance increased and their range expanded from the late 1960s through the 1980s. There was high habitat and diet overlap between bighorn sheep and elk on the Mount Everts/Gardiner basin winter range where both species ate primarily grass, but spatial segregation appeared to limit competition (Houston 1982, Singer and Norland 1994, Barmore 2003). On the Cinnabar Mountain winter range further north, bighorn sheep ate a high proportion of browse during winter (Keating 1982). Thus, there was the potential for competition between elk and bighorn sheep during severe winters when elk also consumed more browse (Greer et al. 1970, Keating 1982, Wagner 2006). However, biologists did not detect any impacts of competition. Bison and elk had high habitat overlap but moderate diet overlap, with bison consuming more grass and far less browse than elk (Houston 1982, Singer and Norland 1994, Barmore 2003). Mule deer and elk had moderate to high habitat overlap but low diet overlap with deer consuming more browse and forbs (Houston 1982, Singer and Norland 1994, Barmore 2003). Bison and mule deer numbers increased during the 1970s and 1980s concurrent with elk, which suggests competition was minimal (Houston 1982, Singer and Norland 1994, Barmore 2003).

Elk and pronghorn had low habitat and diet overlap, with pronghorn eating far more browse and forbs (Houston 1982, Singer and Norland 1994, Barmore 2003). However, concentrated browsing by elk substantially reduced the amount of sagebrush on the pronghorn winter range in the Gardiner basin. The abundance of sagebrush decreased by 43% between 1957 and 1990 as browsing reduced heights and the recruitment of seedlings (Singer and Renkin 1995). Thus, pronghorn could no longer rely on sagebrush as a staple food source during winter but instead used a variety of habitat types to meet their nutritional needs (White et al. 2022c). Adult pronghorn maintained relatively high reproductive and survival rates despite this decrease, however, and there was no evidence of widespread malnutrition (White et al. 2022c).

There was a decrease in counts of elk in northern Yellowstone from about 19,000 in the mid-1990s to 3,915 by 2013 following the restoration of large predators and substantial annual hunter harvest outside the park (MacNulty et al. 2020b). This substantial decrease reduced elk densities and competition for resources on the winter range, especially at middle to upper elevations in the park (White et al. 2012). However, as elk numbers declined the number of bison in northern Yellowstone increased from about 1,500 in 2005 to 4,000 in 2016 (Geremia 2022). The exact causes of this increase are unknown but include substantial dispersal from central to northern Yellowstone due to high bison densities, high wolf predation on calves, intense management actions along the western boundary to keep bison in the park, and the large decrease in elk numbers (White and Wallen 2012). To date, there is no evidence increased bison numbers in northern Yellowstone are competing with elk and decreasing their reproduction and survival, but research and monitoring are ongoing. Most elk spend winter outside the park, while most bison spend winter inside the park, which may contribute to the apparent absence of bison-elk competition (White et al. 2012, Geremia et al. 2015b, Northern Yellowstone Cooperative Wildlife Working Group 2022). Monitoring of grasslands in northern Yellowstone during 2015 to 2022 indicated soil organic matter was stable and within ranges supporting nutrient cycling, water holding potential, and physical structure. Grazed plant communities sustained production compared to areas where grazing was excluded (Geremia and Hamilton 2019, 2022). The compositions of plants in some grassland areas have changed in recent decades, but most of these communities are resilient and still productive with healthy soils and energy, nutrient, and water cycles (Geremia and Hamilton 2019, 2022).

Since the early twentieth century, browsed plant communities have been reduced due to concentrated elk use of willow and aspen and the concomitant loss of beavers creating a negative feedback loop and an ecological state change from a carnivore-beaver-woody vegetation state to an elk-grassland state. The recent decline of elk and the winter range shift to outside the park has increased woody plant growth in some areas where water is not limiting, restoring some to woody communities; yet so far there is no evidence of an ecological state change back to its earlier condition (Wolf et al. 2007, Bilyeau et al. 2008, Brice 2020, Peterson et al 2020).

Predation

Predation occurs when one animal attacks and kills another for food (Caughley and Sinclair 1994). Predators, such as wolves, are usually not successful at killing large dangerous prey, such as adult elk, unless they can exploit an injury, weakness, or environmental conditions, such as deep snowpack or fallen timber, that restrict the maneuverability of the prey (Smith et al. 2000, 2004; Mech et al. 2001, 2015; Bergman et al. 2006, Dunkley 2011, MacNulty et al. 2012, 2020a). The susceptibility of an elk to predation depends on age, body size, nutritional condition, injuries, habitat selection, defensive responses, and experience (Metz et al. 2020a,b; Smith 2021). Adult elk in their prime are relatively invulnerable to predation unless they get trapped in terrain, habitat, or snowpack conditions that restrict their mobility and escape (Bergman et al. 2006, Dunkley 2011, Metz et al. 2020b). Smaller calves with less experience and older adults with deteriorated condition are generally more susceptible to predation (Wright et al. 2006, Mech et al. 2015, Metz et al. 2020b). This vulnerability increases during severe weather or crowded conditions that decrease forage availability, nutrition, and body condition (Coulson et al. 2001, Smith 2021).

Adult male elk feeding along a river surrounded by deep snow in Yellowstone National Park. Photograph by J. R. Douglass, National Park Service.

Predators in the Yellowstone area were poisoned, shot, and trapped during the late 1800s and early 1900s to reduce competition with settlers, such as livestock depredations (Stahler et al. 2020). People eradicated wolves and decimated numbers of bears and cougars by the 1930s (Rush 1932, White et al. 2017, Stahler et al. 2020). However, conservation and management actions increased the number of grizzly bears in Yellowstone National Park from perhaps 100 or fewer during the 1970s to as many as 150 to 200 by the mid-1990s (Craighead et al. 1974, White et al. 2017). Numbers of black bears also increased to between 150 and 275 in northern Yellowstone (Bowersock 2020), while cougars reestablished a viable population by the mid-1980s, and then continued to increase to as many as 50 animals (Murphy 1998, Ruth et al. 2019, Anton 2020, Stahler et al. 2020).

During the late 1980s, predation by bears, cougars, and coyotes killed about 23% of the elk calves in northern Yellowstone each year but few adults (Singer et al. 1997). Despite this predation, biologists consistently counted between 15,000 and 19,000 elk (Taper and Gogan 2002). Survival of adult females was high with most deaths being harvests of elk migrating outside the park and starvation of older animals (White and Garrott 2005a). Recruitment was highly variable among years because occasional severe winters exacerbated competition for food on the winter range and led to substantial starvation (Coughenour and Singer 1996, Singer et al. 1997, White and Garrott 2005a). Wolves were reintroduced to Yellowstone during 1995 to 1997 and the number in northern Yellowstone increased from 21 in 1995 to 98 in 2003 before decreasing to an average of 45 (range = 34 to 79) thereafter (Smith et al. 2020). The reintroduction of wolves was a transformational event because it completed the restoration of the most abundant and diverse predator community in the continental United States (White 2016, Garrott et al. 2020). The following sections assess the effects of this restoration on elk in northern Yellowstone and surrounding areas.

<u>Prey Selection</u>—Prey selection by cougars and wolves depends largely on vulnerability and reducing their risk of injury rather than maximizing intake (Hoy et al. 2021). Elk availability and vulnerability for predators changes through the seasons. In spring, elk from as many as eight populations migrate into portions of Yellowstone National Park for the summer (Kauffman et al. 2018, Stahler et al. 2022). Adult elk are in relatively poor nutritional condition after prolonged undernutrition through the winter and the energetic costs of late gestation and lactation (Cook 2002, 2004a,b). In late spring through summer, young calves are plentiful, and adults are recovering their body condition by consuming nutritious, growing forage (Metz et al. 2020b). In autumn and early winter, calves are larger and generally in good condition, as are adult females (Metz et al. 2020b). Mature males deplete their energy reserves during the rut and attempt to replenish their condition to the extent possible (Houston 1982, Metz et al. 2020b). By late winter, elk are in relatively poor nutritional condition, especially calves and older adults (Metz et al. 2020b). Thus, the typical predation pattern is more smaller elk (calves) are killed through summer, calves and depleted bull elk are killed early in winter, and more adult elk are killed during late winter and spring, especially bulls that have dropped their antlers and older females (Metz et al. 2018, 2020b)

A wolf, grizzly bear, coyotes, and ravens at a carcass on Swan Lake Flat in Yellowstone National Park. Photograph by Jim Peaco, National Park Service.

Grizzly bears in Yellowstone are carnivorous with ungulate meat comprising about 45% to 80% of their diets (Mattson 1997, Stahler et al. 2020). Black and grizzly bears rarely kill adult elk, but they are effective hunters of newborn elk calves (French and French 1990, Gunther and Renkin 1990). They intensely search areas near solitary female elk during the birthing season to locate calves in hiding. Bears accounted for about 60% of elk calf deaths from 2003 to 2005, almost entirely during the first month after calving (Barber-Meyer et al. 2008). This percentage was about 3 times higher than during a similar study from 1987 to 1990 (23%; Singer et al. 1997). It appears bear predation increased as their abundance increased which, in turn, decreased the survival of elk calves (Barber-Meyer et al. 2008, Proffitt et al. 2014). In addition, grizzly bears frequently steal and scavenge on the kills of cougars and wolves (Stahler et al. 2020). Prior to wolf restoration, carcasses primarily were available in late winter when elk died from starvation (Stahler et al. 2020). Black and grizzly bears emerging from their dens after hibernating through the winter fed on these carcasses. However, wolves changed this pattern by killing elk through the year (Wilmers and Getz 2005, Metz et al. 2012, 2020b; Stahler et al. 2020).

Predation studies conducted on the recolonizing cougar population between 1987 and 1994 found their diets in northern Yellowstone consisted of 60% elk, 18% mule deer, and about 22% other prey, such as bighorn sheep, pronghorn, marmots, porcupines, and coyotes (Murphy 1998, Ruth et al. 2019, Stahler et al. 2020). Following wolf reintroduction, predation studies between

1998 and 2006 found cougars increasingly used elk (74%), relying less on deer (14%) and other prey (12%; Ruth et al. 2019, Stahler et al. 2020). More recent studies (2016 to 2022) have found cougar diets shifting to less use of elk (49%) than in prior decades, with increasing use of deer (35%) and about 16% other prey (Stahler et al. 2021). These patterns of prey selection through time are likely most influenced by changes in elk abundance and carnivore competition in northern Yellowstone (Stahler et al. 2020). When hunting elk, cougars kill primarily calves (62%) and adult females (30%), but occasionally kill bulls (Ruth et al. 2019, Stahler et al. 2020). Cougars kill more elk calves as summer progresses and continue through winter as calves move around the landscape with groups of adult females (Ruth et al. 2019, Stahler et al. 2020). After wolf restoration, cougars began killing more adult female elk, probably due to fewer available calves (Ruth et al. 2019, Stahler et al. 2020). Cougars sometimes lose kills to bears and wolves and need to kill more frequently, especially when they are raising kittens (Ruth et al. 2019, Stahler et al. 2020). As a result, their kill rates of elk increased after wolf restoration, and are about twice the per capita kill rate of wolves (Ruth et al. 2019, Anton 2020, Stahler et al. 2020).

A male cougar in a tree in Yellowstone National Park. Photograph by Jacob W. Frank, National Park Service.

Wolves in northern Yellowstone typically hunt in packs during winter and travel long distances through relatively flat grasslands close to rivers and streams (Kauffman et al. 2007). This strategy facilitates the detection of elk foraging in grasslands or near habitat transitions, such edges between grasslands and forests, and allows wolves to scan groups for individual elk susceptible to attack (Bergman et al. 2006, Kauffman et al. 2007). Snow cover in these areas can hinder elk maneuverability while obstacles, such as river or forest edges, can hinder rapid escape (Bergman et al. 2006, Kauffman et al. 2007). Wolves are successful in less than 10% of their attacks on adult elk in northern Yellowstone due to their large body size and defensive tactics (Smith et al. 2000, Mech et al. 2001, MacNulty et al. 2012, 2020a). Prime-age adult elk are generally not susceptible to predation unless injured or chased into an environmental trap, such as downed timber or deep snowpack, where their vulnerability increases rapidly and substantially (Bergman et al. 2006, Kauffman et al. 2007). As a result, packs of wolves generally scan for calves, older, or injured elk, which are highly susceptible (Kauffman et al. 2007, MacNulty et al. 2007, Mech et al. 2015). The odds of wolves killing calves increases with elk abundance (Wilmers et al. 2020).

Elk comprised about 94% of kills by wolves in northern Yellowstone during winters from 1995 to 2017, and about 82% of kills during spring and summer (Metz et al. 2020b). Wolves preferred calves which comprised about 20% of kills during spring, 65% of kills during summer after calves emerged from hiding, 45% during early winter when the smaller body size of calves made them more vulnerable, and 23% during late winter and spring when there were fewer calves and more old, debilitated adults (Metz et al. 2012, 2020b). Adult females comprised about 35% to 40% of wolf-killed elk during winter and spring but less than 20% during summer (Metz et al. 2020b). Adult males comprised about 30% of wolf-killed elk during spring, 12% in summer and autumn, 21% during early winter, and 37% during late winter when they were in their poorest nutritional condition (Metz et al. 2020b). Wolves killed more mature bulls during early winter following poor summer forage conditions when they had relatively poor body condition after the rut (Metz et al. 2020b, Wilmers et al. 2020). The average age of adult elk killed by wolves was about 8 years for males and 14 years for females (Smith et al. 2004, Wright et al. 2006, Metz et al. 2020b). This pattern remained consistent, even following a 70% decrease in elk abundance (Metz et al. 2012, 2020b).

As elk numbers decreased and bison numbers increased in northern Yellowstone, wolves began to scavenge on carcasses of bison that died during calving, from injuries sustained during the rut, starvation, or other causes (Tallian et al. 2017, MacNulty et al. 2020b; Metz et al. 2020a,b). Scavenging increased as bison abundance increased, and bison carcasses now comprise about 25% of the meat wolves eat during winter (MacNulty et al. 2020b, Metz et al. 2020b). This scavenging reduced predation on elk from about 18 to 12 elk per wolf each year based on kill rates during winter (Metz et al. 2020a).

Wolf pack feeding on a bison carcass in Yellowstone National Park. Photograph by Jacob W. Frank, National Park Service.

Likewise, wolves in the Madison headwaters area of west-central Yellowstone strongly preferred elk calves during winter because of their high vulnerability compared to other prey (Becker et al. 2009a). Wolves killed more adult elk as the duration and accumulation of snow increased, likely due to its debilitating influence on body condition which, in turn, increased elk vulnerability to predation (Becker et al. 2009a). The number of elk killed by wolves decreased as elk numbers decreased substantially (Becker et al. 2009b). Wolves killed more bison when calves were abundant, especially after snowpack increased, but these kills did not reduce kill rates on elk (Becker et al. 2009a,b).

<u>Effects on Elk Abundance</u>—Studies on predation in the years preceding wolf restoration found recolonizing cougars removed less than 2% of adult elk and 9% to 17% of calves (Murphy 1998, Ruth et al. 2019). This degree of predation, even combined with coyotes and bears, had no detectable limitation on elk population growth, which continued after the 1988 fires (Singer et al. 1997). Prior to the reintroduction of wolves in northern Yellowstone, some scientists predicted a 10 to 30% reduction in elk numbers while others predicted reductions of 50% or more (Mack and Singer 1993, White and Garrott 2005b, Boyce 2018). Following wolf reintroduction, wolf predation was one of several factors that decreased elk numbers, along with predation by bears, cougars, and coyotes, the continuation of liberal human harvests of prime-aged, female elk, and sporadic severe weather events, such as deep snowpack and sustained drought (Eberhardt et al. 2003, 2007; Vucetich et al. 2005, White and Garrott 2005a, MacNulty et al. 2020b, Smith 2021).

There were relatively few wolves during the late 1990s and the predation rate did not exceed 3%, which had little effect on elk recruitment, survival, and trends (Mech et al. 2001, Smith et al. 2004, Metz et al. 2020a). However, decreasing elk abundance along with increasing wolf abundance gradually resulted in wolves killing a higher portion of the population each year, which contributed to a rapid decrease in numbers as wolves killed about 5% of the adult female elk annually from 2004 through 2009 (Eberhardt et al. 2007, Metz et al. 2020a). Thereafter, wolf predation rates on elk decreased as wolves scavenged more on bison carcasses and killed fewer elk (Metz et al. 2012, 2020a).

The trend in the Madison headwaters elk population was remarkably similar following wolf restoration. Wolves killed more than 20% of the population in west-central Yellowstone from 2004 through 2009 (Garrott et al. 2005, 2009c, 2020). The probability of an elk dying was strongly influenced by terrain and weather that increased its susceptibility to predation by wolves (Garrott et al. 2009c, 2020). Elk at higher elevations with deeper snows were more likely to be killed by wolves, as were elk in geothermal areas or meadows from which they could be chased into deeper snow or burned timber with downfall that impeded their escape (Bergman et al. 2006, Dunkley 2011, Garrott et al. 2020). In both northern and west-central Yellowstone, the predation rate of wolves on elk increased, rather than decreased, as elk numbers decreased to lower levels (Garrott et al. 2009d, Tallian et al. 2017, Metz et al. 2020b). For example, as elk numbers decreased to between 10,000 and 5,000 elk in northern Yellowstone, wolves killed a larger portion of the population (White and Garrott 2005a, Metz et al. 2020a). Both populations were regulated at substantially lower abundance than prior to predator restoration, with the Madison headwaters population at less than 10% of its pre-wolf abundance and the northern Yellowstone population at about 40% of its pre-wolf abundance (Garrott et al. 2009c,d; Metz et al. 2020a). Whether this regulation will persist is the subject of ongoing research.

The death of prime-aged females 2 to 14 years old has the largest influence on trends in elk populations (Eberhardt 1977, 2002; Gaillard et al. 1998, 2000; Eberhardt et al. 2007, Smith 2021). Females 2 to 9 years old are resistant to predation and rarely killed even in severe environmental conditions, such as deep snowpack or sustained drought (Garrott et al. 2009b,c; MacNulty et al. 2016, 2020b; Smith 2021). However, females 10 to 14 years old are more susceptible to wolf predation during severe conditions and females greater than 14 years old are more likely to be killed by wolves than other causes of mortality, such as starvation, harvest, and other predators (Smith 2021). Thus, wolf predation on adult females generally focuses on older elk that are less fertile and comprise a smaller portion of the population (Smith 2021). The main contribution of predators to the decreasing trend in numbers of elk in Yellowstone was their role in reducing recruitment and contributing to an older age structure (White and Garrott 2005a, Raithel et al. 2007, Garrott et al. 2009c, Griffin et al. 2011, Proffitt et al. 2014, MacNulty et al. 2020b, Smith 2021). For example, cougars removed less than 5% of adult female elk following wolf arrival, but their predation on calves increased from 10% in the early wolf restoration years to 20% to 60% as calves became less available once wolves fully colonized (Ruth et al. 2019, Stahler et al. 2020, Smith 2021). Research across multiple elk populations in the northwestern United States estimated wolves reduced recruitment by about 5 calves per 100 adult females and grizzly bears by another 7 calves per 100 adult females (Lukacs et al. 2018). Calf survival is now a major driver of elk population trends in northern Yellowstone because about one-half of the elk killed by wolves and about 60% of those killed by cougars are calves, primarily during summer and early winter (Smith et al. 2004, Wright et al. 2006, Metz et al. 2012, 2020a,b). Additionally, grizzly bears and black bears, which occur at higher abundances in northern Yellowstone than wolves and cougars combined, continue to be the primary predators on calf neonates in early summer (Barber-Meyer et al. 2008, Griffin et al. 2011, Proffitt et al. 2014, Bowersock 2020). Ongoing research is evaluating the relative effects of different predators on elk population dynamics through time.

Effects of Weather—Severe winters with deep or crusted snow increase energetic costs and nutritional stress and decrease mobility and maneuverability, thereby increasing susceptibility to predation and mortality (Houston 1982, Robbins 1993, Cook 2002, Brodie et al. 2013). Kill rates by wolves in Yellowstone increase in deeper snowpack even at relatively low elk densities and persistent drought also decreases nutrition and body condition which increases the susceptibility of calves and older elk to predation (Coughenour and Singer 1996, Singer et al. 1997, Mech et al. 2001, Cook et al. 2004b, Becker et al. 2009a,b; Metz et al. 2020a,b). Thus, animals in poor condition die sooner in a predator-rich environment than before predator restoration (Becker et al. 2009a,b; Metz et al. 2020a,b; Smith 2021). In addition, as the portion of the population in the older age class increases due to lower recruitment, the portion of adult elk susceptible to wolf predation increases and population growth decreases (Proffitt et al. 2014, Hoy et al. 2020, Smith 2021).

Reintroduced wolf running in deep snow in Yellowstone National Park. Photograph by Barry O'Neill, National Park Service.

Prior to wolf restoration, the survival of calves varied widely from year-to-year depending on population density, forage production, and snowpack that limited forage availability and increased energy expenditures (Coughenour and Singer 1996, Singer et al. 1997). With less forage and deeper snowpack, more calves and older elk died, and calves born the following spring were smaller and less likely to survive (Houston 1982, Coughenour and Singer 1996, Singer et al. 1997). Higher densities of elk exacerbated these effects because less forage was available for each elk (Houston 1982, Coughenour and Singer 1996, Singer et al. 1997). Conversely, calf survival increased with warmer spring temperatures that shortened winter and commenced the growth of new vegetation earlier (Coughenour and Singer 1996, Singer et al. 1997). This likely enabled better milk production for nursing females and increased the growth of calves (Parker et al. 2009).

Following wolf restoration, poor forage production during summer increased the odds of wolves killing mature bulls early in winter following the energy demands of the rut (Metz et al. 2020b, Wilmers et al. 2020). This pattern was more pronounced during years of persistent drought. In years with good forage production, wolves primarily killed calves during early winter, probably because they were most vulnerable due to their small body size (Metz et al. 2020b, Wilmers et al. 2020). However, this pattern was influenced by forage conditions during the summer preceding their mother becoming pregnant (Griffin et al. 2011, Wilmers et al. 2020). Better forage conditions and body condition of the mother before she became pregnant contributed to higher survival of her calf during its first winter (Houston 1982, Cook et al. 2004a, Parker et al. 2009). The odds of wolves killing adult female elk increased during severe snowpack because these conditions made all elk vulnerable and adult females were most abundant (Wilmers et al. 2020).

Similarly, elk in the Madison headwaters population experienced extensive starvation during severe winters with deep snowpack prior to wolf restoration, but few elk died during mild winters with shallow snowpack (Garrott et al. 2003, 2009b). This pattern was stronger for calves. Prior to wolf restoration, calves had relatively high survival during the lightest snowpack years, but most calves starved during winters with severe snowpack (Garrott et al. 2003, 2009b). Following wolf restoration, predation reduced the survival of prime-aged females by less than 3%, younger females by 2% to 4%, and older females by 8% to 10% (Garrott et al. 2009c). However, wolf predation reduced calf survival by 25% to 50%, even during winters with mild snowpack (Garrott et al. 2009c).

Prey Switching—Prey switching occurs when a predator starts killing more of a different type of prey that is relatively abundant as their preferred prey decreases to comparably lower numbers (Murdoch 1969, Garrott et al. 2009d, Tallian et al. 2017). Elk are the preferred prey of wolves in northern Yellowstone, but they also kill bison, especially calves and older adults during winter (Metz et al. 2012, 2020b). Counts of northern Yellowstone elk decreased substantially from more than 19,000 in the mid-1990s to about 3,915 in 2013 following the restoration of large predators, including wolves (MacNulty et al. 2020b). Concurrently, the number of bison in northern Yellowstone increased from about 1,500 in 2005 to 4,000 in 2016 (Geremia 2022). Despite this drastic change in the relative abundance of bison and elk, wolves continued to kill predominantly elk; even as the abundance of elk continued to decrease (Metz et al. 2012, 2020b; Smith 2021). Wolves did kill some bison calves and scavenging on bison carcasses increased over time, but prey-switching from elk to bison did not occur (Tallian et al. 2017, Metz et al. 2020a). Biologists observed a similar sustained selection for elk by wolves in the Madison headwaters area of west-central Yellowstone following a drastic decrease in elk numbers and much higher abundance of bison during winter (Garrott et al. 2009d). Wolves killed more bison as their numbers increased relative to elk, but there was not a corresponding decrease in wolf preference for elk (Becker et al. 2009a,b; Garrott et al. 2009d).

The lack of prey switching from elk to bison probably reflects decisions by wolves to attack prey with less risk of injury (Tallian et al. 2017). Adult bison are the largest prey in Yellowstone and even their smaller calves are dangerous to attack given the group defense strategies employed by bison (Tallian et al. 2017). Thus, bison are formidable prey and less than 5% of observed attacks by wolves resulted in a kill (MacNulty et al. 2007, Mech et al. 2015, Tallian et al. 2017). Likewise, wolves are less successful attacking elk that remain in tight groups with multiple animals using defensive tactics like kicking (MacNulty et al. 2007, Mech et al. 2015). However, elk are smaller and often run when attacked by wolves, which makes it easier for wolves to select younger or older animals without engaging the entire group (MacNulty et al. 2007, Mech et al. 2015). Pursued elk also can be chased into environmental traps, such as downed timber or deep snowpack, where their vulnerability increases (Bergman et al. 2006). As a result, wolves continued to select elk and usually only large packs of more than 10 wolves occasionally hunted smaller groups of 10 to 20 bison with calves (MacNulty et al. 2012, Tallian et al. 2017). Instead of attacking large groups of bison, wolves began scavenging more on carcasses as the abundance of bison in northern Yellowstone increased and more bison died due to injuries and starvation (Tallian et al. 2017). By 2014, the scavenging of bison carcasses provided wolves with nearly as much meat as they acquired from killed elk. In turn, this strategy decreased the kill rates of elk by 30% to 40% (Metz et al. 2020a,b).

Changes in Elk Distribution—The number of northern Yellowstone elk on upper-elevation portions of their winter range, where elk were exposed to high predation risk from wolves during winter and bears during spring, decreased by 80% after wolf restoration (White et al. 2012, MacNulty et al. 2020b). In contrast, the portion of the population that spent winter at lower elevations outside the park increased (White et al. 2012). Elk in Yellowstone National Park encountered wolves, on average, once every 9 days (range = 7 to 12 days; Middleton et al. 2013b, Cusack et al. 2020). This shift in the distribution of elk during winter may continue in future years due to higher adult female survival outside the park with reduced harvests and higher recruitment than in higher-elevation areas (Evans et al. 2006, Hamlin et al. 2009, White et al. 2012). As elk density decreased in northern Yellowstone after carnivore restoration, the primary factor influencing habitat selection by elk switched from more efficiently obtaining food to choosing safer terrain (Smith et al. 2022). Biologists observed a similar switch in Banff National Park in Canada (Hebblewhite and Merrill 2009). Similar changes in the distribution of elk occurred in the Madison headwaters area after wolf recovery. Prior to wolf restoration, about one-third of the elk were distributed in each of three major river drainages (White et al. 2009c, Dunkley 2011). However, elk were eliminated from the two highest elevation drainages where deep snowpack made them more vulnerable to predation and about 95% of the remaining population concentrated in the lowest elevation drainage (White et al. 2009c, Dunkley 2011).

These shifts in elk distribution following wolf restoration primarily were due to the predation of more-vulnerable elk in higher-elevation areas with deeper snowpacks, and decreased recruitment to replace these animals, rather than elk redistributing on the landscape (White et al. 2009c, 2012; Dunkley 2011). Wolves frequently traveled through areas with relatively high densities of elk without attempting to making kills (Bergman et al. 2006, Kauffman et al. 2007). Thus, differences in predation risk among areas likely were due to differences in the vulnerability of elk once attacked rather than differences in detection or encounter probabilities (Bergman et al. 2006, MacNulty et al. 2007).

Group of adult female and calf elk grazing near Mammoth in Yellowstone National Park. Photograph by Jim Peaco, National Park Service.

Conclusions

Predator restoration transitioned the Yellowstone system from bottom-up regulation of the elk population via forage limitation and starvation during severe winters as elk numbers increased to top-down regulation from predation which reduced recruitment and led to an older, less productive population (Garrott et al. 2009b,c; MacNulty et al. 2020b). Wolves specialized on elk and strongly selected for more vulnerable calves and older animals (Becker et al. 2009a,b; Metz et al. 2020b). This selection was greater in areas of the park where there were more wolves and snowpack was deeper. In addition, bears and cougars became more significant predators on elk calves as their numbers and distribution increased (French and French 1990, Gunther and Renkin 1990, Mattson 1997, Murphy 1998, Barber-Meyer et al. 2008, Ruth et al. 2019). Surprisingly, cougars kill as many elk as wolves in northern Yellowstone because their abundance is similar, and cougars kill more elk as carcasses are stolen by grizzly bears and wolves (Ruth et al. 2019, Metz et al. 2020a,b; Stahler et al. 2020). The winter distribution of elk contracted to lower snowpack areas in the park after the restoration of large predators, and a much larger portion of the smaller elk population spent winter outside the park where predators were fewer and recruitment higher (White et al. 2009c, 2012; MacNulty et al. 2016, 2020b).

The effects of predators on elk population dynamics vary considerably within the same region because of differences in land use, vegetation communities, densities of large predators and their management, local environmental conditions, elk migratory patterns, and human harvests (Garrott et al. 2005, Hamlin et al. 2009). Populations of elk in the Greater Yellowstone Area decreased in abundance in areas where preservation was the main land use, such as Yellowstone National Park, due to predation by high numbers of wolves, cougars, and black and grizzly bears consistently reducing recruitment (Garrott et al. 2005, Hamlin et al. 2009). In contrast, populations remained stable or increased in areas where agriculture was the predominant land use, with low numbers of predators due to hunting and control actions and moderate numbers of elk harvested by hunters (Garrott et al. 2005, Hamlin et al. 2009). The survival of adult female elk decreased at high numbers of wolves relative to elk and recruitment was consistently lower for populations with high numbers of wolves relative to elk, especially in areas with relatively high numbers of grizzly bears (Garrott et al. 2005, Hamlin et al. 2009). This consistently low recruitment dominated trends in the northern Yellowstone, Madison headwaters, and Gallatin elk populations, especially in areas with moderate hunting; though recent counts of northern Yellowstone elk have increased somewhat (Garrott et al. 2005, Hamlin et al. 2009, Profitt et al. 2014).

Vigilant adult female elk in Yellowstone National Park. Photograph by Neal Herbert, National Park Service.

Chapter 7
Ecological Role and Adaptive Capabilities

Keystone Species

Elk play a prevalent role in the Yellowstone ecosystem by enhancing the productivity of grasslands through grazing, transferring nutrients across the landscape, converting grass to animal tissue, and providing sustenance for predators, scavengers, and decomposers (Houston 1982, Singer and Norland 1994, Frank et al. 2013, Stahler et al. 2020). Prior to wolf restoration, elk intensively grazed some wet grassland areas in northern Yellowstone (up to 55%) but grazed plants recovered (Frank and McNaughton 1993). Elk increase the availability of nitrogen in the soil by depositing fertilizers (feces and urine) and breaking down plant litter, which helps grass roots and associated fungi intake nitrogen and water (Frank and McNaughton 1992, Frank and Evans 1997, Frank and Groffman 1998). As a result, precipitation becomes the main factor affecting grass production by influencing soil moisture, which can stimulate or limit production (Frank and McNaughton 1992, Coughenour and Singer 1996, Frank et al. 2013). In areas with sufficient soil moisture, low to moderate grazing has a strong, positive influence on grasses and soil microbes that increases the availability of light, moisture, nutrients, and the growth of new tissue (Frank and McNaughton 1993, Frank and Groffman 1998, Frank et al. 2002). Grazing by abundant elk in northern Yellowstone during the 1980s and 1990s stimulated grass production in wet areas by about 40%, which allowed grazed grasses to maintain nutritious growth with 10% to 35% higher protein content (Frank and McNaughton 1992, Frank and Groffman 1998, Frank et al. 2002). These stimulating effects of moderate grazing on plant production were lower or not observed in dry areas and during droughts due to a lack of soil moisture (Frank 2007, Frank et al. 2013, Geremia and Hamilton 2019). Grazing and nitrogen cycling decreased by 25% to 50% from 1999 to 2001 as elk numbers decreased substantially, which resulted in less forage production and lower forage quality in some areas (Frank 2008). Elk also represent a key food source for species ranging from wolves to magpies to beetles and bacteria in the soil (Metz et al. 2020a,b, Stahler et al. 2020). In the end, their carcasses contribute to nutrient surges that greatly enhance the productivity of nearby plants (Frank et al. 2013).

A wolf chases magpies and ravens from an elk carcass near Soda Butte in Yellowstone National Park. Photograph by Jim Peaco, National Park Service.

Trophic Cascades

Predators reduce numbers of their prey and alter their behavior to some extent, especially immediately before, during, and after encounters. The word 'trophic' means feeding, and 'cascade' refers to how predation affects the prey's forage (Hobbs and Cooper 2013). Trophic cascades occur when predators reduce the density of their prey or induce them not to use certain areas where predation risk is higher (Hobbs and Cooper 2013). Scientists wondered how the restoration of wolves to Yellowstone after being absent for almost a century would change elk numbers and behavior and, in turn, their browsing and grazing effects on plants (Hobbs and Cooper 2013, Peterson et al. 2020, Hobbs et al. 2023) .

During the 1800s, there were tall communities of aspen trees in the uplands and cottonwoods and willows along rivers and streams in northern Yellowstone (Houston 1982, Meagher and Houston 1998). Many of the smaller stream channels with willows had dams maintained by beavers (Smith and Tyers 2012, Tyers 2020). Although these aspen and riparian communities only comprised about 4 to 6% of northern Yellowstone, they supported a diversity of wildlife (Houston 1982, Meagher and Houston 1998). However, many of these communities changed, or transitioned, into grasslands following many decades of intense browsing by abundant elk following the extirpation of wolves and cougars in the 1920s and the concentration of elk inside the park due to hunting outside the park and feeding inside the park (Houston 1982, Kay 1990, National Research Council 2002, Beyer et al. 2007, Hobbs and Cooper 2013, Peterson et al. 2020, Hobbs et al. 2023). Remaining sprouts or saplings were less than 3 feet (1 meter) tall, whereas a height of 8 to 10 feet (2.5 to 3 meters) is necessary to extend beyond the reach of browsing elk and enable the tree to keep growing (Brice 2022, Brice et al. 2022). The loss of beavers and their dams due to a lack of tall willows contributed to a lowering of water tables and the down-cutting (incision) of streambeds (Wolf et al. 2007). Faster flows straightened channels and separated them from their historic flood plains where fine sediments allowed cottonwoods and willows to establish (Wolf et al. 2007). Likewise, concentrated browsing by elk decreased the abundance, recruitment, and stature of sagebrush on the lower-elevation winter range in the Gardiner basin by the 1950s (Singer and Renkin 1995, Wambolt and Sherwood 1999, Wagner 2006). In contrast, grazing by at least 16,000 to 19,000 elk in the late 1980s had little effect on grass production compared to earlier decades with fewer elk (Coughenour and Singer 1996, Frank and McNaughton 1992, 1993).

Following wolf restoration, along with increasing numbers of bears and cougars, large carnivores contributed to a substantial decrease in elk abundance in northern Yellowstone and changed their distribution, with fewer elk in the middle and upper portions of the winter range and a larger portion of fewer elk at lower elevations in and outside the park (White and Garrott 2005a, White et al 2012, Middleton et al. 2013a,b; 2018). Reduced browsing by elk in higher-elevation areas led to increases in the heights and growth rates of aspen in some areas over the next 15 years, especially in the eastern portion of the winter range (Ripple and Beschta 2007, 2012; Painter et al. 2014, 2015). By 2016, about 10% of aspen stands in northern Yellowstone had plants greater than 6.5 feet (2 meters) tall (Brice 2022, Brice et al. 2022). Many biologists attributed this finding to altered elk behavior, such as the avoidance of these areas due to an increased risk of predation (Laundré et al. 2001, Ripple et al. 2001, Ripple and Beschta 2004).

However, recent data indicates less than 25% of young aspen in northern Yellowstone grow tall enough to escape browsing and the regeneration of young aspen has ceased at many sites, suggesting stand deterioration is continuing (MacNulty 2023). Elk have continued to forage in risky areas at night (when wolves were usually were not actively hunting), including aspen stands, and many aspen stands were in low-risk areas (Fortin et al. 2005, Kauffman et al. 2010, Kohl et al. 2018, 2019; Cusack et al. 2019). Others demonstrated wolves indirectly contributed to increased aspen recruitment by helping to reduce the elk population size (along with other predators), but elk response to predation risk did not reduce elk foraging in a way that measurably increased aspen recruitment (Kauffman et al. 2010, MacNulty 2023). Most importantly, hunter harvests of elk north of the park reduced elk density and played a significant role in increased aspen recruitment (Kauffman et al. 2010, Painter et al. 2014, 2015, 2018). Collectively, the current body of evidence indicates the strength of trophic cascades across northern Yellowstone are highly variable, and influenced by multiple predators, including humans (Hobbs and Cooper 2013, Peterson et al. 2020). Climate warming may limit the cascading effects of wolves on aspen because many stands are in areas forecast to become increasingly unsuitable for aspen due to drying and moisture stress (Piekielek et al. 2015, Brice et al. 2022).

Cottonwoods on the banks and floodplains of streams and rivers in the upper elevation portion of northern Yellowstone initially showed signs of recovery following wolf restoration and decreased browsing by elk (Beschta 2003). Biologists found thousands of seedlings and saplings in 2001 and 2002 and these young trees continued growing at higher elevations along the upper Lamar River and Soda Butte Creek with less browsing from elk (Rose and Cooper 2016). However, browsing by abundant bison kept saplings short in the Lamar Valley, which is likely to continue into the near future (Ripple and Beschta 2003, Beschta and Ripple 2010, 2015; Ripple et al. 2010, Painter and Ripple 2012).

Experiments from 2001 to 2017 in the middle elevation portion of the northern winter range indicated browsing of willows remained high (60% of growth each year) in the 2000s after the restoration of wolves (Bilyeu et al. 2008). Willows with adequate water could withstand these high levels of browsing, while willows within fenced areas without browsing grew slowly without access to elevated water tables (Hobbs and Cooper 2013, Hobbs et al. 2023). Conversely, willows in fenced areas with access to high water tables grew rapidly and were about 13 feet (4 meters) tall by 2016 (Bilyeu et al. 2008, Marshall et al. 2013, 2014). In other words, the historic loss of beaver dams slowed the recovery of willows, even with reduced browsing, due to lowered water tables (Johnston et al. 2007, 2011; Tercek et al. 2010). Biologists from the Custer Gallatin National Forest released 46 beavers at four sites in the Absaroka wilderness north of the park between 1986 and 1999 and these animals successfully established with some dispersal into areas of the northern winter range (Tyers 2020). With reduced browsing, willows naturally grew taller in some areas in middle and upper elevations of the northern range and beavers colonized them during 2011 to 2017. There was only one known beaver colony in northern Yellowstone from 1996 to 1998 but 20 existed by 2015 (Smith and Tyers 2012; D. Smith, unpublished data; Tyers 2020). It is uncertain whether beavers will persist in these areas given their need to frequently cut willows for food and dams (Hobbs and Cooper 2013, Peterson et al. 2020, Tyers 2020, Hobbs et al. 2023). Biologists are monitoring this situation to see if beavers will eventually recolonize a larger portion of northern Yellowstone.

Physiology

Male elk have evolved to retain their antlers long after the breeding season ends. The primary function of antlers is for displays and fights to establish dominance during the autumn breeding season when males compete for females (Geist 2002). However, bulls do not cast their antlers until a 2- to 3-month period in late winter or early spring (Hudson et al. 2002). Males that drop their antlers early can begin regrowth sooner and develop larger antlers before the next breeding season, thereby potentially achieving greater reproductive success (Metz et al. 2018, 2020b). However, antlers also have an important secondary function as weapons for deterring predators. Biologists in Yellowstone found males that cast their antlers early are selectively hunted and killed by wolves, even though they are in better condition than males retaining their antlers (Metz et al. 2018, 2020b). There is less risk of injury to attacking wolves when elk have no antlers. Thus, male elk may retain their antlers longer after the breeding season as weapons for fighting off wolves (Metz et al. 2018, 2020b).

Adult male elk that recently cast its' antlers in Yellowstone National Park. Photographer unknown. National Park Service photograph collection.

Elk are dietary and habitat generalists that can adapt to a variety of environmental conditions, as evidenced by their use of diverse ecological regions, habitats, and forages (Christianson and Creel 2007). They are well adapted to the predictable changes in seasons in temperate environments and can withstand chronic undernutrition through the winter due to their insulating fur, large rumen capacity to process low quality forage high in fiber, and abilities to reduce activities and metabolism to save energy, recycle urea for protein, and break down fat and protein for energy (Cook 2002, Hudson et al. 2002, Parker et al. 2009). They also have adapted behaviorally and physiologically to opportunistically exploit non-typical forages in Yellowstone (Garrott et al. 2009e).

Fires during the summer of 1988 burned extensive areas of conifer forest in the park used by elk as summer range, and large portions of the year-round range of the non-migratory Madison headwaters population in west-central Yellowstone. In subsequent years, biologists frequently observed elk eating burned bark during winter even when grasses and sedges were available (White et al. 2009a). This was surprising because bark was relatively poor-quality food with low crude protein, high fiber, and low digestibility compared to other forages (Jakubas et al. 1994). Biologists determined the fires had substantially reduced the levels of toxic compounds in the bark and loosened it from the trunks of the burned trees. Thus, even though it was far from optimal, bark was readily available above the snowpack and could be consumed rapidly and efficiently compared to other forages (Jakubas et al. 1994). Similarly, bark was absent from the rumens of northern Yellowstone elk during the 1960s except during severe winters when it was found in up to 60% of rumens (Greer et al. 1970, Craighead et al. 1973).

Some plants in geothermally warmed areas of Yellowstone grow through winter in run-off and along the banks of warm waterways, thereby providing relatively higher nutrition. Aquatic plants, such as water milfoil, in thermally warmed rivers had high crude protein and low fiber levels compared to many other winter forages (Garrott et al. 2009e, White et al. 2009a). Biologists frequently observed elk feeding on these forages in the Madison headwaters area, which was surprising because geothermal waters contain high levels of arsenic from magma sources under the earth's crust, which is absorbed by plants in these areas (Garrott et al. 2009e, White et al. 2009a). Arsenic can be toxic at the high concentrations present in many of these plants and reduce the life span of animals consuming it (Kocar et al. 2004). The high dietary intake of arsenic was confirmed by sampling bones from elk that died in the Madison headwaters area (Garrott et al. 2002, Garrott et al. 2009e). However, biologists determined elk had apparently evolved the capability to detoxify much of the ingested arsenic through reactions with microflora in the rumen (Garrott et al. 2002, Kocar et al. 2004, Garrott et al. 2009e).

Adult male elk feeding in a thermal area in Yellowstone National Park. Photograph by George Marler, National Park Service.

Anti-Predator Behaviors

Predation risk depends on where and when predators hunt and the behavior, condition, and habitat use of potential prey that make them vulnerable to detection and attack (Mech and Peterson 2003, Bergman et al. 2006, Kauffman et al. 2007, White et al 2009c). In Yellowstone, elk tend to return to the same areas each season, likely because familiarity helps them attain the resources they need to survive (White et al. 2010, MacNulty et al. 2020b). Wolves frequently move through areas occupied by elk without provoking a strong behavioral response until they focus on a group with potentially vulnerable individuals (Mech and Peterson 2003, MacNulty et al. 2007). As a result, differences in predation risk likely are primarily due to differences in the vulnerability of detected elk rather than the chance of encounters, with risk escalating during confrontations and dissipating relatively quickly thereafter (Bergman et al. 2006, Gude et al. 2006, White et al. 2009c). To reduce the probability of detection and attack, elk could alter their behavior, distribution, grouping tendencies, habitat use, or vigilance. However, these responses potentially could affect their energy expenditures and foraging behavior and, in turn, decrease their nutrition, body condition, pregnancy, and survival (Creel et al. 2007, Christianson and Creel 2010). The following sections provide our understanding of how elk responded to the restoration of predators and increased predation risk.

Seasonal Ranges and Habitat Selection—Northern Yellowstone elk did not substantially alter their seasonal ranges after wolf restoration (Mao 2003, Mao et al. 2005, White et al. 2010, Cusack et al. 2019, Kohl 2019). In winter, when accessible forage was constrained by deep snows, elk could not spatially separate themselves from wolves because they needed to access these areas for forage (Fortin et al. 2005, Mao et al. 2005, Kauffman et al. 2007, Gregory et al. 2009). Elk did not shift the location or configuration of their winter ranges to reduce overlap with wolves, even at high wolf densities (Mao 2003, Fortin et al. 2005, Mao et al. 2005, Kauffman et al. 2007). Instead, elk selected less steep terrain with lower snowpack that permitted easier movements to escape if attacked (Mao et al. 2005, Kauffman et al. 2007). Elk also moved between open grasslands and forested areas at different times of day to evade predators (Fortin et al. 2005, Gregory et al. 2009, Kohl et al. 2018, 2019).

There was no indication of any considerable change in overwinter nutrition following wolf restoration (Cook et al. 2004b, White et al. 2011, Middleton et al. 2013a). In summer, when nutritious forage was abundant, most elk distanced themselves from concentrated areas of wolves in northern Yellowstone by migrating to higher-elevation areas throughout the park and selecting more forested areas, particularly burned areas with a diversity of forbs and grasses with high nutritional value (Mao 2003, Mao et al. 2005, White et al. 2010, Nelson et al. 2012). This seasonal movement reduced encounter rates with wolves (Mao et al. 2005). Elk selected slopes on steeper terrain when wolves were present, perhaps to provide a better vantage point and make it more difficult for wolves to attack (Mao 2003, Mao et al. 2005).

Similarly, most elk in the Madison headwaters population showed fidelity to their home ranges after wolf restoration, but their movements became more dynamic and home ranges became larger (Gower et al. 2009b). Nineteen radio-collared elk dispersed more than 9 miles (15 kilometers) from areas with very high densities of wolves (Gower et al. 2009b). The Madison headwaters area experiences deep snowpack which limits the ability of elk to modify their activities and movements to mitigate predation risk (Gower et al. 2009b). Elk selected portions of the landscape with lower snowpack and terrain features, such as near rivers or steep slopes, that increased their probability of escape if attacked (Mao et al. 2005, Bergman et al. 2006, Kauffman et al. 2007, White et al. 2009b,c; Dunkley 2011). However, they did not make broad changes in habitat selection that altered their diets or nutrition (White et al. 2009b,c). Elk continued to select areas with higher food availability during winter, even though wolves frequently were present in these areas (White et al. 2009b,c). There was no change in over-winter nutrition after wolves became established, but predation reduced elk numbers by 70% in the area (White et al. 2009b,c).

Grouping Behavior—Elk in northern Yellowstone congregated in larger groups after wolf restoration with typical group sizes of about 85 elk in summer and 200 elk in winter (Mao 2003). Group sizes were larger in open grassland areas with higher wolf densities, which may have increased the probability of elk detecting predators or escaping attack by being one of many prey (Mao et al. 2005). In addition, larger group sizes and more dynamic grouping behavior may be an effective strategy when other defensive tactics, such as fleeing, do not work well in deep snow or thick vegetation that hinder efficient escape (Mao 2003, Mao et al. 2005, Gower et al. 2009c).

Elk in the Clarks Fork, Madison headwaters, and Madison Valley populations also congregated into larger groups in open areas after wolf restoration (Grigg 2007, Gower et al. 2009c, Proffitt et al. 2009). Elk altered their grouping behavior depending on wolf presence and whether a kill had recently occurred in the area. In contrast, elk in the Gallatin population decreased group sizes and shifted habitats from grasslands to forests to reduce their level of predation risk (Creel et al. 2005). These differences in behavioral responses among areas are likely due to differences in snowpack, habitats, and other factors that influence predation risk and prey vulnerability (Gower et al. 2009c, Proffitt et al. 2009, 2010, 2013; Rickbeil et al. 2019).

Vigilance—Elk in the northern Yellowstone and Gallatin populations increased their visual awareness when wolves were present. Thus, several biologists concluded the risk of predation reduced time for foraging by elk, which could decrease their nutrition, body condition, pregnancy, and survival (Laundré et al. 2001, Childress and Lung 2003, Wolff and Van Horn 2003, Lung and Childress 2007, Winnie and Creel 2007, Liley and Creel 2008). However, the likelihood of a foraging bout by elk in the Madison headwaters population was slightly higher in the presence of wolves, possibly because wolves hunted primarily during crepuscular hours (daylight and dusk) and were relatively inactive during the day when behavioral studies were conducted (Gower et al. 2009a). Elk could remain more vigilant during the high-risk crepuscular hours but compensate by increasing foraging during the lower-risk daytime hours (Gower et al. 2009a). Scans of their surrounding environment by feeding elk were short and usually occurred while elk were chewing food prior to swallowing (Gower et al. 2009a). Thus, there was little reduction in foraging efficiency. Elk from the Clarks Fork population that also spent summer in northern Yellowstone increased their vigilance when wolves approached within about one-half mile (1 kilometer; Middleton et al. 2013a). However, the feeding rates of elk were not reduced, suggesting small increases in vigilance did not reduce food intake (Middleton et al. 2013a).

The contrasting results among studies likely reflect a focus on different behavioral activities by researchers, the subjective nature of classifying vigilance behavior, and the potential for several behaviors to occur simultaneously (Gower et al. 2009a). Regardless, heightened behavioral alertness is an obvious response by elk when wolves are present and threatening to attack (Gower et al. 2009a). A loss of foraging efficiency certainly occurred during or immediately following a direct encounter with wolves (Gower et al. 2009a). However, this interruption of feeding only lasted a short time because elk were undernourished during winter and needed to resume foraging (Gower et al. 2009a).

Adult female elk in Yellowstone National Park. Photograph by Neal Herbert, National Park Service.

Movements—Northern Yellowstone elk did not substantially alter their migration pathways or summer use areas after wolf restoration, and there was no evidence of an increase in long-distance dispersal movements (White et al. 2010). Elk mortality from wolves was low during migration and on the summer range because elk migrated away from the most concentrated area of wolf activity and selected habitats at higher elevations that allowed them to obtain high-quality growing forage (Mao et al. 2005, White et al. 2010). During winter, factors such as habitat, snowpack, and terrain strongly influenced elk distribution and wolf kill sites, creating good hunting areas for wolves and places of relative safety for elk (Kauffman et al. 2007, Kohl et al. 2018, 2019). Groups of elk only encountered wolves about every 7 to 11 days and most elk quickly adjusted their behavior to survive these encounters (Middleton et al. 2013a, Cusack et al. 2020). After wolf restoration, elk tended to make longer movements during the crepuscular hours and shorter movements during other times of day (Forester et al. 2007). When attacked by predators, elk often moved into rivers, up steep terrain, into human developed areas, or along forest or cliff edges (Mao et al. 2005, Kauffman et al. 2007, MacNulty et al. 2012, 2020a).

Elk in northern Yellowstone responded to varying predation risk from cougars and wolves by moving between different places at different times of day to avoid one predator while remaining relatively safe from the other (Kohl et al. 2018, 2019). Elk moved out of forests and into open areas at night to avoid cougars while wolves were relatively inactive. They moved into forested areas during the day when cougars were relatively inactive, and wolves were searching for prey in open areas (Kohl et al. 2018, 2019). These behaviors enabled most elk to remain relatively safe from both predators by foraging in areas where there were lulls in predator activity (Kohl et al. 2018, 2019). Likewise, elk in the Gallatin and Madison Valley populations made relatively short movements of about 1 mile (2 kilometers) from open to forested areas when wolves were expected or nearby (Creel et al. 2005, Gude et al. 2006).

Elk from the Clarks Fork population that spent summer in northern Yellowstone also increased their movements when wolves approached to within about one-half mile (1 kilometer, Middleton et al. 2013a). Wolves generally left the area within 8 hours, so movements of elk decreased within 24 hours (Middleton et al. 2013a). Likewise, elk in the Madison Valley population increased movements when wolves were within 3 miles (5 kilometers) and after encountering wolves, with movements dissipating between 8 and 48 hours later (Gude et al. 2006, Grigg 2007, Proffitt et al. 2009). Movements by elk in the Madison headwaters population were more frequent and variable across the landscape as wolves increasingly encountered and attacked them (Gower et al. 2009b). Thus, there were increases in home-range sizes and some changes in the locations of home ranges after wolf colonization (Gower et al. 2009b). Some elk left the Madison headwaters area or became migratory following wolf colonization (Gower et al. 2009b). Biologists did not detect these dispersal and migratory movements prior to wolf colonization, suggesting they were an attempt to avoid predation risk by spatially segregating themselves from high wolf-use areas (Gower et al. 2009b).

Elk moving along Specimen Ridge in Yellowstone National Park. Photograph by J. R. Douglass, National Park Service.

Body Condition and Pregnancy—The probability of pregnancy in northern Yellowstone elk decreases as body fat decreases (Cook et al. 2004a,b). Thus, some scientists suggested predation risk from wolves could indirectly contribute to lower pregnancy rates in elk by altering foraging patterns, decreasing nutrient intake, and resulting in insufficient body condition for breeding, conception, and gestation (Creel et al. 2007, 2009; Christianson and Creel 2010). However, forage is generally abundant and nutritious during summer and autumn when most elk leave the northern winter range and distribute throughout the park in areas with lower wolf densities (Mao et al. 2005, White et al. 2010). In addition, the body fat levels of adult female elk during mid-winter remained high after wolf restoration (2000 to 2006) and at levels comparable to before wolf restoration (1962 to 1968; White et al. 2011). In turn, pregnancy rates of young females were high (90%) and similar between periods (White et al. 2011, MacNulty et al. 2020b). There was little evidence for predation risk effects from wolves or other predators on the nutrition, body condition, or pregnancy rates of northern Yellowstone elk (White et al. 2011). Similar conclusions were reached for migratory elk in the Clarks Fork, non-migratory elk in Madison headwaters area, and other populations in the Greater Yellowstone Area (Gower et al. 2009a,b ; White et al. 2009b,c; Middleton et al. 2013a).

Conclusions

Since the recovery of large predators, the grazing system in northern Yellowstone has switched from being dominated by elk to being dominated by bison (White et al. 2022a,b). Most bison in northern Yellowstone spend summer in the Lamar Valley and nearby areas before moving downslope to the Blacktail Deer Plateau during the winter (Geremia et al. 2015b). Fewer female elk with calves spend winter at higher elevations in the park, such as the Lamar Valley or Blacktail Deer Plateau, due to the increased risk of predation in deeper snowpack (White et al. 2010, 2012; see Chapters 4 and 6). Studies prior to predator restoration found minimal competition between bison and elk (Houston 1982, Singer and Norland 1994, Barmore 2003), but the current grazing and predator communities are unlike any since the park's establishment (Geremia and Hamilton 2019, 2022). Biologists are continuing to monitor the effects and stability of this transition.

Elk reduce the risk of predation from multiple predators by making temporal and spatial changes in where they forage to avoid predator activity and quickly execute anti-predator behaviors in the presence of wolves (Gower et al. 2009a-c; White et al. 2009b,c; Middleton et al. 2013a, Kohl et al. 2018, 2019). These behaviors enable elk to maintain their body condition, pregnancy rates, and gestation without having to resort to more energetically costly antipredator behaviors such as using suboptimal habitats, shortening foraging time, or increasing vigilance at the expense of feeding time (Gower et al. 2009a-c; White et al. 2009b,c; Middleton et al. 2013a, Kohl et al. 2018, 2019).

Adult male elk herding females during the breeding season (rut) in Yellowstone National Park. Photograph by Neal Herbert, National Park Service.

Chapter 8
Human Influences

Introduction

Although public lands form the core of the Greater Yellowstone Area, most elk populations, including northern Yellowstone elk, use private lands extensively during winter when they migrate out of mountainous landscapes, such as Yellowstone National Park, to lower-elevation valleys (Haggerty and Travis 2006, Haggerty et al. 2018, Tilt 2020, Gigliotti et al. 2022, 2023). Residents in the Yellowstone area have strong favorable attitudes toward migratory wildlife, which are a primary reason they live in the area and a major benefit to the economy (Metcalf et al. 2016). Elk provide extensive recreational opportunities through hunting, photography, and wildlife watching, and are a major part of the social character of communities in the area (Metcalf et al. 2016, Middleton et al. 2019). At the same time, these areas contain more cultivation, development, fences, livestock, and roads, which sometimes leads to conflicts over crop depredation, disease transmission, and property damage (Gude et al. 2007, Hansen and Phillips 2018, Tilt 2020, Gigliotti et al. 2022, 2023). The following sections discuss some of the major human influences on northern Yellowstone elk and their environment which, in turn, affect their adaptations, behaviors, distribution, habitats, population dynamics, and management.

Visitor photographing an adult elk in Yellowstone National Park. Photograph by J. Hemphill, National Park Service.

Brucellosis

Cattle brought into the northern Yellowstone area infected wild bison and elk with the non-native disease brucellosis by 1917 (Rush 1932, Meagher and Meyer 1994). This disease is caused by the bacterium *Brucella abortus* and can induce abortions and be transmitted back to cattle if they contact infectious birthing tissues (Cheville et al. 1998). Brucellosis concerns livestock producers because, if cattle become infected, there is lost income from killing infected cattle, additional testing requirements, and possible restrictions on interstate transport and international trade (Bidwell 2010). The prevalence of brucellosis in about 1,700 elk captured or shot in the northern Yellowstone area during 1961-1962 was less than 1% (Greer 1962). The northern Yellowstone elk population expanded its winter range north of the park and into the Paradise Valley during the late 1970s in response to increasing abundance and other factors (Houston 1982, Lemke et al. 1998). The number of elk using this area increased after the extensive fires in the park during the summer of 1988 and varied thereafter around 3,000 elk (Lemke et al. 1998). This range expansion resulted in the mingling of elk and cattle in the Paradise Valley during the potential abortion and birth period for elk from February through mid-June (Lemke et al. 1998, Rickbeil et al. 2019, Tilt 2020). Thus, the timing of spring migration and duration elk remain on winter range north of the park affect the risk of brucellosis transmission to cattle (Cross et al. 2010, Rickbeil et al. 2019). Risk is higher following winters with increased snowpack when elk initiate spring migrations later and many elk spend the brucellosis transmission period in areas where mingling with cattle occurs (White et al. 2012, Rickbeil et al. 2019, Tilt 2020).

During 1985 to 2009, the prevalence of brucellosis in about 2,900 elk harvested during the Gardiner late season hunt north of the park in hunting district 313 was 2% to 4% (Lemke 2009). However, the prevalence of brucellosis in elk harvested north of the park from 2010 to 2020 was about 13% to 15%, and the prevalence further north in the southern Paradise Valley was about 20% to 30% (Montana Fish, Wildlife and Parks 2017, 2018b, 2020). Elk have become more concentrated in the Paradise Valley of Montana during the last several decades, in part, due to accessing irrigated alfalfa fields (Rayl et al. 2019, Tilt 2020). This nutritious, year-round forage source decreases the tendency for elk to migrate away from these areas during late winter and spring (Garroutte et al. 2016, Haggerty et al. 2018, Barker et al. 2019a,b). Many large groups totaling thousands of elk are spending more time in this area, which presents significant challenges for landowners including competition with livestock for forage and hay, damage to fences, and brucellosis transmission (Tilt 2020, Gigliotti et al. 2022, 2023).

Montana has implemented hazing and shooting efforts in recent years to disperse some elk, but many elk still mingle with cattle during the potential transmission period (Rayl et al. 2019, Tilt 2020). There are no substantive efforts being implemented to prevent brucellosis transmission from elk like the intrusive measures (vaccination, culling, test-and-slaughter, fertility control, relocation) the State of Montana has suggested the National Park Service take with bison in Yellowstone National Park (White et al. 2015). State biologists have concluded these methods are not likely to be effective, feasible, or politically or socially acceptable to implement on wide-ranging elk populations (Rayl et al. 2019). Instead, biologists indicated the primary strategy for managing brucellosis transmission risk to livestock is to prevent mingling by hazing, hunting, fencing or removing haystacks, and improving forage on public lands (Rayl et al. 2019). Brucellosis is spreading in elk throughout the Greater Yellowstone Area and genetic data indicate elk have infected cattle herds with brucellosis more than 30 times since 1998 (Kamath et al. 2016). Elk exposed to brucellosis now inhabit an area encompassing about 17 million acres and the current spread is not linked to Yellowstone bison or elk, but rather to other lineages in elk (Kamath et al. 2016). The eradication or suppression of brucellosis would require eliminating the disease in elk by attempting to capture, test, and vaccinate or slaughter many elk across the entire Greater Yellowstone Area, which most people consider unacceptable and impossible at this time (National Academies of Sciences, Engineering, and Medicine 2017).

Predators and scavengers may reduce the transmission of brucellosis by removing infectious birthing materials from the environment (Cross et al. 2013, Garrott et al. 2013). The recovery of bison, wolves, cougars, and grizzly bears in the Yellowstone area has increased the amount of carrion and, in turn, the abundance of scavengers that could remove brucellosis-infected tissues before they are discovered by susceptible bison, cattle, or elk (White et al. 2015, Stahler et al. 2020). The Wyoming Game and Fish Department protects scavengers such as coyotes and red foxes on some elk feed grounds to reduce the time infectious tissues remain on the landscape (Cross et al. 2013).

Adult female elk and calves crossing a river in Yellowstone National Park. Photograph by Harlan Kredit, National Park Service.

Climate Warming

The climate patterns of winter snowpack and summer precipitation and plant growth in the Yellowstone area have strongly influenced elk adaptations in behavior, movements, and physiology and, ultimately, their population dynamics over many thousands of years (Houston 1982). However, average annual temperatures increased about 2.3° Fahrenheit (1.3° Celsius) during 1950 to 2018 in the Greater Yellowstone Area (Hostetler et al. 2021). In northern Yellowstone, these changes have resulted in less snow at lower elevations, earlier snow melt and plant growth, longer and drier growing seasons, and more frequent drought (Tercek et al. 2015, Thoma et al. 2015). The regional warming trend is predicted to continue, with an increase in average annual temperatures of another 2° Fahrenheit across all seasons, milder winters with fewer days below freezing, and earlier spring vegetation green-up (Hostetler et al. 2021).

Continued climate warming would further alter precipitation patterns, snow melt and forage green-up, elk migration patterns, timing of parturition, and calf growth rates and survival in complex and unforeseen ways (Wilmers and Getz 2005, Parker et al. 2009, Wilmers et al. 2013, Middleton et al. 2018, Barker et al. 2019a,b). Elk give birth to calves when new plant growth enables higher nutrition to support lactation, calf growth, and the replenishment of body condition (Parker et al. 2009). By adjusting the timing of migration to a warming climate, northern Yellowstone elk have demonstrated resilience and maintained access to nutritious vegetation during summer (Rickbeil et al. 2019). Migrant elk began departing their summer ranges later in autumn, arriving at their winter ranges about 50 days later than in the early 2000s, and then leaving their winter ranges earlier in spring (Rickbeil et al. 2019). However, if climate warming eventually alters the ability of elk to predict or track the green-up in vegetation by even a few weeks, then body condition in autumn and pregnancy rates could decrease (Middleton et al. 2018).

Milder winters should lead to increased survival of elk because temperature and snowpack influence energy depletion and nutrition which, in turn, influence body condition and vulnerability to predation (Cook et al. 2004b, 2013; Parker et al. 2009, Smith 2021). Snowpack also influences the timing of elk migration outside the park which affects the number of elk exposed to harvests in Montana (Rickbeil et al. 2019). Decreased snowpack as winters become milder could decrease the susceptibility of elk to predation and harvest, and increase forage availability, body condition, survival rates, and population growth (Mech et al. 2001, Metz et al. 2012, 2020a,b; Smith 2021). Earlier spring green-up could improve nutrition for elk during the latter stages of gestation and lactation, which would contribute to increased birth weight, growth, and survival of calves (Merrill and Boyce 1991, Cook et al. 2004a,b; Parker et al. 2009, Frank et al. 2013, Middleton et al. 2018).

However, a continued drying and warming trend could result in more hotter days and more frequent droughts with continued climate warming (Gross and Runyon 2020, Yellowstone Center for Resources 2021). Hotter, drier summers could result in the senescence of vegetation earlier in the summer with fewer green grasses available by middle to late summer (Merrill and Boyce 1991, Frank et al. 2013, Lachish et al. 2020). There was a 20% reduction in grass and forb production in northern Yellowstone during a severe drought from 1988 to 1989 and no stimulating effects of grazing on plant production during a drought in 2000 and 2001 due to decreased soil moisture (Frank and McNaughton 1992, Frank 2007). An early decrease in food quality and quantity could result in lactating adult females entering autumn and winter with marginal fat reserves for pregnancy and survival (Cook et al. 2004a,b; Middleton et al. 2013b, 2018). Elk in Yellowstone were severely malnourished with low fat reserves during the winter of 1989 following the severe drought the previous summer (DelGiudice et al. 2001). In addition, levels of body fat in adult female elk in northern Yellowstone during the winters of 2000 to 2002 were marginal, suggesting some nutritional limitation occurred on the summer range, especially for females that nursed through summer (Cook et al. 2004a,b).

These potential divergent impacts of climate warming on the nutrition and body condition of elk make predicting the future consequences of climate change in Yellowstone difficult (Wilmers and Getz 2005, Wilmers et al. 2013, Lachish et al. 2020). Research on elk populations in the northwestern United States has already detected a decrease in recruitment from 1989 to 2010 due, in part, to changes in precipitation patterns and forage conditions (Lukacs et al. 2018). Continued climate warming will modify the timing and production of forage, as well as elk body condition, movement patterns, and demographic rates, in complex and contrasting ways (Wilmers et al. 2013, Lachish et al. 2020).

Elk migrating along a ridge in Yellowstone National Park. Photograph by Jacob W. Frank, National Park Service.

Land Use

There are decreasing trends in ungulate migration world-wide, including in the Greater Yellowstone Ecosystem, due to barriers and impediments, habitat fragmentation, and the loss of herd knowledge and memory (Berger 2004, Middleton et al. 2013b, 2019; Kauffman et al. 2018). Fragmentation of habitat or barriers to movements eliminated most historic migration pathways for ungulates in North America, including perhaps as many as 75% in the Greater Yellowstone Area (Berger 2004). Human activities have shortened, disrupted, or threatened most pathways elsewhere. Protective parks and wilderness areas are often inadequate for conserving long-distance migration corridors which generally cross many jurisdictions (Berger et al. 2006, Berger and Cain 2014, Kauffman et al. 2018, Middleton et al. 2019). If ungulates cannot move across the landscape due to barriers, such as development or fences, they may become more concentrated and forage in smaller areas with adverse consequences, such as overgrazing, increased competition for forage, and disease transmission (White et al. 2013c). Impaired migration also diminishes the transfer and deposition of nutrients across the landscape in the form of feces, urine, and carcasses, which spatially reorganizes energy and nutrient dynamics in ecosystems (White et al. 2013c). In addition, diminished dispersal could impact population genetics due to less gene flow among herds and populations.

Changes in land use and predator restoration have interacted with a warming climate to contribute to fewer elk migrating into the park (White et al. 2012, Middleton et al. 2013a,b; 2018). Elk spending winter outside the park often choose areas close to irrigated livestock pastures that can provide more nutritious forage, even during winter, than elk that remain at higher-elevations (Barker et al. 2019a,b; Gigliotti et al. 2023). Many of these elk have shown a reduced tendency to migrate back into the park during summer and, instead, remain year-round in valleys with irrigated pastures (Middleton et al. 2013a,b; 2018; Barker et al. 2019a,b; Tilt 2020). This trend in resident elk numbers increasing outside the park with less migration into the park may be exacerbated in future years with a shorter peak growing season at higher elevations that contributes to summer-autumn nutritional limitations and lower pregnancy rates in lactating elk (Cook et al. 2004b, 2016; White et al. 2012, Middleton et al. 2013a,b, 2018). Elk in the North Sapphire Mountains in southwestern Montana tended to migrate less if they had areas irrigated during summer in their winter range, especially if the occurrence of native forage was unpredictable on migrant summer ranges either due to droughts, fires, or other disturbances (Barker et al. 2019a,b). Thus, the migratory tendencies of elk may be reduced under these circumstances or migrants may have lower pregnancy rates and recruitment into the population (Barker et al. 2019a,b).

Adult female elk in Yellowstone National Park. Photograph by Neal Herbert, National Park Service.

Hunting

Human harvests can contribute substantially to variations in adult female mortality among years because survival rates are usually much higher in elk populations not subject to harvests (Brodie et al. 2013). Liberal harvests can be a major factor influencing the survival and population growth of elk, often exceeding the effects of predators (Eberhardt et al. 2003, 2007; Vucetich et al. 2005). From 1976 to 2009, hunters north of the Yellowstone National Park boundary killed large numbers of prime-aged females during the late-season elk hunt (Evans et al. 2006, Wright et al. 2006). However, hunters harvested few calves and predation was low until after the restoration of grizzly bears by the late 1980s and wolves by the late 1990s (Evans et al. 2006, Wright et al. 2006, Eberhardt et al. 2007, MacNulty et al. 2016, 2020b). High calf survival compensated for the harvests of adult females, as evidenced by the rapid increase in elk numbers from 1976 to 1988 (MacNulty et al. 2016, 2020b). By the early 2000s, however, the restored predator community was killing a substantial number of calves and older elk while hunters continued to harvest large numbers of prime-aged female elk during the late hunt (Vucetich et al. 2005, Evans et al. 2006, Wright et al. 2006, Eberhardt et al. 2007, Proffitt et al. 2014). Thus, state managers reduced harvest permits to offset predation (Evans et al. 2006, Wright et al. 2006, Montana Fish, Wildlife and Parks 2019).

Responses of elk to human hunters can be as strong, or stronger, than responses to carnivore predation risk. There were fewer and smaller groups of females and young in open grasslands, and movement rates increased substantially, after the rifle hunting season began in the Madison

Valley (Proffitt et al. 2009, 2010). Many elk moved to privately owned lands where owners limited public hunting, thereby reducing their susceptibility to harvest (Proffitt et al. 2009, 2010, 2013). High-quality forage is more abundant in irrigated pastures outside the park than in grasslands therein, which can strongly influence the movement patterns and demographic rates of elk (Garroutte et al. 2016, Barker et al. 2019a,b; Gigliotti et al. 2022, 2023). Outside hunting seasons, some elk in the Madison Valley used habitats on public lands more often, but females tended to remain on private ranchlands through winter and calving (Proffitt et al. 2010, 2013). As a result, state wildlife managers may need to decrease elk use of private refuge areas to increase harvests (Haggerty and Travis 2006, Proffitt et al. 2010, 2013; Barker et al. 2019a,b).

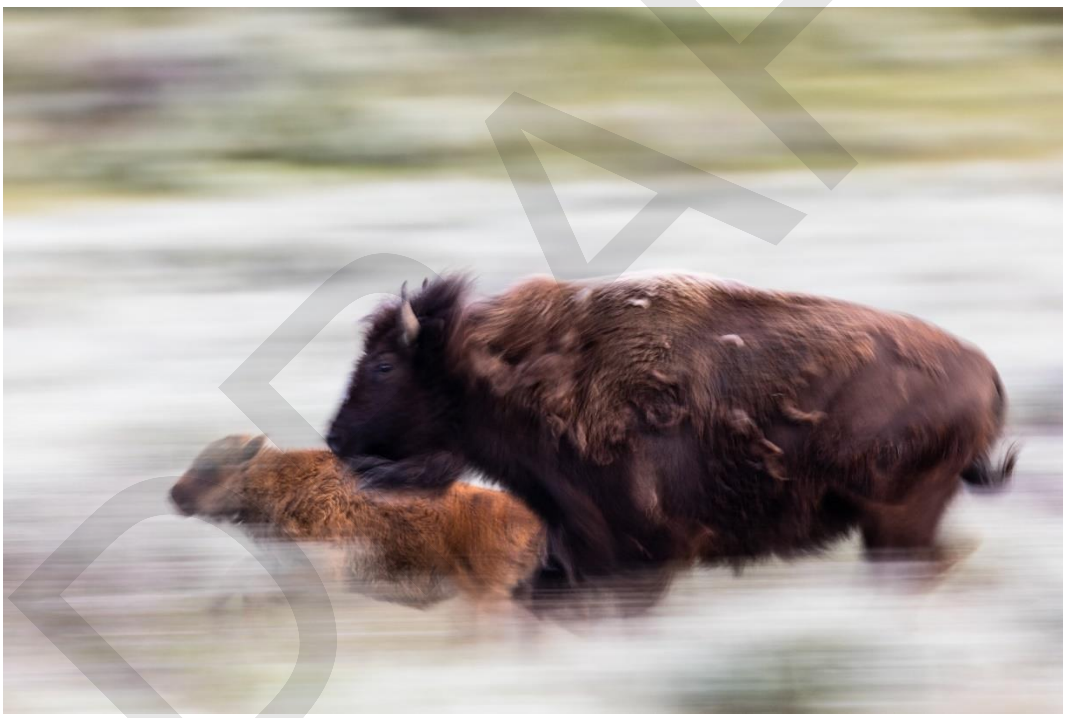
Invasive Plants

Abundant ungulates in the Yellowstone area increase the availability of nitrogen in the soil by depositing fertilizers (feces, urine) and breaking down plant litter, which helps roots and associated fungi take in nitrogen and water (Frank et al. 2013). As a result, climate is the main factor influencing grass production each year because variations in precipitation and temperature strongly influence soil moisture, which can limit production (Frank et al. 2013). There has been a substantial increase in the amount of carbon dioxide in the atmosphere over the past two centuries, which can increase plant growth by reducing water loss and facilitating photosynthesis (Friedlingstein et al. 2019, Frank 2022). This increase may have indirectly contributed to more grass production and abundant forage for ungulates in Yellowstone, especially in wetter areas like the Lamar Valley where park managers planted nonnative cool-season grasses, such as clover, oats, smooth brome, and timothy, for hay during the early 1900s (White et al. 2022a,b). These grasses inefficiently use water but thrive in wet areas and remain productive under grazing, which enabled them to outcompete native plants and spread (Geremia and Hamilton 2019, 2022; Renkin 2022, Wacker 2022).

Trends towards warmer and drier conditions with more frequent drought could worsen the spread of invasive winter annual grasses which threaten native bunchgrass communities in the warmer and drier areas of the park (Renkin 2022, Wacker 2022). Invasive species usually have short generation times and high productivity, which enables them to disperse more quickly than natives into areas as the climate warms (Wilmers et al. 2013, Renkin 2022, Wacker 2022). Winter annuals germinate in autumn and begin to grow early in the spring, which enables them to outcompete native plants in dry areas where water and nutrients typically are only available during short periods in spring and autumn (Renkin 2022, Wacker 2022). Drier grassland and shrub-steppe areas in the lower and middle elevation areas of northern Yellowstone are vulnerable to invasions of winter annuals, which have displaced native bunchgrass communities in large portions of the Gardiner basin near the northern park boundary (Geremia and Hamilton 2019, 2022; Yellowstone Center for Resources 2021). Many hundreds of acres in this area were irrigated, cultivated for hay, and grazed by livestock until the 1940s, and managers eventually planted crested wheatgrass in many of these hayfields (White et al. 2022a,b). More recently, high nitrogen deposition by wild ungulates and a warming climate allowed annual wheatgrass and desert alyssum to spread into these disturbed areas (Yellowstone Center for Resources 2021).

The regional warming trend is predicted to continue in northern Yellowstone with milder winters, earlier spring vegetation green-up, and more frequent drought; though there is substantial uncertainty around these predictions (Hostetler et al. 2021). If summers become hot and dry, there could be decreased production across grasslands and shrub-steppe due to lower soil moisture which, in turn, limits absorption of water and nutrients by plants (Gross and

Runyon 2020, Yellowstone Center for Resources 2021). Short ephemeral pulses of nutrient availability in wet grassland areas could promote the growth of drought-tolerant plants, including annuals, winter-annuals, and slow-growing bunchgrasses and other graminoids (Gross and Runyon 2020, Yellowstone Center for Resources 2021). Shrub and bunchgrass-dominated plant communities in dry upslope areas on the Blacktail Deer Plateau, Little America, and the slopes of the Lamar Valley could be invaded by annual plants (Yellowstone Center for Resources 2021, Wacker 2022). As a result, there could be a decrease in numbers of elk due to lower plant production contributing to decreased body condition, pregnancy, and survival (Yellowstone Center for Resources 2021). More intense droughts would further limit forage availability in late summer and winter (Wilmers et al. 2013). These changes could reduce the capacity of the park to support elk and other ungulates, with some animals being unable to obtain adequate fat and protein reserves for pregnancy and survival (Yellowstone Center for Resources 2021). In turn, there could be larger migrations and dispersal out of the park, with more elk remaining outside the park on agricultural land (White et al. 2012, Geremia et al. 2014, Middleton et al. 2013b, 2018).



Bison female and calf running in the Lamar Valley of Yellowstone National Park. Photograph by Jacob W. Frank, National Park Service.

If summers begin earlier but are wetter, higher decomposition rates in warm, wet soils could make more carbon, nitrogen, and phosphorus available to plants. Prolonged nutrient and water availability could favor faster-growing grasses, including rhizomatous and shallower rooted forms, as well as annual plants (Gross and Runyon 2020, Yellowstone Center for Resources 2021). These conditions also could enhance grazing feedbacks that further promote primary production, especially in higher-elevation wet areas with grazing-tolerant, cool-season grasses

(Geremia and Hamilton 2019, 2022). This could contribute to an increase in numbers of bison in northern Yellowstone, with more bison remaining in the park during winter due to increased forage availability (Yellowstone Center for Resources 2021). This could potentially increase competition for forage with elk.

Conclusions

Residents of the Greater Yellowstone Area have been extremely supportive of efforts to conserve elk in the region. However, human presence and rural residential development has increased rapidly in the past several decades, with land use modifications and changes in ownership to people with more diverse needs and values (Haggerty and Travis 2006, Haggerty et al. 2018). Many elk in the Yellowstone area are used to the day-to-day activities of people and often feed, move, and rest near houses, roads, agricultural fields, and recreational areas (Tilt 2020). These animals have adjusted their behaviors and movements to recurring activities, though some unexpected disturbances may cause short-term movements with minor energetic costs. The continued protection of habitat, migration corridors, and herd knowledge of the broader landscape in the face of increased development will require strong partnerships among government agencies, local communities, and private landowners (White et al. 2013a, 2022; Berger and Cain 2014, Middleton et al. 2019, Gigliotti et al. 2022).

In 2003, the Montana Legislature directed the Fish and Wildlife Commission to manage elk populations at or below sustainable population numbers by 2009 based on habitat assessments (Montana Code Annotated [MCA] 87-1-301, 87-1-323). The primary method used by the Commission and Montana Fish, Wildlife and Parks to reduce numbers of elk is regulated public harvests in designated hunting districts (MCA 87-1-301). These harvests are not always effective at limiting elk numbers, however, with more than 60% of hunting districts over objective and 50,000 elk above objective for the entire state in 2021 (Montana Fish, Wildlife and Parks 2021b, United Property Owners of Montana 2022). Increasing elk numbers on agricultural lands has led to conflict and litigation, with state personnel attempting to remove elk from some areas in recent years using hazing and hunting or shooting (Rayl et al. 2019, Tilt 2020, United Property Owners of Montana 2022).

At the same time, the Montana Legislature mandated a substantial reduction in the number of wolves, the primary predator of elk. In 2021, the Fish and Wildlife Commission established a harvest threshold of 450 wolves statewide (population estimate of 1,100 wolves), including 82 wolves in the administrative region including the winter range used by northern Yellowstone elk (Montana Fish, Wildlife and Parks 2021a). The State of Montana indicated wolf-related livestock depredation and decreasing elk numbers were the primary reasons for implementing aggressive wolf population reduction across the state (Sholly 2021, 2022a,b; Popper 2022). According to Montana's livestock loss numbers, however, less than one wolf-related livestock depredation has occurred each year since 2013 within the winter range used by northern Yellowstone elk (Sholly 2021, 2022a,b). Data also show counts of northern Yellowstone elk in hunting district 313, north of the park, have been within the range of Montana Fish, Wildlife and Parks' population objective of 3,000 to 5,000 elk since at least 2004 and above 4,000 elk since 2017 (Montana Fish, Wildlife and Parks 2018, 2019, 2021c; Sholly 2021, 2022a,b). In addition, the average number of brow-tined bull elk harvested from this population during the past decade was higher than during 1999 to 2009 (Montana Fish, Wildlife and Parks 2018a, 2019, 2021c).

By effectively eliminating the major predator of elk from many agricultural areas, the Montana Legislature and Fish and Wildlife Commission have inadvertently created a human-induced refugia for elk with substantial nutritional subsidies that contribute to high pregnancy and recruitment rates. During 2021-2022, about 19% of the wolves primarily living in Yellowstone National Park were harvested in surrounding states, including 19 wolves in the winter range area for northern Yellowstone elk (Sholly 2022a,b). The harvest of 20% of the wolves in this area annually for many years is predicted to decrease wolf numbers by about 50% over time, while a 30% harvest would decrease numbers by 80%. This decrease in wolf numbers likely would contribute to a substantial increase in elk numbers, with the ecosystem trending back towards conditions prevalent during the 70-year period when wolves were absent, elk were far more abundant, and liberal harvests were needed to reduce numbers (Dr. Tim Coulson, University of Oxford, UK, personal communication).

An article published by park biologists in 2016 (Smith et al. 2016) recommended a maximum harvest rate of 5% to 7% for wolves primarily living within Yellowstone National Park. This recommendation allows for the harvest of some wolves that leave the park and adjusting the quota among years based on a consistent rationale as the number of wolves in the park varies. A July 2022 letter from the Superintendent to the Montana Fish and Wildlife Commission recommended a quota of 6 wolves for the wolf management unit along the north boundary of the park, which would equate to about 5% of the wolves primarily living in the park, while allowing for additional harvest of wolves along other boundaries (Sholly 2022b). In August 2022, the Commission decided to institute a quota of 6 wolves in that unit based on this rationale (Montana Fish, Wildlife and Parks 2022). By early February 2023, 6 wolves had been killed in this unit, with 4 of these wolves belonging to packs based in the park and 3 wearing radio collars. The future of wolves and their role in regulating elk numbers, along with the effects of other predators like cougars, bears, and humans (through hunting or land management practices), will continue to require information provided by ongoing research and monitoring.

While numbers of northern Yellowstone elk have increased towards about 7,500 elk after a low count of 3,915 in 2013 in this multi-predator system, there is still substantial uncertainty about their long-term dynamics due, in large part, to the ongoing human influences described in this chapter. Successful wildlife management within the Greater Yellowstone Area depends on agencies with different jurisdictions and mandates collaborating and taking actions to promote the best possible outcomes for the broader common interest (Clark 2021). Even if their objectives are in conflict at times, it is essential that federal and state agencies work together and with private landowners to support each other's interests wherever possible (Clark 2021).

Female elk grooming a young calf in Yellowstone National Park. Photograph by Jacob W. Frank, National Park Service.

Chapter 9
Current Management

Introduction

Managers in Yellowstone National Park are directed by statute and policy to conserve resources therein unharmed, with minimal human intervention when possible. The Yellowstone National Park Act of 1872 set apart a vast expanse of land in the future states of Wyoming, Montana, and Idaho "as a public park or pleasuring ground for the benefit and enjoyment of the people." It requires the Secretary of the Interior to preserve "from injury or spoilation" the "wonders" of Yellowstone and to ensure "their retention in their natural condition." The Secretary is also required to "provide against the wanton destruction of the fish and game found within the park, and against their capture or destruction for the purposes of merchandise or profit" (16 USC 21 *et seq*., 17 Stat. 32). After the creation of the park in 1872, Congress sent a detachment of U.S. Cavalry to protect its wonders and the remnant populations of wildlife. Public sentiment to protect these animals was widespread and led to some of the first efforts to preserve and restore wildlife populations (Olliff et al. 2013).

In addition, the National Park Service Organic Act of 1916 created the Park Service and mandated managers "conserve the scenery and the natural and historic objects and the wild life therein and to provide for the enjoyment of the same in such a manner and by such means as will leave them unimpaired for the enjoyment of future generations" (54 USC 100101a,b). Subsequent management policies clarified park managers will preserve "components and processes in their natural condition" which was defined as "the condition of resources that would occur in the absence of human dominance over the landscape" (National Park Service 2006:36). Additional principles for managing biological resources included: "preserving and restoring the natural abundances, diversities, dynamics, distributions, habitats, and behaviors of native plant and animal populations and the communities and ecosystems in which they occur; restoring native plant and animal populations in parks when they have been extirpated by past human-caused actions; and minimizing human impacts on native plants, animals, populations, communities, and ecosystems, and the processes that sustain them" (National Park Service 2006:42).

These efforts were successful and as northern Yellowstone elk numbers increased during the 1900s about 14,150 animals were shipped elsewhere to facilitate restoration efforts across North America (Houston 1982, Yellowstone National Park Archives Box N-64). These practices helped define our national conservation ethic where wildlife are considered a public resource for all Americans and certain areas, such as Yellowstone, are considered so magnificent and unique they are preserved by the federal government for all citizens in perpetuity (White 2016, 2021). However, the goal of preserving parks in a natural condition free from the influence of modern society was unattainable due to changes to ecosystems and environmental conditions over the past century (Cole and Yung 2010). These changes included the massive slaughter of wildlife populations in the late 1800s, widespread human development, fire suppression, introduced diseases, accelerating climate warming, exotic species invasions, and global pollution (Cole and Yung 2010). Humans have already altered most ecosystems so much that eliminating the original causes of these problems will not revert the systems back to their original conditions (Hobbs et al. 2010). Thus, attempts to use past conditions, such as pre-settlement, as targets for preservation or restoration are unattainable (White et al. 2013b, White 2016). Furthermore, the boundaries of parks and wilderness areas do not encompass entire ecosystems or meet all the needs of various wildlife species therein (Stephenson et al. 2010).

Despite these irreversible changes, it is possible to attain the goal of minimizing human dominance and intervention in parks to the extent feasible, rather than implementing management actions based on prevailing political and social values (Boyce 1998, 2018; National Park Service 2006, White et al. 2013b). To achieve this goal, elk and other wildlife are generally allowed to move freely and unpursued within Yellowstone National Park, with their behaviors, movements, and reproductive success primarily affected by their decisions and natural selection, which is more commonly called survival of the fittest (Darwin 1859, White 2016). Within the park, elk live in an environment not dominated by people and coexist with a full suite of native ungulates and predators under environmental conditions that vary seasonally and among years and can be quite severe at times (White et al. 2013b). As a result, northern Yellowstone elk have retained their adaptive capabilities.

Collaborative Conservation

Today, the Greater Yellowstone Area is famous for its large, migratory elk herds that millions of visitors watch each year and thousands of sportspersons pursue in spectacular wilderness hunts (Kauffman et al. 2018). However, the management of these elk has prompted bitter debates regarding appropriate numbers, grazing effects, harvest levels, and predator impacts (Olliff et al. 2013). At various times over the past century, managers in Yellowstone National Park have culled thousands of elk due to concerns about overgrazing, let numbers increase with minimal human interference, and restored a diverse and abundant predator association to reduce elk numbers (Olliff et al. 2013). Laypersons, politicians, and scientists have intensely debated these actions. Some people were concerned about too few elk following market hunting in the late 1800s, others were concerned about too many elk and overgrazing during the 1920s through the mid-1990s, and hunters became concerned about too few elk after the restoration of wolves in the late 1990s (Houston 1982, Barmore 2003, Eberhardt et al. 2007, Olliff et al. 2013, MacNulty et al. 2016, 2020b).

Wildlife watchers in the Lamar Valley of Yellowstone National Park. Photograph by Diane Renkin, National Park Service.

Current management in Yellowstone lets nature take its course and, whenever possible, human intervention is discouraged (White et al. 2013a, White 2016). Thus, there are no plans to control numbers of predators, such as bears, cougars, coyotes, or wolves, inside the park. Predator numbers necessarily decrease in response to fewer prey and wolf numbers in Yellowstone decreased from about 170 in 2007 to 95 in 2013 as elk numbers decreased (Smith et al. 2020). In addition, managers decreased harvests of female elk in nearby areas of adjacent states to compensate for lower recruitment due to predation and a shift to an older age structure (Wright et al. 2006, Montana Fish, Wildlife and Parks 2019, Brodie et al. 2013, Hoy et al. 2020, Smith 2021). The elk population should respond to lower predator numbers and harvests with increased survival and recruitment of young (White and Garrott 2005a, Eberhardt et al. 2007, MacNulty et al. 2020b). However, the days of 20,000 or more elk in northern Yellowstone are gone for the foreseeable future given the abundant, diverse predator community.

The wildlife community in the Yellowstone area is always changing, with predators responding to prey numbers and vulnerabilities, and vice versa. In turn, these responses induce other changes in the ecosystem through scavengers, decomposers, and vegetation communities. The recovery of large predators is relatively recent in ecological time, and it is unclear how the system will continue to change as an increasing human presence, warming climate, and multiple predators and their prey interact across the vast Yellowstone landscape (White et al. 2009d, 2013b). In addition, the National Park Service continues to allow natural disturbance processes, such as wildfires, to occur in wilderness areas of the park. During the last 45 years, Yellowstone has experienced an average of about 2 dozen fires per year that burned an average of about 5,900 acres annually, excluding the extensive fires during 1988 (Yellowstone Center for Resources 2018). Thus, habitat shifts to early seral stages with highly nutritious forage for several years thereafter is an ongoing activity.

During the first century after the park's establishment, managers focused on developing best practices for preserving wild, wide-ranging animals and restoring imperiled species of iconic wildlife, such as bison, grizzly bears, and pronghorn (Olliff et al. 2013). In recent decades, biologists are attempting to restore ecosystem processes by suppressing nonnative species, reestablishing top-down processes such as predation, and facilitating bottom-up processes like herbivory by large aggregations of bison which modify the grasslands they depend on (White et al. 2009d, 2013b, White 2021). The recovery of large predators in the Greater Yellowstone Area was a transformational event that eventually facilitated and maintained a substantive decrease in elk numbers and had many other indirect effects on other ungulates, predators, producers, scavengers, and decomposers throughout the ecosystem (White 2016, Garrott et al. 2020). Current projects are examining changes in food webs, vegetation communities, and biodiversity over time with a recovered large-predator community. Biologists also are assessing how elk, mule deer, bighorn sheep, and pronghorn respond spatially and temporally to predation risk from black bears, cougars, grizzly bears, and wolves.

Biologists assessing the nutritional condition of a bull elk killed by wolves in Yellowstone National Park. Photograph by Jacob W. Frank, National Park Service.

Despite this extensive and ongoing research, science is unlikely to change the viewpoints of many people or lead to consensus about elk or predator management (White et al. 2009d). Scientific investigation rarely results in clear indisputable evidence that creates immediate widespread consensus on the issue or process under investigation (White et al. 2009d, White 2016). It is hard to understand complex and interacting ecological processes and unequivocally identify the precise causes of changes with complete certainty (White 2016). In addition, the restoration of large predators and bison made it more difficult to forecast future trends in elk abundance by adding layers of complexity, such as the top-down effects of predation on elk and the bottom-up effects of competition for available forage with bison (National Research Council 2002, Geremia et al. 2019, 2022; MacNulty et al. 2016, 2020b). All debates about natural resource issues and policies have a strong component of human values underlying the interpretation of the science. We are all biased by our attitudes, experiences, and alliances, and people tend to support findings they like based on these preconceived notions (White 2016). Thus, debates about northern Yellowstone tend to reflect competing visions of what the speakers think it should look or be like to suit their own beliefs and values, regardless of the science (McNaughton 1996, National Research Council 2002, MacNulty et al. 2016, 2020b, White 2016).

For these and other reasons, federal and state managers have struggled to integrate the National Park Service's objectives of minimal interference with ecosystem processes with state objectives for sustained harvests of elk and wolves outside the park following predator restoration and changes in elk distribution and migratory patterns (Eberhardt et al. 2007, Smith et al. 2016). While these objectives are different, there is tremendous overlap in the overall missions of both agencies: to manage wildlife as public trust resources for the benefit of present and future generations. In addition, both approaches focus on conserving habitats and ecological processes that sustain viable populations of wildlife. As a result, these agencies need to reinvigorate collaborative efforts on scientific investigations and cooperative dialogue regarding the cross-jurisdictional management of elk, wolves, and other wildlife and their habitats (Clark 2002, 2021). The challenge of managing wildlife across jurisdictions is prioritizing common interests beneficial to each agency and the broader community over special interests primarily benefitting one or a few parties (Brunner et al. 2002, 2005; Clark et al. 2014). The agencies need to consider valid and appropriate concerns, both biological and social, and develop solutions to problems that work in the real world. In practice, this means addressing a diversity of issues based on reliable information instead of perpetuating disputes based on self-serving beliefs and values (Clark 2002, Clark and Vernon 2016). It also means promptly addressing landowner conflicts with wildlife to maintain their support for conservation (Tilt 2020). This endeavor is difficult and requires trust to develop strong partnerships, creativity to advance novel ideas, confidence to take bold actions, courage to withstand criticism, and determination to adapt and persevere (White 2016). In other words, it will require strong and visionary leadership to coalesce rather than divide participants and progress towards common, democratic interests (Clark 2021).

Harvests and Disease

Habitat and land use differences among areas may strongly influence the behavioral responses of elk to wolf presence and the degree to which these behaviors are manifested

(Garrott et al. 2005, Hamlin et al. 2009). Trade-offs between foraging conditions and the risk of predation or harvest as constrained by snow vary considerably among elk populations in the Greater Yellowstone Area due to differences in land use, vegetation communities, large predator densities and management, local environmental conditions, elk migratory patterns, and human harvests (Hamlin et al. 2009). With a restored large predator community, state managers need to closely monitor and manage elk harvests to ensure they do not precipitate a substantial decrease in numbers (White and Garrott 2005a, Wright et al. 2006, Eberhardt et al. 2007). Antlerless harvests likely will need to remain at a reduced level to offset kills by predators and not accelerate a decrease in adult female survival and elk abundance (Brodie et al. 2013, Smith 2021). This reduced hunter opportunity has decreased the economic benefits of hunting to local communities. However, tourism to observe wolves and other large predators in and near the park can offset these economic losses (Duffield 1992, Wright et al. 2006, Varley et al. 2020). Excluding elk from irrigated pastures through fencing, hazing, or hunting may reduce resident tendencies in elk, eliminate human-induced refugia and nutritional subsidies, and offset benefits of higher pregnancy and recruitment; thereby increasing the benefits of migration (Barker et al. 2019a,b).

When CWD is detected in the park, biologists and rangers will increase visual surveillance, the investigation of carcasses, collection of samples for testing, and targeted culling of animals demonstrating clinical signs (Treanor et al. 2021). Biologists will evaluate potential predation effects on CWD, including predation rates and the age and sex distribution of deer and elk killed by predators, for comparison to pre-CWD data. They also will collect samples from captured deer and elk for testing CWD (ear punch, feces), pregnancy (blood, genetics), and body condition, and then monitor survival and eventual cause of death via telemetry. The greatest challenge for park staff will be obtaining enough samples to identify infected animals, estimate prevalence, and track changes across space and time. Effective monitoring to detect CWD at low infection rates and assess subsequent increases in prevalence requires testing samples from many hundreds of deer and elk in a timely and cost-effective manner. There is no hunting in the park and predators rapidly consume carcasses. Thus, park biologists currently rely on monitoring information about prevalence and spread from surrounding states. Biologists need a reliable noninvasive diagnostic test to detect infected animals and track the spread of CWD. Deer and elk infected with CWD excrete prions in their feces long before they exhibit clinical signs of the disease (Tamgüney et al. 2009). Predators and scavengers also excrete prions in their feces for several days after ingesting infected material from their prey (Nichols et al. 2015). Scientists have developed methods for detecting CWD in feces, but they are not yet accredited, commercially available, or reliable (Treanor et al. 2021; see Chapter 3).

The CWD response plans of states surrounding Yellowstone are to use hunter harvests as a primary tool for monitoring disease prevalence and slowing spread. The wildlife departments remove animals showing clinical signs of disease and use culling as necessary to slow disease spread. The National Park Service is tasked with maintaining native plants and animals. The origin of CWD is unknown, but its distribution and prevalence were influenced by human actions, such as the translocation of captive deer and elk between facilities and the concentration of wildlife by feeding and habitat loss (Williams et al. 2002). Thus, human actions likely have increased the chances of CWD transmission and, as a result, it is appropriate for the National Park Service to consider CWD management actions (National Park Service 2006).

However, a primary purpose of Yellowstone National Park is to preserve abundant and diverse wildlife in one of the largest remaining intact ecosystems on earth. Disease management actions such as substantial population reductions by culling may be inappropriate for the park because they would remove many healthy animals, substantially reduce the prey base for predators and scavengers, and result in reduced visitor enjoyment (National Park Service 2006). In addition, Yellowstone supports a robust large-predator complex and scavenger guild that rapidly remove debilitated animals and carcasses (Stahler et al. 2020). Selective predation and scavenging could remove a greater proportion of CWD-infected animals than culling or harvest, reduce environmental contamination and, perhaps, suppress CWD prevalence (Brandell et al. 2022). Potentially, predators could selectively remove animals with late-stage infections, which are the primary source of transmission (Krumm et al. 2010, Wild et al. 2011, Brandell et al. 2022).

Conclusions

Elk are a keystone species that play a prevalent role in the Yellowstone ecosystem by enhancing the productivity of grasslands through grazing, transferring nutrients across the landscape, converting grass to animal tissue, and providing sustenance for predators, scavengers, and decomposers (Frank et al. 2013, Metz et al. 2020a,b; Stahler et al. 2020). They also are an economic boon to the Greater Yellowstone Area because tourism and recreational activities have a large and growing influence on the regional economy. Visitors traveling through the area have an exceptional opportunity to observe hundreds of elk moving across the vast landscape, competing for breeding opportunities during the rut, and nursing and protecting their newborn calves. In addition, sportsmen and women flock to the region to experience superb wilderness hunts (Middleton et al. 2019). Tourism to Yellowstone National Park supports thousands of jobs and has an estimated overall benefit of $640 million to the area's economy (Cullinane-Thomas and Koontz 2020). In addition, wildlife that summer in the park and migrate into surrounding states during autumn drive a large portion of a $300 million big game and hunting industry in the region (Southwick Associates 2017). As a result, elk are an integral part of the social fabric of most communities in the region (Metcalf et al. 2016). With a bit of tolerance and conservation, the resiliency and adaptive capabilities of elk will continue to perpetuate viable populations in the Yellowstone region for many thousands of years.

Mature male elk bugling near Canyon in Yellowstone National Park. Photo by Eric Johnston, National Park Service.

Acknowledgments

Primary funding and support for the studies and management activities described in this book came from the American taxpayers, National Park Service, Montana Fish, Wildlife and Parks, Wyoming Game and Fish Department, U.S. Fish and Wildlife Service, U.S. Forest Service, U.S. Geological Survey, Montana State University, University of Wisconsin, University of Montana, Utah State University, University of Wyoming, University of Alberta, Michigan Technological University, Annie and Bob Graham, Frank and Kay Yeager, Valerie Gates, Canon USA, Inc., Yellowstone Forever, and the Yellowstone Park Foundation. In addition, funding or support were provided by the Pittman-Robertson Federal Aid in Wildlife Restoration, National Aeronautics and Space Administration, National Park Foundation, National Science Foundation, Rocky Mountain Cooperative Ecosystems Studies Unit, Rocky Mountain Elk Foundation, National Geographic Society, Natural Sciences and Engineering Research Council of Canada, Safari Club, University of Wyoming-National Park Service Research Center, Washington Department of Fish and Wildlife, Oregon Department of Fish and Wildlife, and the National Council for Air and Stream Improvement.

For their diligence and expertise in implementing monitoring and research efforts, we are grateful to Dean Anderson, Colby Anton, Shannon Barber-Meyer, William Barmore, Matt Becker, Wes Binder, Eric Bergman, Bob Beschta, Hawthorne Beyer, Daniel Bilyeu Johnston, John Borkowski, Mark Boyce, Ellen Brandell, Jedediah Brodie, Jason Bruggeman, Kira Cassidy, Steve Cherry, Susan Clark, John Cook, Rachel Cook, David Cooper, Mike Coughenour, Tim Coulson, Elizabeth Covelli Metcalf, Bob Crabtree, Jeremy Cusack, Troy Davis, Glenn DelGuidice, Don Despain, Andy Dobson, Shana Drimal, Lee Eberhardt, Les Eberhardt, Shaney Evans, James Forester, Daniel Fortin, Wayne Freimund, Erica Garroutte, Chris Geremia, Andrew Gregory, Kathy Griffin, Jamin Grigg, Bill Hamilton, Andy Hansen, Mark Hebblewhite, Tom Hobbs, Doug Houston, Sarah Hoy, Rosemary Jaffe, Matt Kauffman, Michael Kohl, Ky Koitzsch, Lisa Koitzsch, Shelly Lachish, Eric Larson, Paul Lukacs, Mark Lung, John Mack, Julie Mao, Kristin Marshall, Rick McIntyre, Sam McNaughton, Mary Meagher, Dave Mech, Jerod Merkle, Evelyn Merrill, Peter Metcalf, Matt Metz, Connor Meyer, Arthur Middleton, Mike Mitchell, Kerry Murphy, Luke Painter, Andy Pils, Rolf Peterson, Jarod Raithel, Gregory Rickbeil, Bill Ripple, Bill Romme, Joshua Rose, Jay Rotella, Toni Ruth, Glen Sargeant, Ulysses Seal, Carly Segal, Frank Singer, Lacy Smith, Erin Stahler, Aimee Tallian, Mike Tercek, John Treanor, Monica Turner, Nathan Varley, John Vore, John Vucetich, Fred Wagner, Fred Watson, Carl Wambolt, Evan Wolf, Greg Wright, and Travis Wyman.

We also thank the following National Park Service employees for their contributions to the efforts described in this book: Lisa Baril, Tami Blackford, Sarah Bone, Wayne Brewster, Colin Campbell, Jennifer Carpenter, John Cataldo, Steve Cater, Mike Coffey, Alana Darr, Sarah Dewey, Laura Dooley, Kerrie Evans, Nancy Finley, Corrie Frank, Jake Frank, Deb Guernsey, Carrie Guiles, Dave Gustine, Wendy Hafer, Neal Herbert, Christie Hendrix, Dave Hallac, Regina Heiner, Michael Keater, Pat Kenney, Allison Klein, Dan Krapf, Doug Kraus, Jan Laye, Chris Lehnertz, Suzanne Lewis, Tana Lindstrom, Jodie Lyle, Wendy Maples, Melissa McAdam, Lauren McGarvey, Tom Olliff, Jim Peaco, Joy Perius, Phil Perkins, Ellen Petrick-Underwood, Glenn Plumb, Charissa Reid, Tim Reid, Roy and Diane Renkin, Mike Robinson, Ann Rodman, Shannon Savage, Paul Schullery, Cam Sholly, Erin Stahler, Kathy Tonnessen, John Varley, Linda Veress, Morgan Warthin, Erin White, Lee Whittlesey, and Becky Wyman.

In addition, we thank Emily Almberg, Kurt Alt, Neil Anderson, Keith Aune, Vanna Boccadori, Julie Cunningham, Pat Flowers, Claire Gower, Ken Greer, Justin Gude, Ken Hamlin, Craig Jourdonnais, Tom Lemke, Karen Loveless, Adam Messer, Abby Nelson, Kelly Proffitt, Jennifer Ramsey, and Mike Yarnall from Montana Fish, Wildlife and Parks; Doug McWhirter, Kevin Hurley, Terry Kreeger, and Tony Mong from the Wyoming Game and Fish Department; Pete Zager and Mark Hurley from Idaho Department of Fish and Game, Scott McCorquodale from the Washington Department of Fish and Wildlife; Walt Allen, Ken Britton, Mary Erickson, Phil Farnes, Mike Thom, and Dan Tyers from the Custer Gallatin National Forest; Paul Cross, Peter Gogan, Mark Haroldson, Bob Klaver, Ed Olexa, Chuck Swartz, and Frank van Manen from the U.S. Geological Survey; Eric Cole and Bruce Smith from the U.S. Fish and Wildlife Service; and Jeff Augustin, JD Davis, and Lisa Diekmann from Yellowstone Forever, Alethea Steingisser from the University of Oregon, and Jim Halfpenny and Bob Landis from Gardiner, Montana.

Flight services were provided by Central Helicopters, Gallatin Flying Service, Hawkins and Powers Aviation, Helicopter Capture Services, Leading Edge Aviation, Montana Aircraft, Pathfinder Helicopters, Quicksilver, Sagebrush Aero, Sky Aviation, Tracker Aviation, and Wildlife Air LLC. Telemetry services were provided by Advanced Telemetry Systems, Lotek Wireless, Televilt/TVP Positioning AB, Telonics, and Vectronic Aerospace GmbH. Annual surveys were coordinated and funded by the Northern Yellowstone Cooperative Wildlife Working Group whose members include Montana Fish, Wildlife and Parks, Custer Gallatin National Forest, Northern Rocky Mountain Science Center (U.S. Geological Survey), and Yellowstone National Park.

Health evaluations including serology, disease analyses, and parasitology were conducted by the New York State Animal Health Diagnostic Center (Ithaca, NY) and the University of Minnesota and the Montana and Wyoming State Veterinary Diagnostic Laboratories. Age determination from teeth cementum was conducted by Matson's Laboratory and pregnancy status was determined from measuring the presence of Pregnancy Specific Protein B in serum by BioTracking LLC. The botanical composition of diets was determined through microscopic examination by the Soil and Plant Analysis Laboratory at the University of Wisconsin and the Wildlife Habitat and Nutrition Laboratory at Washington State University.

We thank the photographers who donated their images to this publication, including Ed Austin, Stan Canter, J. R. Douglass, William Dunmire, Jacob W. Frank, John Good, Hadley, J. Hemphill, Neal Herbert, Eric Johnston, Herb Jones, Harlan Kredit, Francis LaNoue, Stephen Larrabee, George Marler, Barry O'Neill, Jim Peaco, Diane Renkin, J. Schmidt, and Ted Scott. We also thank Allison Klein, Alethea Steingisser, and the Spatial Analysis Center of the Yellowstone Center for Resources for preparing figures. Special thanks to Charissa Reid for formatting the book. Last, but certainly not least, we thank the numerous private landowners that provide secure habitat for elk in the Yellowstone area. The views and opinions in this book are those of the authors and should not be construed to represent any views, determinations, or policies of federal or state agencies. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Adult male elk in the morning mist in Yellowstone National Park. Photograph by J. Schmidt, National Park Service.

Adult male elk bedded on the Blacktail Deer Plateau in Yellowstone National Park. Photograph by Neal Herbert, National Park Service.

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Adult male elk in downed timber near the Sepulcher Mountain trail in Yellowstone National Park. Photograph by Neal Herbert, National Park Service.

Two bedded adult, female elk by Jacob W. Frank, National Park Service.

P. J. White is the Natural Resource Program Manager for Yellowstone National Park.

Daniel R. Stahler leads the Wolf, Cougar, and Elk Programs for Yellowstone National Park.

Douglas W. Smith retired after 28 years in Yellowstone National Park leading the Wolf, Elk, and Bird Programs.

Daniel R. MacNulty is an Assistant Professor in the Department of Wildland Resources at Utah State University who has worked extensively in Yellowstone National Park.

Robert A. Garrott is Professor Emeritus of Ecology at Montana State University who worked extensively in Yellowstone National Park.