# YELLOWSTONE PRONGHORN

## RECOVERING
from the brink of extirpation

P. J. White,
Kerey K. Barnowe-Meyer,
Robert A. Garrott,
& John A. Byers

*Pronghorn buck in the Gardiner basin portion of Yellowstone National Park with Electric Peak in the background. Photo by Jacob W. Frank, National Park Service.*

*Cover photo by Neal Herbert, National Park Service.*

*Back cover photo by Jim Peaco, National Park Service.*

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*Featuring the photography of Jacob W. Frank, Neal Herbert, and Jim Peaco, National Park Service*

# Contents

*Pronghorn mother and fawn near Slough Creek in Yellowstone National Park. Photo by Jacob W. Frank, National Park Service.*

*Pronghorn buck growing new horn sheaths on the winter range near Stephens Creek in Yellowstone National Park. Photo by Jim Peaco, National Park Service.*

*Pronghorn buck and does traveling in the Gardiner basin portion of Yellowstone National Park. Photo by Jim Peaco, National Park Service.*

# Preface

John A. Byers, Professor Emeritus of Zoology, University of Idaho

In many bars in the American West, you are likely to hear of a jackalope. There may be a taxidermic mount on the wall of the bar. As the name implies, a jackalope is an imagined, rabbit-like mammal with horns or antlers on its head. Jackalopes are not entirely bar talk. Twenty million years ago, in North America, rabbit-sized ungulates with horns existed. They were members of a subfamily called the Merycodontinae. They gave rise to and were replaced by larger antelope-like creatures (Antilocaprinae) that adapted well to the vast grasslands of North America. One of the grassland adaptations that the Antilocaprinae evolved was running ability in response to the presence of North American lions, cheetahs, speedy hyenas, fast running bears, and other dangerous predators. To escape this diverse lot of predators, the Antilocaprinae evolved a blinding sprint speed, as well as the ability to run at high speed for several miles. They became open country running specialists with the ability to detect predators from afar and then to outrun them should the predators approach.

Then about 11,000 years ago, an extinction event occurred in North America. All the major predators and all but one of the Antilocaprinae disappeared. The cause of the extinction event is not known, but some biologists have pointed out that extinction was coincident with the arrival of one wave of humans in North America. The sole surviving antilocaprid was the pronghorn, Antilocapra americana, the subject of this book. Pronghorn inherited the North American grassland which they shared with bison, elk, grizzly bears, wolves, and coyotes. This unique, beautiful, native American ungulate did quite well in the grassland until European humans with plows and rifles appeared. The pronghorn story since then has been one of range reduction, decline, and partial recovery.

The pronghorn in Yellowstone National Park are a remnant of a once larger population that surged up and down the Yellowstone River valley. In fall, the animals would travel the 50 miles or so (easy for such mobile creatures) to the open plains that are now traversed by Interstate 90. In spring, they would ascend the Yellowstone, to occupy the high moist grasslands that are now within the Park. For pronghorn, a safe winter habitat is one in which they can run and the windswept high plains along the lower Yellowstone filled the bill. In spring, pronghorn females need a high level of nutrition to fuel, through milk, the rapid growth of two relatively large fawns. The upper elevation grasslands provided this.

This vital annual migration was cut off by human occupation and development in the Yellowstone River valley. Now, in late summer, the Yellowstone pronghorn descend only as far as the open slopes above Gardiner, Montana. Fences impede them. The area above Gardiner offers relatively open terrain which pronghorn prefer in winter, but it offers poor food. In winter, pronghorn have a steady diet of plant parts that are so loaded with smelly toxic compounds that they would gag a human. As this book recounts, some pronghorn now remain in the area above Gardiner year-round. New growth in spring relieves the toxic monotony of the winter diet. Most pronghorn, however, continue to recreate a portion of the ancestral migration. They ascend to the Blacktail Deer Plateau, Hellroaring Canyon, Little America Flats, Specimen Ridge, and the Lamar Valley. They move within what is called the Northern Range, a relatively narrow strip of grassland that is closed, to the south, by dense forest.

As this book reports, pronghorn in Yellowstone have struggled for more than a century. The population has never come close to its natural limit, the ecological carrying capacity of its environment. The principal reason for poor performance is the density of coyotes which are specialized as opportunistic predators of pronghorn fawns. In Yellowstone, and elsewhere in the American West, coyotes consume so many pronghorn fawns that they severely limit population growth. This situation, known as mesopredator

release, followed the extirpation of wolves from the American West by poisoning, trapping, and shooting. With no wolves to regulate their numbers or their habitat use, coyotes reached densities sufficient to depress pronghorn recruitment.

The reintroduction of wolves into Yellowstone had several cascading ecological effects which are now well documented. One of these was an improvement in pronghorn fawn survival in areas of high wolf density. This occurs because wolves are intolerant of coyotes and, as a result, areas with high wolf density are areas with low coyote density. The other change that would obviously benefit Yellowstone pronghorn would be an expansion of winter range to include lower-elevation areas of the Yellowstone River valley where more palatable food exists. More long-term conservation agreements and incentives with landowners along the Yellowstone River valley from Gardiner, Montana, about 50 miles north through the Paradise Valley are needed to provide better winter range for pronghorn and restore their historic migration and dispersal pathways.

The keys to a better future for Yellowstone pronghorn are thus known. One key, the reintroduction of wolves, is accomplished. The other, a significant expansion of winter range remains, at present, a work in progress.

*Pronghorn buck with new growing horn sheaths feeding in Yellowstone National Park. Photo by Diane Renkin, National Park Service.*

# Introduction

Pronghorn, commonly called antelope, are unique to western North America; they are not related to the true antelope in Africa and Asia. Pronghorn are the sole living member of the North American family *Antilocapridae* and are quite distinct in appearance with both sexes having horns and males having a patch of black fur behind the jaw. Pronghorn are sometimes called "speed goats" because they can run at more than 45 miles (72 kilometers) per hour with entire groups turning together as though their movements were choreographed.

Historical accounts suggest thousands of pronghorn once used the mountainous grassland and sagebrush-steppe areas in and near present-day Yellowstone National Park during summer before moving long distances to lower-elevation river valleys north and west of the Park to spend winter. By the 1960s, only a small population of less than 200 pronghorn remained in the northern portion of the Park during summer with few animals moving to winter ranges outside the Park. Most pronghorn congregated on a small sparsely vegetated winter range near the northern Park boundary. The population appears to have been isolated from other pronghorn for almost a century and had low survival of fawns due to high predation by coyotes.

In 1998, the U.S. House Appropriations Committee directed the National Park Service to "initiate a National Academy of Sciences review of all available science related to the management of ungulates and the ecological effects of ungulates on the range land of Yellowstone National Park, and to provide recommendations for implementation by the Service." The National Research Council convened a Committee on Ungulate Management in Yellowstone National Park who conducted the review and published its findings in a book entitled *Ecological Dynamics on Yellowstone's Northern Range*. The Committee concluded "[t]his pronghorn herd faces a serious risk of extinction. The risk could be reduced by eliminating harvest, by increasing harvest of coyotes and bobcats, by restricting recreational access to critical winter range, by reducing disturbances within the winter range, and by management actions that result in enhanced growth and vigor of sagebrush within winter range." They also found "[t]he pronghorn population has fluctuated widely and has been declining recently. Adverse factors include coyote predation and hunting on private land outside the Park. Pronghorn may be affected by competition with elk, mule deer, and bison during severe winters." The Committee recommended the National Park Service evaluate the current and likely future trajectories of the pronghorn population and human disturbances to this population.

Park managers commissioned Dr. Kim Keating from the Northern Rocky Mountain Science Center, U.S. Geological Survey, to compile information regarding the population dynamics and management of Yellowstone pronghorn. They distributed Dr. Keating's report to a group of 33 pronghorn experts who assembled at the *Yellowstone Pronghorn Conservation Assessment Workshop* in January 2002 to assess the conservation status of the Yellowstone pronghorn population. The primary objectives of the workshop were to identify threats to the persistence of the population and recommend research and management actions to reduce the risk of a catastrophic decrease in numbers. The panel recommended the implementation of a rigorous monitoring program to estimate reproduction, survival, recruitment, and age structure. They also recommended identifying and monitoring movement routes, fawning areas, and segments of the population using different fawning areas. The panel recommended research to evaluate mortality and recruitment among the various fawning areas in relation to predator densities and use, the effects of weather, forage, and habitat conditions on pronghorn nutrition and recruitment, and the extent of genetic diversity and relatedness to other populations.

Over the next two decades biologists from the National Park Service, University of Idaho, Montana State University, Montana Fish, Wildlife and Parks, National Parks Conservation Association, and the Yellowstone Ecological Research Center worked to address these recommendations, conserve the pronghorn population, and restore movement corridors and behaviors thought to be essential for their persistence. This book summarizes these efforts. Chapter 1 provides general information on the behavior and traits of pronghorn while Chapter 2 outlines the management history and population trends of pronghorn in and near Yellowstone National Park. Chapters 3 through 6 provide specific information on the demographics, habitat use, seasonal movements, and diets of Yellowstone pronghorn. Chapter 7 provides information on their genetics and population structure while Chapter 8 provides information on current management practices, restoration efforts, and recommendations for the future. The authors provide original sources of information at the end of each paragraph to make additional details available. 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.

*Pronghorn doe bedded in Yellowstone National Park. Photo by Bryan Harry, National Park Service.*

# Chapter 1
# Natural History: "Ghosts of Predators Past"

## *Distribution*

Pronghorn are only found in the central and western portions of North America. Prior to Euro-American settlement, they were abundant and widespread from present-day southern Alberta, Manitoba, and Saskatchewan in Canada, south through western Minnesota to western Texas and the state of Hidalgo, Mexico, and west to eastern Oregon, Nevada, California, and Baja California, Mexico. Native people hunted them for food and clothing using a variety of techniques including ambushes, stalking, driveways (fences) to cliffs or corrals, and shooting arrows or throwing lances from horses (*Equus ferus caballus*, see Chapter 2). (Yoakum 2004a)

Tens of millions of pronghorn likely occupied North America prior to Euro-American colonization. However, settlement, unregulated killing, and habitat loss decimated their numbers by about 99% during the latter half of the 19th century. Conservation organizations and sportsmen's groups supported proper hunting practices and habitat acquisition, while government agencies implemented hunting and livestock grazing restrictions, habitat protection measures, and predator control efforts. Congress passed the Lacey Act in 1900 to prohibit the interstate transport of game killed in violation of state laws which curtailed market hunting and poaching somewhat. Only about 31,000 pronghorn remained in North America by the 1920s, mostly in small and isolated populations. Agencies and organizations increased efforts to protect pronghorn from overharvest and their habitats from overgrazing by livestock. The federal government established wildlife refuges and allocated revenues from an excise tax on sporting gear and ammunition (Federal Aid in Wildlife Restoration, Pittman-Robertson Act of 1937) to the states for wildlife management and habitat protection. Federal and state agencies also captured and relocated (translocation) more than 30,000 pronghorn from well-populated areas to restore or augment other populations. (Nelson 1925, Yoakum 1986, Byers 1997, O'Gara and McCabe 2004, O'Gara et al. 2004, Yoakum 2004a)

These successful conservation measures contributed to a gradual increase in numbers to more than 1 million pronghorn by the 1980s with about 50% to 60% in Wyoming, 20% in Montana, 7% in South Dakota, and the remainder elsewhere. Wildlife agencies now implement sustainable harvests in most states. Pronghorn are now found from southern Alberta and Saskatchewan in Canada, south through western North Dakota to western Texas, and west to southeastern Oregon, Nevada, northern and central California, and the states of Baja, Chihuahua, and Sonora in northern Mexico. (Yoakum 1986, O'Gara and McCabe 2004, Yoakum 2004a, Morton et al. 2008)

## *Physical Characteristics*

Pronghorn (*Antilocapra americana*) belong to the mammalian order Artiodactyla which are even-toed ungulates (hooved animals). They are the sole living member of the family *Antilocapridae* and their appearance is quite distinctive. Both sexes have permanent horns of bone covered by an outer sheath of protein called keratin, a compacted, fibrous material. Pronghorn males (bucks) shed these sheaths annually in October or November and regrow them by the following March. The horns of females (does) generally are short straight spikes about 0.1 to 3 inches (0.25 to 8 centimeters) in length, while adult males have horns about 12 to 14 inches (30 to 36 centimeters) long covered by forked (or pronged) sheaths. (Byers 1997, O'Gara 2004a)

Pronghorn have hollow, brittle hair with large air cells and good insulation qualities. They have white fur on the belly, chest, lower jaw, rump, and throat with reddish-brown to tan fur elsewhere. Males also have a patch of black fur, the subauricular skin gland, behind the jaw. They are 4 to 5 feet (1 to 1.5 meters) long and about 3 feet (1 meter) tall at the shoulders. Males generally weigh between 90 to 145 pounds (41 to 66 kilograms) and females 75 to 110 pounds (34 to 50 kilograms). Fawns weigh about 7 to 9 pounds (3 to 4 kilograms) at birth and grow about 0.6 pound (0.25 kilogram) per day. They gain about 60 pounds (27 kilograms) by autumn. (Byers 1997, O'Gara 2004a)

Pronghorn have large eyes set high on the sides of their head and excellent vision in a wide arc of about 320 degrees for detecting movements of predators and other animals in their surroundings. They have good hearing and sense of smell and often mark their territories or ranges with scent glands. They also use an array of vocalizations from grunts to snorts to growls for communication. (Byers 1997, O'Gara 2004a)

## *Adaptive Capabilities & Behaviors*

Pronghorn have long, slender legs and large hearts and lungs for their body size. They are the fastest land animal in North America and can run about 45 miles per hour (72 kilometers per hour) for more than one mile (1.6 kilometers) which is faster than any of their current predators such as wolves (*Canis lupus*), cougars (mountain lions; *Puma concolor*), and coyotes (*Canis latrans*). Dr. John Byers from the University of Idaho attributed this speed and endurance to "ghosts of predators past" which refers to a relic capability from natural selection on ancient pronghorn when they lived with faster predators such as the North American cheetah (*Miracinonyx trumani*) and hyena (*Chasmaporthetes ossifragus*) for millions of years.

*Pronghorn buck horn sheath. Photo by Jacob W. Frank, National Park Service.*

These predators vanished from North America over 10,000 years ago, but pronghorn still retain their evolved speed and other anti-predator behaviors. (Byers 1997, O'Gara 2004a)

Pronghorn generally gather in groups which may be related to a group defense (safety in numbers) strategy. When an animal congregates with others it reduces or dilutes its risk of being attacked because it is now one of many available prey. It also provides increased awareness (vigilance) due to additional eyes, ears, and noses to detect predators and communicate within the group. This social behavior may also be a relic of evolutionary history from ancient pronghorn living with faster but now extinct predators for millions of years. Pronghorn form larger groups in winter consisting of both sexes and all ages. These groups are loose aggregations and vary regularly in composition and size, with individuals frequently joining and leaving. Adult males segregate from these groups in late winter or spring and become solitary (3+ years old) or congregate in small bachelor groups (1 to 3 years old) through the summer. Pregnant females remain in larger groups except for 2 to 3 weeks from mid-May to mid-June when they seek an isolated birthing site with nearby hiding places for their newborn fawns. They then re-join other females and young but in smaller groups than during winter. (Byers 1997, O'Gara 2004b)

Pronghorn are primarily active during daylight with peaks of activity after sunrise and before sunset. Daily movements usually are longer in autumn and winter when forage plants are senescent (dead and dry) and scarce compared to spring and summer when plants are green, abundant, and nutritious. Pronghorn can jump quite high but rarely use this capability, preferring instead to crawl or duck underneath obstacles such as fences if the bottom wire is smooth (not barbed), 16 or more inches (41 centimeters) above ground, and not blocked by dirt, snow, or vegetation. They often cross rivers and streams that are quite rapid during the spring run-off but sometimes appear nervous and uncomfortable about such crossings and restart many times. Regardless, they are good swimmers and drownings are not common. (O'Gara 2004b,f)

## *Habitat Use & Diets*

About 67% of pronghorn in North American live in relatively flat to rolling grassland communities, while 33% live in shrub-steppe and less than 1% live in desert (see Chapter 4). They prefer habitats with low vegetation and open views and generally avoid steep and densely forested areas. They are very selective feeders and prefer habitats with a variety of forbs and shrubs. Pronghorn obtain moisture from succulent plants such as forbs but also drink from available water sources during summer. Pronghorn use tall shrubs or trees for shade during summer and swales and depressions for shelter from high winds and blowing snow. They often forage in recently burned areas with a proliferation of nutritious forbs for several years after wildfires. (Schwartz and Nagy 1976, Yoakum 2004b,c)

Pronghorn spend much of the day feeding on a wide variety of plants such as forbs, grasses, and shrubs. They have dexterous lips which they use to select specific plants or parts of plants such as leaves, flowers, and fruits. Pronghorn are ruminants with a four-chambered stomach containing microbes such as bacteria and protozoa to help them digest ingested plant materials. They regurgitate and re-chew their food (called cud) to break ingested plants into smaller fragments before re-swallowing so more nutrients can be absorbed. The rumen microbes ferment plant fragments into volatile fatty acids which are absorbed for energy. The relatively small rumen stomachs of pronghorn are inefficient at digesting plants high in fiber, so animals often select leafy parts of plants with higher digestibility and protein. (Byers 1997, O'Gara 2004b,c)

Pronghorn change their foraging strategies among seasons in grassland and shrub-steppe habitats to select the most nutritious and digestible plants or plant parts available at that time of year (see Chapter 6). Grasses tend to have high digestibility and protein content during spring green-up, while forbs have

high digestibility and protein content during summer. Shrubs have high protein content during winter compared to forbs and grasses. As a result, pronghorn feed on new grass growth in the spring and early summer but select more forbs and shrubs during the rest of the year because their leaves and buds are higher in nutrients and more digestible than senescent grasses. Pronghorn generally move to lower-elevation windswept areas with snow less than 10 inches (25 centimeters) deep during winter where forage is exposed, or they can paw snow away with their front hooves to reach forage underneath. When snow depths exceed 12 inches (31 centimeters) pronghorn often rely on sagebrush (*Artemesia*) and other exposed shrubs for food and survival. (Byers 1997, O'Gara 2004b, Yoakum 2004b)

The diets of pronghorn in grassland areas usually consist of about 60% forbs, 20% grasses, and 20% shrubs. Forbs are often favored when they are available, generally during spring and summer green-up. Grasses are consumed in all seasons but especially during spring and summer green-up. In shrub-steppe habitats, pronghorn diets usually consist of about 60% shrubs, 30% forbs, and 10% grasses. In these areas, shrubs like sagebrush are a staple food in all seasons but forbs are still preferred compared to their availability. (Yoakum 2004b)

## *Seasonal Movements*

Pronghorn make some of the longest seasonal round-trip movements (called migrations) of any ungulate in the contiguous United States (see Chapter 5). One herd in western Wyoming migrates each autumn from Grand Teton National Park about 100 miles (161 kilometers) south to the upper Green River basin during the winter months. They return to the Park along the same corridor the following spring. Other pronghorn populations migrate shorter distances of 5 to 30 miles (8 to 48 kilometers), or even not at all (non-migratory). In some circumstances, populations may be partially migratory with only some animals moving seasonally between summer and winter ranges and others remaining on the same range year-round. In varied landscapes, migrants typically gain access to more favorable resources like nutritious food or safer areas with fewer predators to raise young. Many ungulates migrate to higher elevations each spring to forage on newly emerging nutritious plant growth through the summer but return to lower elevations each autumn to avoid deep snows that limit food availability during the winter. However, migratory individuals also can face additional risks compared to non-migratory residents such as traversing less-open habitats with increased risk of predation between seasonal areas of use. (Fryxell and Sinclair 1988, Fryxell et al. 1988, Kaitala et al. 1993, Sawyer et al. 2005, Kauffman et al. 2018, Middleton et al. 2020)

Fragmentation of habitat or barriers to movements eliminated most historic migration pathways for ungulates in North America including about 75% in the Greater Yellowstone Area. Human activities have shortened, disrupted, or threatened most pathways elsewhere. For example, fences, highways, housing, and energy development threatened the Grand Teton to Green River corridor which pronghorn used for more than 6,000 years with several constricted areas as narrow as 132 yards (121 meters). Protective parks and wilderness areas are often inadequate for conserving long-distance migration corridors which generally cross many jurisdictions. Thus, the protection of migration corridors and herd knowledge of the broader landscape requires strong partnerships among government agencies, local communities, and private landowners with prompt responses to alleviate human-animal conflicts. (Berger 2004, Sawyer et al. 2005, Berger et al. 2006, White et al. 2013c, Berger and Cain 2014, Kauffman et al. 2018, Middleton et al. 2020)

The history of overexploitation of pronghorn and nearly all the native ungulates of western North America during the era of Euro-American colonization likely contributed to the loss of migratory behaviors. Migration behaviors in ungulates are believed to be learned as young animals follow their mothers or other members of their social group during their first annual cycle of seasonal movements. In

this way, young animals gain knowledge of broader landscapes, locations of important resources distant from their birth site, and pathways to effectively travel from one important area to the next. In essence, migratory behavior is culturally transmitted through social learning and is transmitted across generations. Over hundreds or thousands of generations, animals occupying complex landscapes may develop many different migratory strategies to cope with seasonal changes in the resources required to survive and reproduce. As a result, a population may develop a portfolio of migratory behaviors with different groups of animals within the same population displaying different seasonal movement patterns. This diversity of migratory behaviors spreads the population across the landscape and helps buffer the overall population from limiting factors and random catastrophic events, thus making the population demographically more resilient. When ungulate populations are extirpated or 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. In those circumstances, it may be difficult for wildlife managers to devise restoration strategies that can help recreate historic migratory behaviors. As a result, recolonization may take many decades and some behaviors may be lost from the population forever. (Jesmer et al. 2018, Lowrey et al. 2019, 2020, 2021; Merkle et al. 2019)

## *Social Organization*

Pronghorn are social animals, although group compositions (sex, age) and numbers vary among areas and seasons. These changes may be due to birthing events, fawn protection, food distribution and quality, predation risk, and human disturbances such as fencing and hunting. Group size may also change when animals balance tradeoffs associated with obtaining adequate nutrition and avoiding aggressive social interactions. Predictable changes in forage quality and quantity through the year may cause animals to vary group sizes among seasons and habitat types. Snow conditions may influence grouping behavior by reducing forage availability and hindering travel due to increased energetic costs. In some areas, groups of

*Pronghorn fawn running in Yellowstone National Park. Photo by Jacob W. Frank, National Park Service.*

pronghorn females during summer appear to be independent social units of related animals. (Jarman 1974, Kitchen 1974, Bromley 1977, Brun 1977, Hirth 1977, Copeland 1980, Pyrah 1987, Byers and Kitchen 1988, Fryxell 1991, Heard 1992, Jędrzejewski et al. 1992, 2006; Byers 1997, O'Gara 2004b, Gower et al. 2009)

## Genetics

Pronghorn have 58 chromosomes, each of which is a molecule of deoxyribonucleic acid (DNA). Diversity or variation in the DNA of individuals provides the potential for populations to adapt to changes in environmental conditions, diseases, or resources. The genetic variation in pronghorn is lower than that of many other mammals because their numbers were reduced by about 99% during the latter half of the 19th century. Such severe reductions in numbers (called bottlenecks) can result in substantial losses of genetic variation (see Chapter 7). Some geneticists thought the Yellowstone population contained much of the genetic diversity formerly widespread in the species but no longer present in other populations. As a result, biologists used pronghorn captured from the Yellowstone population to establish or augment populations in numerous western states (see Chapter 2). (Lee et al. 1994, Reat et al. 1999, O'Gara 2004c, Scott 2004, Flesch et al. 2021)

## Diseases & Parasites

Pronghorn are susceptible to a wide variety of diseases and parasites, many of which apparently spread from domestic livestock. However, large outbreaks with long-term chronic effects on population dynamics appear to be infrequent (see Chapter 3). Viruses that can infect pronghorn include adenoviruses, bluetongue, epizootic hemorrhagic disease, bovine respiratory syncytial virus, bovine virus diarrhea, contagious ecthyma (sore mouth), and parainfluenza. Bluetongue can cause large die-offs of pronghorn with more than 3,200 deaths reported in eastern Wyoming during an outbreak in 1976. Bacterial infections include actinomycosis, anaplasmosis, anthrax, chlamydial infections, leptospirosis, pasteurellosis, plague, and tuberculosis. Actinomycosis (lumpy jaw) was common in some pronghorn populations (including Yellowstone) in the late 1800s and early 1900s. Pronghorn can be infected by internal parasites such as flukes, tapeworms, roundworms (nematodes), and coccidian protozoans, as well as ectoparasites such as ticks. (Hornaday 1913, Skinner 1922, Byers 1997, O'Gara 2004e)

## Population Dynamics

Pronghorn are polygynous with males 3 years and older attempting to breed multiple females in late summer or early autumn (the September-October rutting period; see Chapters 6 and 7). Competition between males for females is intense as they attempt to defend harems and control the movements of females. Males attempt to concentrate females into tight groups while also detecting and repelling other males. In a morning of harem maintenance and defense, a male may run 10 miles (16 kilometers) or more. Occasionally, when a harem contains a female in estrus, an intruding male cannot be chased away. The result is a fight. Fighting in pronghorn is vicious and dangerous; the risk of injury or death per fight is approximately 10%. Because of the energy they expend during rut, as well as a reduction in time devoted to feeding, males enter winter with less fat than females. As a result, males are much more likely to die in a severe winter. (Byers 1997, O'Gara 2004a,b)

Females generally begin breeding at 16 to 17 months old and breed every year thereafter. They become pregnant in late summer or autumn and give birth to one or two grayish brown to chocolate-colored fawns during mid-May to mid-June after a gestation period of about 8 to 8½ months. Pronghorn make

a very high maternal investment in reproduction relative to their body size. They usually produce twins and sometimes triplets to increase the likelihood of at least one fawn surviving. Fawns hide in rocks or vegetation for about two weeks to prevent detection by predators after which they travel with their mother through the summer before becoming independent. They stop nursing (become weaned) after about 12 weeks. (Byers 1997, O'Gara 2004a-d)

Pronghorn fawns have a high risk of being killed by predators like coyotes until about 45 days of age. Coyotes often cue in on solitary females, searching the area nearby to locate fawns in hiding. The presence of a coyote near mothers with young fawns often elicits a defensive reaction, with mothers attempting to chase the coyote away from the immediate area. After the fawns begin traveling with their mothers, small groups of coyotes may attack one or two fawns from several directions to distract the female and confuse or scare the fawns into making a fatal misstep. Bobcats (*Lynx rufus*) and golden eagles (*Aquila chrysaetos*) are important predators of fawns in some areas. Black bears (*Ursus americanus*), cougars, and grizzly bears (*U. arctos*) also kill some fawns. Overall, mortality rates of fawns often are quite high and can range from 60% to 90% with predation accounting for about 75% of the deaths and abandonment, accidents, birth defects, diseases, malnutrition, and severe weather accounting for the remainder. The high reproductive rates of pronghorn generally compensate for these high mortality rates when forage availability and quality (nutrition) is high and numbers of pronghorn in an area are relatively low. (Byers 1997, O'Gara 2004b-f)

The average adult pronghorn generally lives about 9 years, with individual does typically dying between 6 to 15 years of age and bucks dying between 4 to 12 years of age. Adult males have higher mortality (lower survival) than adult females across all ages due to their dangerous and exacting competitions for mates during the rut. Potential predators of adult pronghorn include cougars, coyotes, golden eagles, and wolves. Cougars are effective at ambushing or stalking pronghorn in areas near rugged terrain and tall vegetation. Pronghorn can outrun coyotes but are sometimes ambushed or trapped against obstacles such as fences and killed. Packs of wolves apparently killed pronghorn by ambush or group pursuit prior to Euro-American settlement and their extirpation from most areas. Wolves also kill pronghorn by trapping them against obstacles like fences. Many pronghorn may die of malnutrition (starvation) during severe winters if their seasonal ranges are deteriorated due to drought or overgrazing or if they are blocked or trapped by obstacles such as fences or deep snow. Most western states and provinces initiated and then increased regulated harvests as pronghorn numbers increased from the 1930s through the 1970s. Today hunters kill more than 100,000 pronghorn each year in a sustainable manner. Vehicles and trains also kill hundreds to thousands of pronghorn annually. (Scott 1992, Byers 1997, Caslick 1998, O'Gara 2004a,f; O'Gara and Shaw 2004, Yoakum 2004e, Kauffman et al. 2018)

Pronghorn historically lived and fed with large groups of bison (*Bison bison*) that created high quality foods by repeatedly and intensely re-grazing grasslands to keep nutritious forbs and grasses growing throughout the summer. There was little overlap in diets (competition) because bison select more grasses and pronghorn prefer forbs and shrubs. Pronghorn also associated with bighorn sheep (*Ovis canadensis*), mule deer (*Odocoileus hemionus*), and elk (*Cervus canadensis*). These species have more dietary overlap with pronghorn but tend to select different areas and habitats in some seasons. Livestock grazing by domestic sheep (*Ovis aries*) can adversely affect pronghorn by reducing the number of digestible and nutritious forbs and grasses in plant communities. Cattle (*Bos taurus*) also are reservoirs for the disease bluetongue which is fatal for pronghorn. (Yoakum 2004d, Geremia et al. 2019)

## *Current Management*

There currently are about 790,000 pronghorn in Wyoming, Montana, and Idaho. The most significant threat to these populations is the destruction or degradation of habitat along movement corridors and in fawning and wintering areas (see Chapter 8). Human development and resource extraction almost certainly will continue to degrade these habitats. A warming climate could affect precipitation and snowmelt patterns, the frequencies of droughts and wildfires, and lead to invasive annual plants dominating more native vegetation communities and negatively affecting productivity and water, energy, and nutrient cycles. Wildlife agencies need to work together and with local communities and private landowners to conserve pronghorn and their habitats, retain or restore migration pathways, and reduce conflicts. (O'Gara and Yoakum 2004, Morton et al. 2008, Berger and Cain 2014)

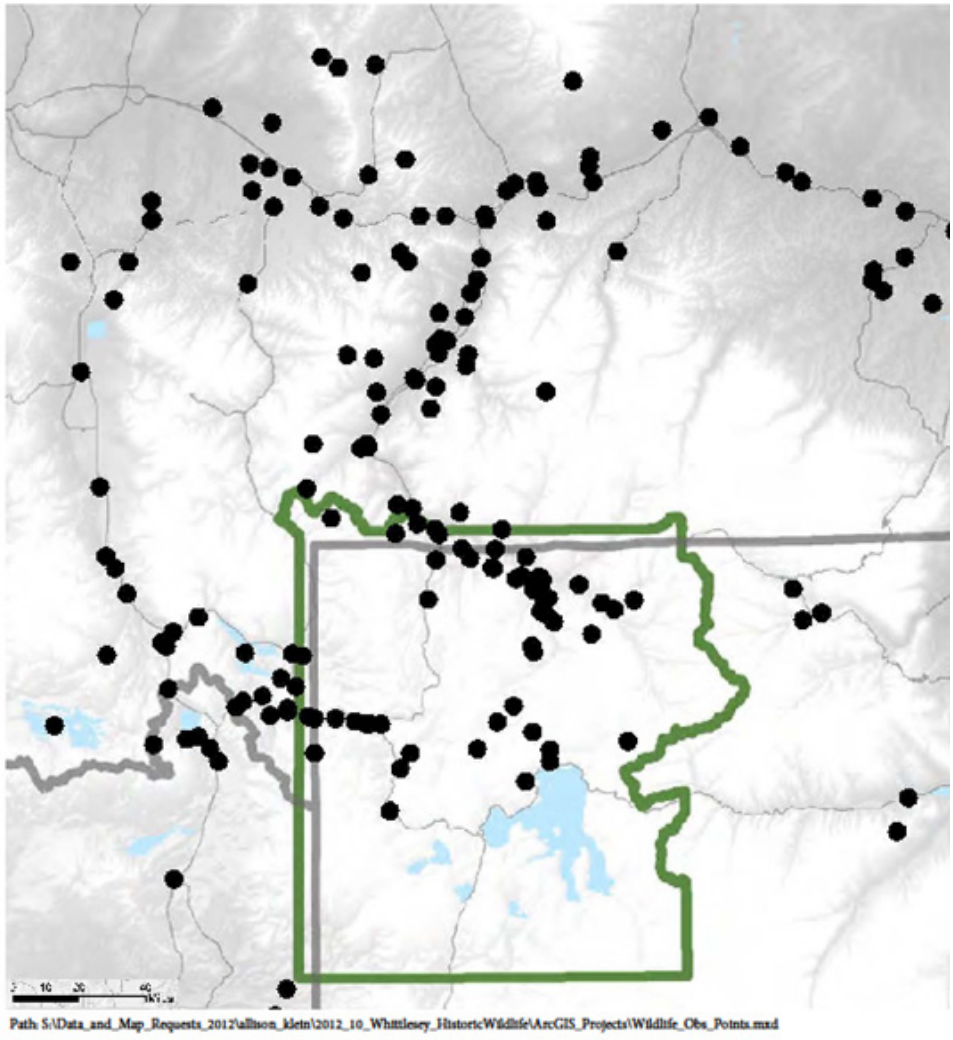
*Bachelor group of pronghorn bucks in Yellowstone National Park. Photo by Jacob W. Frank, National Park Service.*

# Chapter 2
# Historical Trends: Slaughter & Near Extirpation

## *Original Distribution*

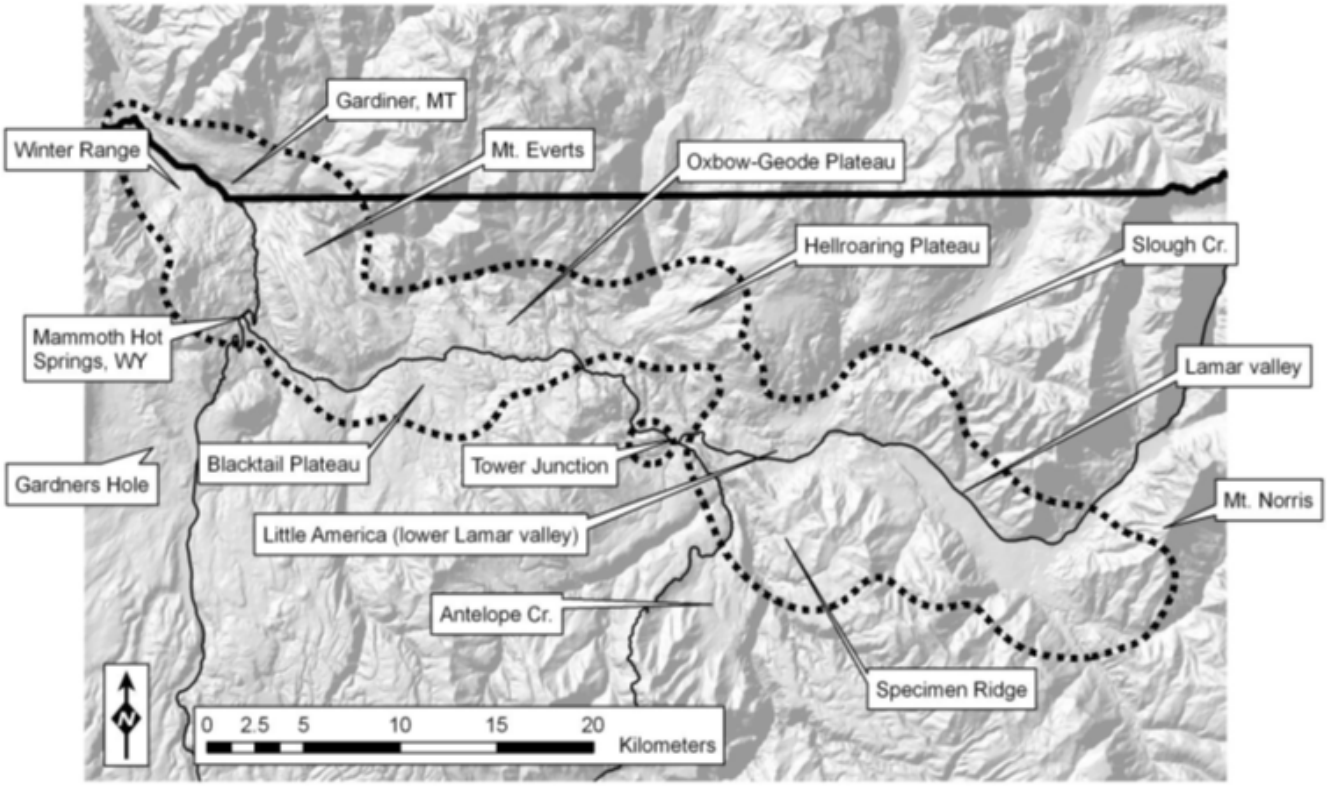
Millions of pronghorn once ranged from southern Canada through the high plains of the western United States to portions of northern Mexico. Early Euro-American travelers to the Greater Yellowstone Area frequently mentioned pronghorn (often calling them antelope) because they were relatively large and unfamiliar animals. Historical accounts indicate pronghorn were abundant and widespread in the Yellowstone area during the early to mid-1800s and made seasonal movements between mountainous grasslands in summer and lower-elevation valleys in winter. Biologists cannot derive accurate estimates of overall numbers from these irregular reports of casual sightings. However, historical accounts suggest thousands of pronghorn once used areas in and near present-day Yellowstone National Park during summer. (Whittlesey et al. 2018, Whittlesey and Bone 2020)

*Pronghorn captured near Reese Creek in Yellowstone National Park circa 1940s or 1950s. Photo by R. Robinson, National Park Service.*




*Pronghorn 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. Map created by Allison Klein and reformatted by Corrie Frank, National Park Service.*

Yellowstone pronghorn spent summer in grassland and sagebrush habitats along the major rivers in the northern and western portions of the Park and moved to lower-elevation winter ranges in the Paradise and Madison valleys of Montana during autumn. In 1881, the gamekeeper in northern Yellowstone reported that "most of the deer and antelope descended into the lower Yellowstone Valley early in the winter." During the late 1800s and early 1900s, people observed pronghorn spending winter between the slopes of Mount Everts in the northern portion of Yellowstone National Park, through the Gardiner basin to the north, and into much of the Paradise Valley; a range of 50 to 80 miles (80 to 130 kilometers) in length. During spring and summer, many of these pronghorn followed the Yellowstone River south and east to the Blacktail Deer Plateau, slopes of Mount Washburn and Antelope Creek, Hellroaring Mountain slopes, Tower Junction, Slough Creek, Specimen Ridge, Lamar Valley, and Soda Butte Creek along Mount Norris. Pronghorn also spent summers in the Hayden Valley, Lower Geyser basin, and along the Madison River in the western portion of the Park. These pronghorn apparently moved from wintering areas in the Madison Valley of Montana along the Madison and Firehole rivers and Nez Perce Creek in the Park. People also

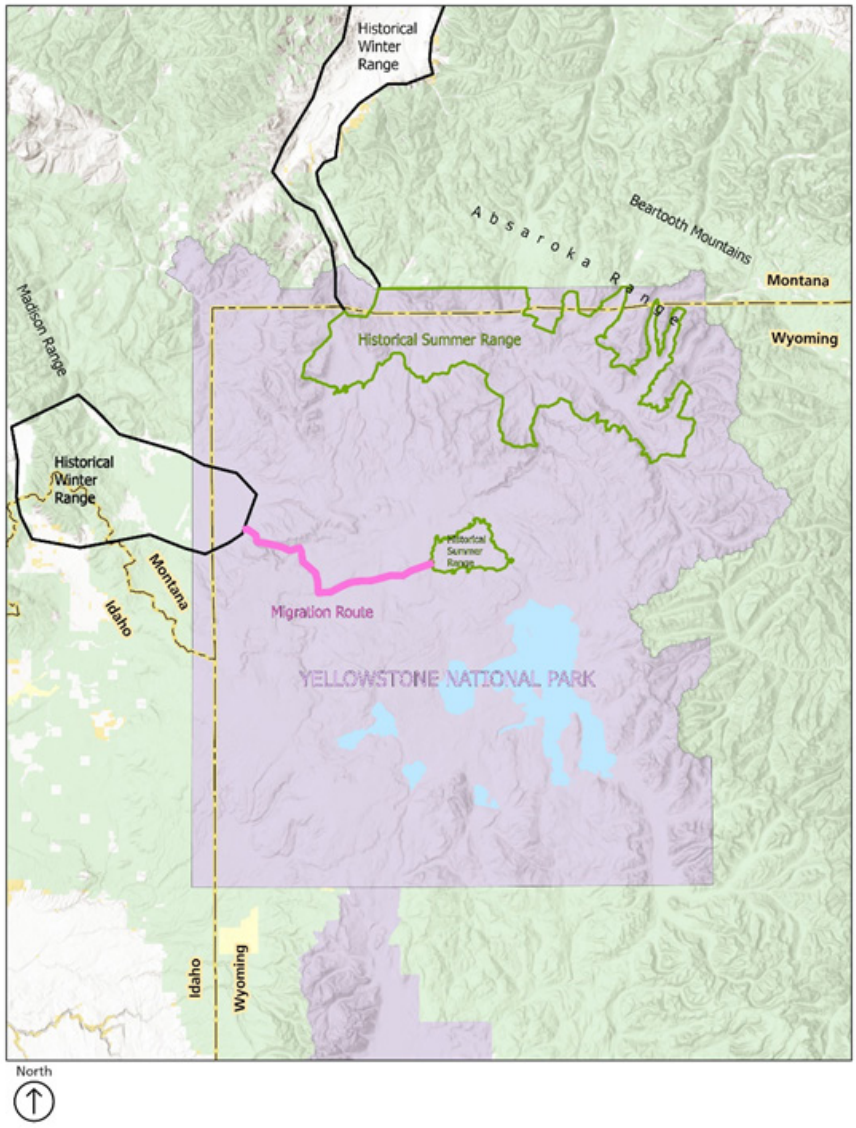



*Map of the area used by pronghorn in the northern portion of Yellowstone National Park. The heavy solid line denotes the northern boundary of the Park and thin solid lines indicate major roads. The dashed line encompasses areas used by radio-collared female pronghorn from 1999 to 2006 (from Barnowe-Meyer 2009).*

observed numerous pronghorn outside the Park east in the Clark's Fork area, south through the Teton Valley and Snake River Plain, and west near Henry's Lake and along the Madison River through the Madison Valley. (Norris 1877, Yount 1881a,b; Wilson 1885, Hofer 1887a,b,c; Grinnell 1918, Skinner 1922, Seton 1929, Murie 1940, Houston 1982, Scott and Geisser 1996, Keating 2002, Yoakum 2004a, Whittlesey et al. 2018, Whittlesey and Bone 2020)

## *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. Some tribes primarily lived in the area year-round, while others moved through the region seasonally. A band of the Shoshone called Sheep Eaters lived year-round in the area and hunted bighorn sheep and other animals for food and clothing. The Crow mainly resided in the eastern portion of the Greater Yellowstone Area and used portions of present-day Yellowstone National Park and surrounding national forests. They primarily hunted bison but also killed pronghorn, elk, deer, and bighorn sheep for meat. They gathered berries, fruits, roots, and seeds for ceremonial, nutritional, and medicinal purposes. The Eastern Shoshone primarily lived further south in the Green and Wind River areas but traveled seasonally through the Yellowstone area to access




*Approximate historical seasonal use areas and migration routes for pronghorn in the northern and west-central portions of Yellowstone National Park and nearby areas of Montana. Figure prepared by Howard Williams, National Park Service.*

bison further north, fish in Yellowstone Lake, and gather obsidian and steatite (soapstone). Members of the Eastern Shoshone tribe used the Yellowstone area more frequently as bison became scarce following European colonization. (Norris 1881a, Meagher and Houston 1998, Nabokov and Loendorf 2004, Historical Research Associates 2006a,b)

Pronghorn were an important food source for most if not all tribes living in the Greater Yellowstone Area. Communal hunters often drove pronghorn into ambushes, jumps, or traps where they were killed with arrows, clubs, spears, or guns. Hunters made game driveways from brush, poles, or rocks at several sites in the northern Yellowstone area including between Reese Creek and the Yellowstone River (northwest of Gardiner, Montana), on Mount Everts near the Gardner Canyon, towards Swan Lake (Gardners Hole), and at the base of Bunsen Peak south of Mammoth. Several tribes hunted pronghorn on horseback, while some hunting parties lit fires to influence the movements of game and regenerate habitat. 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 bones for tools. (Norris 1881a, Nabokov and Loendorf 2004, O'Gara et al. 2004, Confederated Salish and Kootenai Tribes 2005, Historical Research Associates 2006a,b; Kuhnlein and Humphries 2017)

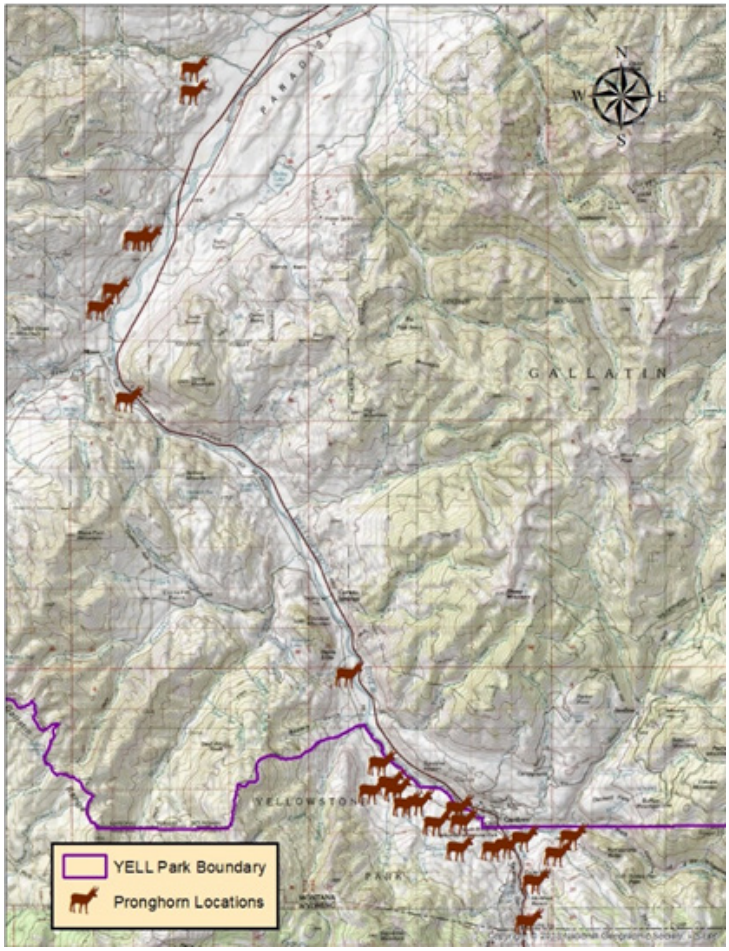
Diseases introduced by colonists, settlement of their lands, slaughter of wildlife populations, and government oppression decimated tribes in the Greater Yellowstone Area by the mid-1870s. Federal treaties limited tribal use of traditional lands and confined them to reservations where they depended on government rations and were urged to adopt farming and ranching lifestyles. When Yellowstone National Park was established in 1872, the eastern portion overlapped the Crow Reservation until the government moved the tribal headquarters further east in 1880. Federal agents moved the Sheep Eater bands living inside the Park to reservations in the Idaho and Wyoming territories by 1880. Reservation agents and soldiers discouraged and prevented indigenous people from using Yellowstone National Park for their traditional hunting and gathering activities. As a result, most tribal foraging, hunting, and spiritual activities in and near the Park ceased during the 1890s. Settlers and Park managers suppressed fires which reduced their regenerating effects and allowed conifers to invade some grassland habitats used by pronghorn. (Norris 1881a,b; Wear 1885, Harris 1889, Meagher and Houston 1998, Nabokov and Loendorf 2004, Confederated Salish and Kootenai Tribes 2005, Historical Research Associates 2006a,b)

## *Effects of Euro-American Settlement*

Settlements were sparse and isolated and livestock uncommon in the American West through the 1840s. 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 near Cooke City, Montana (1870). The influx of miners led to the building of settlements in the Gardiner basin and nearby areas including Gardiner (1880), Cinnabar (1883), Horr/Electric (1894), Aldridge (1896), and Jardine (1898). A railroad line was built to near the northern boundary of Yellowstone National Park (Cinnabar) in 1883. Settlers removed native vegetation along the Yellowstone River valley to create settlements and grow crops. Farmers and ranchers erected fences to contain many thousands of livestock and exclude wildlife. These actions impeded the movements of pronghorn and other wildlife from higher-elevation summer ranges in the Park through the Gardiner basin to lower-elevation winter ranges further north in the Paradise Valley of Montana. (Pitcher 1905, Whittlesey 1995, Keating 2002, Gill 2010)

There was a massive slaughter of pronghorn and other ungulates by market hunters during the 1870s and 1880s. In 1874 traders shipped 33,407 pounds (15,153 kilograms) of pronghorn hides from Bozeman, Montana which equates to between 11,000 and 12,000 animals. The Superintendent of Yellowstone reported market hunters took nearly 2,000 hides of pronghorn out of the Park in the spring of 1875. A trader in Fort Benton (where many hides from the Yellowstone area were shipped down the Missouri River) purchased 33,980 pounds (15,413 kilograms) of deer and pronghorn hides in 1875 which equates to roughly 11,325 animals. In 1877 the Superintendent of Yellowstone reported "thousands" of pronghorn in the Park, but by 1880 he indicated "no other animal has suffered such severe slaughter, not alone within the Park, but upon the great plains, below the Gate of the Mountains, and upon the Yellowstone, where in their migrations they were wont to winter." A fur trading company in Bozeman shipped another 5,000 pounds (2,268 kilograms) of pronghorn hides from October 1881 to July 1882 which equates to roughly 1,820 animals. This mass slaughter essentially eliminated the native grazer and predator community in the Yellowstone area for more than a century, causing substantial and often irreversible effects on native plant communities. (Avant Courier 1875, Norris 1877, 1881a; Angler 1883, Wear 1885, Skinner 1922, Meagher and Houston 1998, Picton and Lonner 2008, Whittlesey et al. 2018, Whittlesey and Bone 2020)

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. However, poaching continued due to a lack of enforcement. By the late 1880s, there were only about 200 pronghorn remaining in the Park. The U.S. Cavalry managed the Park from 1886 to 1917 and protected pronghorn and other game species by herding them back into the Park as well as killing their predators. Soldiers and Park staff killed about 4,350 coyotes in Yellowstone from 1907 to 1935. 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 pronghorn from moving out of the Park and being killed. This fence was not a permanent barrier to movements due to disrepair and other factors. The U.S. Cavalry began growing hay on about 50 acres (20 hectares) in this area in 1904 to feed pronghorn and other ungulates during winter. This feeding and protection contributed to an increase in abundance to perhaps 2,000 pronghorn by 1908 and apparently induced some animals to remain in the basin year-round. This resident non-migratory segment of the population still exists today. (Wear 1885, Harris 1889, Hofer 1905, Pitcher 1905, Benson 1910, Skinner 1922, Murie 1940, Barmore 1981, Houston 1982, Whittlesey 1995, Scott and Geisser 1996, Keating 2002, Scott 2004, Olliff et al. 2013, Whittlesey and Bone 2020)




*A representation of the historic winter range for pronghorn during the late 1800s and early 1900s. The historic winter range extended into the southern Paradise Valley and further north to Livingston, Montana, as depicted by the pronghorn symbols in the upper left portion of the figure, while the truncated winter range by the 1920s primarily was within and adjacent to the northern boundary of Yellowstone National Park (lower right). Figure prepared by Travis Wyman, National Park Service.*

Further north, settlement and fencing by ranchers in the Gardiner basin and Paradise Valley and unregulated hunting outside the Park effectively ended movements of pronghorn north of the Park. The Acting Superintendent reported in 1905 that "[t]he valley of the Yellowstone north of the Park is now completely taken up by ranchers, and their wire fences running in every direction have completely shut off the old winter range of the antelope, and they are now compelled to remain at all times entirely within the limits of the Park or very close to its borders." Pronghorn use of the Hayden Valley in central Yellowstone and their seasonal movements along the Madison River west of the Park also ceased in the early 1920s for unknown reasons. (Pitcher 1905, Young 1907, Skinner 1922, Murie 1940, Barmore 1981, Houston 1982, Scott and Geisser 1996, Caslick and Caslick 1997-2001, Keating 2002, Scott 2004, 2014)

Ranchers brought livestock into the Greater Yellowstone Area by 1867, and numerous ranches were established during the 1870s in areas used by pronghorn. Some ranchers grazed livestock on grasslands in the northern portion of Yellowstone National Park from about 1875 to 1922. There were no restrictions on numbers, seasonal use, or type of livestock (cattle, horses, sheep) within or outside the Park, leading to habitat degradation from overgrazing and soil erosion as well as competition for forage with pronghorn. These effects were exacerbated after 1879 when the completion of the transcontinental railroad led to a substantial increase in livestock numbers and additional pressures on remaining wildlife. 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. In 1900, the Superintendent established regulations to impound and dispose of loose livestock found grazing or being herded in Yellowstone National Park. However, grazing by cattle in the Gardiner basin continued and combined with cultivation almost completely altered the vegetation communities on the valley floor. (Benson 1910, Rush 1933, Houston 1982, Whittlesey 1994, Meagher and Houston 1998, Keating 2002, Gill 2010, Tyers et al. 2017, U.S. Department of Agriculture 2020, White et al. 2021c)

There were only about 8,400 pronghorn in Wyoming and 3,000 in Montana by 1920. Settlers and market hunters extirpated pronghorn from present-day Grand Teton National Park near Jackson, Wyoming, and decimated and fragmented populations to the west in Idaho. They also eliminated populations in the Madison Valley west of Yellowstone National Park and the Paradise Valley north of the Park. Market hunting, poaching, range curtailment, and a series of severe winters and starvation from 1907 to 1917 reduced pronghorn numbers in Yellowstone from thousands to between 200 and 300. (Nelson 1925, Bailey 1930, Beer 1944, Yeaman 1965, Keating 2002, Barnowe-Meyer et al. 2017b)

## *Conservation Efforts*

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. Idaho, Montana, and Wyoming passed seasonal restrictions and limits on pronghorn harvest 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 prohibited the hunting, harassment, and possession of wildlife in the Park in 1894. These and other efforts preserved remaining wildlife and began restoring populations in some areas. They also 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. (O'Gara and McCabe 2004, Rocky Mountain Elk Foundation and Conservation Visions 2006, Picton and Lonner 2008, Gill 2010, Olliff et al. 2013, Tyers et al. 2017)

The National Park Service assumed management of Yellowstone National Park in 1918 and continued several of the agricultural and husbandry practices instituted by the U.S. Cavalry for decades including predator control and the cultivation of hay. A private corporation called the Game Preservation Company bought adjacent land north of Yellowstone National Park in the Gardiner basin of Montana and operated the Game Ranch during the 1920s to protect the remaining winter range for pronghorn. Staff irrigated fields using water from springs and creeks to grow hay and feed pronghorn 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, and other game animals of Yellowstone National Park and the adjacent land." Congress formally added this area to the Park and the Absaroka and Gallatin national forests in 1932. (Hofer 1905, 1908; Acting Superintendent 1912, 1913; Skinner 1922, Seventieth Congress, Session I, Chapter 626, May 18, 1928; Barmore 1981, Houston 1982, Whittlesey 1995, Scott and Geisser 1996, Keating 2002)

Park staff removed fences to allow pronghorn 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, a program which ended in 1934. Despite a severe drought from 1930 to 1936, pronghorn counts increased from 321 in 1934 to 811 in 1940 due to increased winter range (resources) and continued feeding and predator control. However, pronghorn movements still stopped near the new northern boundary of the Park in the Gardiner basin. (Skinner 1922, Murie 1940, Keating 2002)

In the following years, concerns about overgrazing and sagebrush degradation in northern Yellowstone led to Park staff capturing and removing or shooting thousands of elk and bison between 1946 and 1968. There also were severe winters in 1948 and 1962 and extended drought during 1953 to 1961. Park staff captured about 966 Yellowstone pronghorn between 1946 and 1968 and sent 868 of them for release in five states including hundreds in the Madison Valley west of Yellowstone and the Paradise Valley and Livingston areas north of the Park from 1947 to 1957. Managers relocated smaller numbers of pronghorn to the National Bison Range in Montana, Theodore Roosevelt National Park in North Dakota, Wind Cave National Park in South Dakota, four sites in Nevada (Smith Valley, Pine Valley, Majuba Mountain, Nine Mile Flat), and the Awapa Plateau in Utah. Managers sent another 23 or more of the captured pronghorn to zoos in Arizona (Disney Productions), Kansas (Great Bend), North Dakota (Bismark), Washington, D.C. (National Zoo), and the United Kingdom (London). Counts of pronghorn in Yellowstone National Park decreased to about 150 animals following these removals and remained low for about 15 years thereafter. These removals also unintentionally reduced the distribution of pronghorn within the Park, with animals apparently no longer moving to the Antelope Creek area and lower slopes of Mount Washburn during summer following the removal of about 240 pronghorn from the Gardiner basin in the winter of 1947. (Skinner 1922, Murie 1940, Houston 1982, Scott and Geisser 1996, Keating 2002, Barmore 2003, Scott 2004, Olliff et al. 2013)

Managers adopted a new approach for managing wildlife in Yellowstone National Park during the 1970s. They stopped culling pronghorn and elk and allowed their numbers to fluctuate in response to forage availability, predators, weather, and hunting outside the Park. Elk numbers increased rapidly under this change in management, while pronghorn counts remained between 100 and 190 until 1981 despite a lack of human harvests or removals. The lack of population growth was surprising because a substantial reduction in pronghorn numbers should have increased the amount of forage available to remaining individuals. However, elk numbers in northern Yellowstone increased from about 4,000 to 16,000 during this period which may have increased competition for forage and degraded sagebrush and other shrubs on the Gardiner basin winter range. The severe drought during 1974 and 1980 also likely reduced forage quantity and quality. Alternatively, some biologists thought culling had reduced pronghorn abundance

*Pronghorn trap near Reese Creek in Yellowstone National Park circa 1940s or 1950s. Photo by R. Robinson, Yellowstone National Park.*

from levels limited by food resources to lower levels maintained by coyote predation, vehicle strikes, and dispersal. High pregnancy and summer predation rates during this period suggested predation rather than competition for food was the primary factor limiting population growth. (Houston 1973, 1982; Keating 2002, Barmore 2003, Scott 2004, White et al. 2007a, 2013c; Olliff et al. 2013)

This consistent low abundance led some biologists to recommend the pronghorn population be augmented by a "reintroduction of 100 animals." Managers did not implement this recommendation, but pronghorn numbers still increased to about 600 during 1982 to 1991 due to high recruitment of about 80 fawns per 100 adult females during 1982 and 1986. The factors inducing this rapid increase in recruitment remain obscure. In response, however, Montana Fish, Wildlife and Parks initiated hunts of pronghorn in the Gardiner basin north of the Park following complaints about crop depredation with harvests of 2 to 58 pronghorn per year (256 total) from 1985 to 1997. A private landowner constructed two miles of buck-and-pole fence along the northern boundary of the Park in 1987 and 1988 to replace a barbed-wire fence in poor repair. This fence was designed to keep cattle out of the Park and bison inside. It hindered movements by pronghorn across the boundary although crossings by crawling underneath the rails and movements through open gates or around the ends of the fence occurred regularly. (O'Gara 1968, Houston 1973, 1982; Scott 1992, Scott and Geiser 1996, Caslick 1998, Keating 2002, Barmore 2003, Scott 2004)

Population growth slowed as counts exceeded 500 pronghorn and severe drought occurred from 1987 to 1994. There was a rapid decrease in pronghorn counts to 235 from 1992 to 1995 driven by a decline in recruitment to between 8 and 22 fawns per 100 adult females. This crash occurred after intense browsing by abundant elk contributed to a decrease in sagebrush (a primary component of pronghorn winter diets) on the Gardiner basin winter range. There also was high predation by coyotes on pronghorn fawns during this period. Counts remained relatively constant between 200 and 235 pronghorn from 1996 to 2005. There was a severe winter in 1997 which resulted in substantial starvation of ungulates like pronghorn and extended drought from 1998 to 2005. Montana Fish, Wildlife and Parks closed pronghorn hunting north of Yellowstone National Park after 1997 due to low numbers. (O'Gara 1968, Singer and Norland 1994, Singer and Renkin 1995, Wambolt and Sherwood 1999, Keating 2002, Scott 2004, Wagner 2006, White et al. 2007a,b; Boccadori et al. 2008, Barnowe-Meyer et al. 2009, White et al. 2013c)

## Conclusions

The steering committee for the *Yellowstone Pronghorn Conservation Assessment Workshop* concluded in 2002 that prompt action was necessary by Park managers to reduce the relatively high risk of a catastrophic, irreversible decrease in pronghorn abundance due to isolation, low abundance, and low recruitment. The workshop participants recommended Park managers implement the following high-priority management actions:

- Estimate demographic rates and identify migration routes, fawning areas, the proportion of the population in each summer use area, and differential fawn mortality among groups.
- Develop aerial and ground survey methods for reliably estimating population size.
- Develop a contingency plan for implementation if abundance continues to decrease.
- Implement a habitat restoration plan for former agricultural lands on the Gardiner basin winter range within the Park boundary.
- Collect fecal samples during summer and winter for various assays to assess diet quality.
- Conduct necropsies of mortalities and sample blood and feces from captured pronghorn for chemical serology, trace elements, and parasites. (White and Treanor 2002)

The workshop participants also recommended Park managers initiate the following high-priority research actions:

- Study the ecological interactions among wolves, coyotes, and pronghorn to evaluate the differences in mortality and recruitment among pronghorn fawning areas in relation to wolf and coyote densities and use.
- Measure genetic diversity and structuring to evaluate inbreeding, genetic uniqueness, and identify other populations with similar genetics for possible future translocations.
- Conduct a study that integrates weather patterns, forage production, pronghorn nutritional condition, and recruitment. (White and Treanor 2002)

Biologists at Yellowstone National Park partnered with biologists from the University of Idaho, Montana State University, Montana Fish, Wildlife and Parks, National Parks Conservation Association, and the Yellowstone Ecological Research Center to address these recommendations over the next two decades. These efforts included five research projects and two restoration initiatives. Given concerns about the viability of Yellowstone pronghorn due to their low abundance and apparent isolation, biologists conducted research to evaluate the demographics and dynamics of the population including reliable estimates of abundance, age and sex composition, births, deaths, recruitment, and trends (Chapter 3). They evaluated if the selection of sagebrush (Artemisia) habitats by pronghorn on their winter range has changed since the late 1980s, corresponding with diminishing sagebrush and increases in other species such as rabbitbrush (Chrysothamnus; Chapter 4). They documented migration patterns, seasonal distributions, and individual fidelity to migration strategies to evaluate changes from historical patterns, population structure, and protection and restoration needs for migration pathways (Chapter 5). They assessed the potential adaptive benefits of migration by evaluating seasonal foraging strategies, nutrition, condition, maternal investment, survival, and the interacting influences of predator density, snow depths, and terrain (Chapter 6). They also evaluated genetic diversity, inbreeding, relatedness (kinship), and structure in the pronghorn population with regards to population viability and gene flow with neighboring herds (Chapter 7). Park and Forest Service biologists began efforts to restore native bunchgrass, forb, and sagebrush habitat for pronghorn on their Gardiner basin winter range, while the National Parks Conservation Association worked with private landowners and federal and state agencies to restore migration pathways by removing impediments (Chapter 8). We describe the findings and results of these efforts through the remainder of the book.

*Pronghorn buck in Yellowstone National Park. Photo by Jacob W. Frank, National Park Service.*

# Chapter 3
# Demography: Status of the Population

## *Introduction*

Given that Yellowstone pronghorn faced a serious and recurring risk of extirpation, there was a need to determine their current demographic status and assess actions needed to increase the viability of the population. 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). 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. Populations with abundant resources tend to grow at their biological maximum. Population growth slows if the number of animals inhabiting an area increases to the point where there are fewer resources for each individual; that, in turn, decreases nutrition, body condition, reproduction, and survival. Environmental factors not related to density such as extended drought or severe snow conditions can intensify these effects by decreasing food availability and increasing energetic costs. (Caughley and Sinclair 1994, Eberhardt 2002, White and Gunther 2013)

The National Park Service is charged with preserving the resources (including wildlife and their habitats) in Yellowstone National Park unharmed and in their natural condition for the benefit and enjoyment of people. To achieve this goal, pronghorn and other wildlife are generally allowed to move freely and unpursued within the Park with their behaviors, movements, and reproductive success primarily affected by their decisions and natural selection (survival of the fittest). Pronghorn within the Park 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 that can be quite severe at times. As a result, Yellowstone pronghorn have likely retained their adaptive capabilities. A major concern, however, is whether the number of pronghorn in the population and gene flow from neighboring populations are high enough to avoid genetic drift and inbreeding depression and maintain the genetic variation necessary for future adaptations to changing conditions. (16 USC [United States Code] 21 and 26, 54 USC 100101 *et seq*.; White 2016)

The International Union for the Conservation of Nature recommends that population sizes of wild ungulates be at least 1,000 animals, with approximately equal numbers of males and females to ensure competition between breeding males for mates and preserve genetic variation over centuries. These animals do not need to be in a single herd but could be in two or three locations with frequent gene flow between them. To reach this objective and increase sustainability, Park biologists would like to increase the abundance of pronghorn in and near Yellowstone National Park and reestablish interactions and gene flow with neighboring populations north and west of the Park in the Paradise and Madison valleys of Montana. (Hedrick 2009, Gates et al. 2010)

This chapter summarizes information about the status of the population including estimates of abundance, age and sex composition, births, deaths, and recruitment. Genetic information is presented in Chapter 7.

*Pronghorn feeding during winter in the Gardiner basin portion of Yellowstone National Park. Photo by Neal Herbert, Yellowstone National Park.*

## Counts and Classifications

Yellowstone pronghorn are typically counted by a single observer from the ground or in an airplane during late March or early April when animals are concentrated on their winter range in the Gardiner basin. Pronghorn begin migrating to their summer ranges several weeks early during some years when mild late-winter conditions and early vegetation green-up make early migration advantageous. If pronghorn migrate prior to the count, it is necessary to survey both the winter and summer ranges of pronghorn, an area stretching eastward to Mount Norris in the upper Lamar Valley of Wyoming. In contrast to counts, classification surveys are typically conducted in late summer or autumn by an observer who records the composition (sex and relative age) of each observed group. Classifications of does include both adult and yearling females because it is not possible to distinguish between them. Bucks are identified by the presence of horns longer than half the ear length and a black cheek patch. Fawns are significantly smaller than adult does and are easily identified.

The detection of pronghorn varies among counts and classifications due to animal behavior, group size, observer experience, snow cover, vegetation cover, and other factors that influence an observer's ability to sight animals. Biologists conducted a series of 11 airplane flights in Yellowstone to test the ability of observers at detecting radio-collared pronghorn in groups of various sizes and improve methods for reliably estimating population size and composition. The detectability of pronghorn in groups with fewer than 10 animals was lower on the much larger summer range than on the smaller winter range. Group size varied from 1 to 61 animals on the winter range and 1 to 27 animals on the summer range. Observers had a higher probability of sighting groups on the winter range (89%) than the summer range (67%). There also was an increase in the detection of groups from 83% to 99% on the winter range and 53% to 97% on the summer range as group size increased from 1 to 50. (White et al. 2006)

*Radio-collared pronghorn doe with fawn on Specimen Ridge in Yellowstone National Park. Photo by Jacob W. Frank, National Park Service.*

Pronghorn numbers declined from about 600 in 1991 to 235 in 1995, remained less than this level until 2006, increased to about 500 pronghorn by 2017, and then decreased to about 420 animals in 2020. During this same period, counts of elk in northern Yellowstone decreased from about 16,000 to 6,000 following liberal female harvests and the recovery of large predators, suggesting competition for forage with elk may have been a factor contributing to pronghorn numbers remaining at lower levels following the population crash in the early 1990s. There have been about 44 adult pronghorn males per 100 females (44:100) in the population since 1969 with annual ratios ranging between 13 and 104 males per 100 females (13:100 and 104:100). Buck to doe ratios were much higher (average = 62:100; range = 33:100 to 104:100) during the 1970s to mid-1990s than thereafter (average = 28:100; range = 13:100 to 62:100). The causes of this substantial decrease in adult males are unknown. (Scott 1994, Keating 2002, White et al. 2006, 2007a; White and Gunther 2013; Scott 2013)

## Reproduction

The annual cycle of reproduction for Yellowstone pronghorn begins when females ovulate and become receptive to mating in late summer. Breeding occurs in late summer or early autumn when pronghorn are in peak body condition, a result of having fed on nutritious forage through the summer and building muscle mass and fat. Gestation lasts about 245 days (range = 237 to 251) through winter. Fawns are born in spring when forbs and grasses are initiating seasonal growth, providing mothers and their fawns with high-quality forage to support nursing, restoration of nutritional condition, and growth prior to winter. (Byers 1997, 2001; Barnowe-Meyer et al. 2011)

Biologists estimated reproductive rates of Yellowstone pronghorn by determining the pregnancy status of captured females from hormone levels in blood samples. Adult female pronghorn had a relatively high

pregnancy rate of 94% (0.94) from 1999 to 2007. Pronghorn usually gave birth to two fawns around June 1st (range = May 20 to June 21). Biologists observed the births of 17 twins and 3 single fawns from 1999 through 2006. Pronghorn gave birth across northern Yellowstone from elevations of about 5,200 feet (1,585 meters) in the Gardiner basin to 8,400 feet (2,560 meters) on the slopes of Mount Norris in the upper Lamar Valley. Births and hiding sites occurred in grasslands, sagebrush, subalpine meadows, talus slopes, and the edges of coniferous forests. (Byers 2001, Barnowe-Meyer et al. 2009, 2010, 2011; Scott 2013)

## Survival

The probability an animal is still alive at some future time, such as one year later, is called the survival rate. The likelihood of survival from year to year depends on an animal's age. It is relatively low from birth through the first year of life for ungulates like pronghorn but quickly increases to a maximum when animals reach adult body size and remains high through prime age after which it decreases. Survival rates for prime-aged females tend to be high and relatively constant from year to year and trends in population size are sensitive to changes in the survival rates of adult females. (Caughley and Sinclair 1994, Eberhardt 2002)

Biologists estimated the survival rates of Yellowstone pronghorn by fitting newborn fawns with ear-tag transmitters and adult females with radio collars. The tags and collars contained sensors that changed the pattern of the transmitted radio signal when they were immobile for an extended period (6-8 hours), suggesting the animal had died. Biologists then located the dead animal and examined the remains to determine the cause of death. They also estimated the ages of pronghorn based on incisor irruption patterns, tooth wear, or extracting an incisor and counting the annual rings of cementum in the root like annual growth rings in a tree.

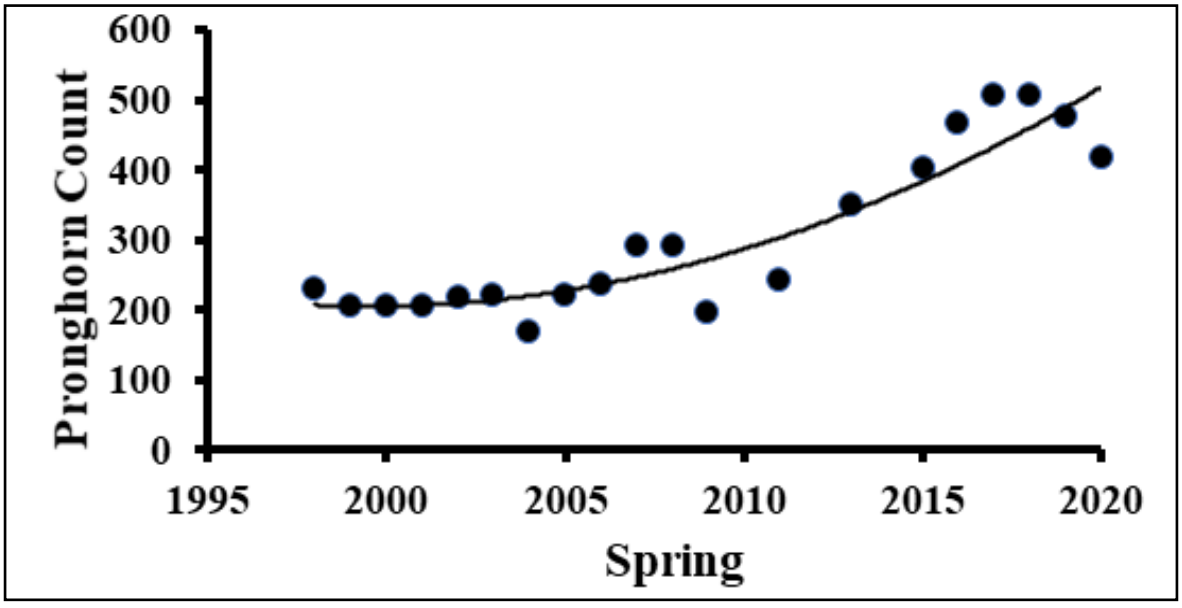
The maximum lifespan of adult female pronghorn in Yellowstone appears to be roughly 10 years. Estimated ages of 46 adult female pronghorn captured from 1999 to 2005 ranged between 2 and 9 years with 14 young 2-year-olds (30%), 27 prime-aged 3- to 6-year-olds (59%), and 5 older 7- to 9-year-olds (11%). Survival rates for adult female pronghorn were about 86% (0.86) overall and ranged from 74% to 99% annually. The average survival rate for Yellowstone pronghorn was somewhat lower than for prime-aged females in other populations because the Yellowstone estimate includes data from older females that typically have lower survival rates.

## Causes of Death

Predators—During 1999 to 2007, coyotes accounted for about 56% of predation on radio-collared adult female pronghorn with cougars (33%) and wolves (11%) comprising the remainder. Coyotes were responsible for up to 79% of predation on ear-tagged fawns with cougars, golden eagles, and black bears comprising the remainder. Coyotes are numerous across northern Yellowstone in open low-lying areas in sagebrush steppe habitats, areas which are chosen by many female pronghorn for birth and fawn hiding sites. Predation risk from coyotes on adult female pronghorn increased immediately following parturition because they selected more rugged or vegetated areas for their fawns to hide, areas where ambushes by predators are more common.

Cougar predation appears to have increased since the 1980s and 1990s when pronghorn comprised less than 1% of prey and fewer pronghorn migrated (~20%) than today (~70%). From 1999 to 2007, bears and golden eagles were more numerous on higher-elevation portions of the summer range than in the Gardiner basin. Wolf predation on pronghorn was relatively low and appeared opportunistic. (Scott and Geisser 1996, Caslick and Caslick 1997-2001, Barnowe-Meyer et al. 2009, 2010, 2011; Scott 2014, Ruth et al. 2019, Metz et al. 2020)

*Pronghorn carcass near Stephens Creek in Yellowstone National Park. Photo by Jim Peaco, National Park Service.*




*Counts of Yellowstone pronghorn each spring prior to migration in the Gardiner basin of Montana from 1998 to 2020. The estimated growth rate of the population averaged about 10% per year from 2005 to 2016.*

Harvests—There was no hunting of Yellowstone pronghorn moving outside the Park into Montana from 1998 to 2015. As pronghorn abundance and movements north of the Park increased, public hunts were resumed by Montana Fish, Wildlife and Parks in 2016. There were 10 permits (licenses) each autumn in hunting district 313 (which includes the southern Paradise Valley) which increased to 11 in 2018 and 21 in 2019 before decreasing to 10 in 2020. Total harvest from 2016 to 2020 was about 53 pronghorn, including 51 males, one female, and one fawn. It is too soon to evaluate the effects of these harvests on the population dynamics and migratory and dispersal movements of pronghorn north from Yellowstone.

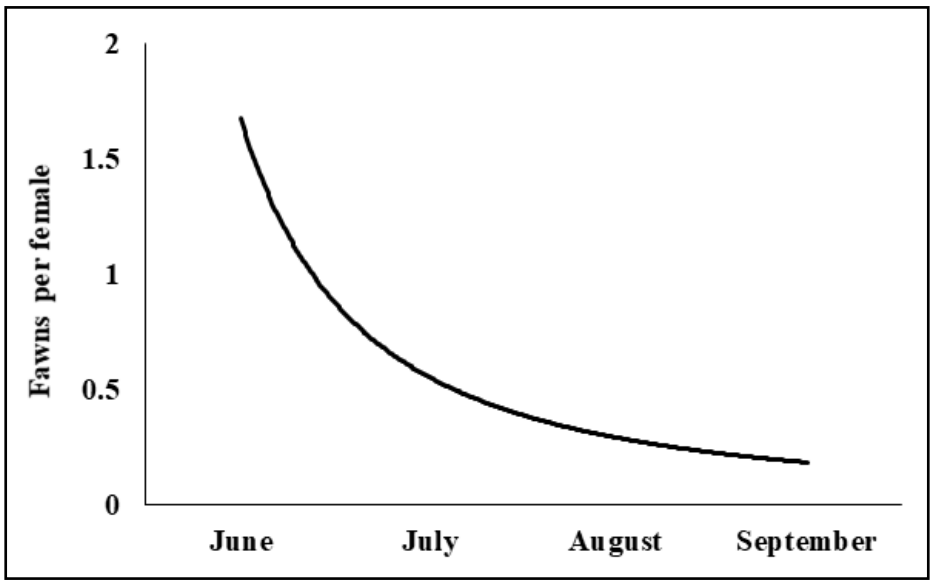
Diseases—Biologists collected blood, feces, and nasal swabs from 32 female pronghorn captured during winter 1999 and analyzed these samples to assess their health. Results indicated a relatively healthy population with no elevated incidence of disease. Serology and blood chemistry values were normal, although four females had low protein and blood urea nitrogen values indicative of nutritional stress. Trace mineral levels of copper, iron, selenium, and zinc were in the normal range as were hematological values for hemoglobin, packed cell volume, and white blood cell count. Fecal egg and oocyst counts detected some protozoans (*Eimeria antilocaprae*) and intestinal and lung nematodes, but overall internal parasite loads were low. (Dunbar 2002)

Laboratory technicians detected antibodies against *Chlamydia psittaci* in 75% of sampled females which is surprising since infection is rare in pronghorn. This bacterium can cause infectious keratoconjunctivitis (pinkeye), arthritis, pneumonia, and reproductive problems. A pinkeye outbreak caused by *Chlamydia* bacteria killed about 60% of the estimated 500 bighorn sheep spending winter on or near Mount Everts in Yellowstone National Park during the 1980s. Biologists did not observe signs of this disease in pronghorn but are continuing surveillance. Technicians detected antibodies in 59% of sampled female pronghorn against parainfluenza 3 (PI3) virus which can cause pneumonia. Biologists did not observe signs of pneumonia in pronghorn but about 36% of bison sampled in northern Yellowstone also had antibodies against this disease. (Meagher et al. 1992, Taylor et al. 1997, Dunbar 2002)

Technicians detected antibodies against bovine viral diarrhea virus in a few sampled females but tests for exposure to *Brucella*, *Pasteurella*, paratuberculosis (Johne's disease), bovine respiratory syncytial virus, bluetongue, and epizootic hemorrhagic disease all were negative. Bluetongue virus infects pronghorn in northern Wyoming and remains a threat to Yellowstone pronghorn. Epizootic hemorrhagic disease is present in eastern Montana where it has devastated several white-tailed deer (*Odocoileus virginianus*) populations. (Dunbar 2002)

## Recruitment

The annual birth pulse adds hundreds of fawns to the pronghorn population each spring which would rapidly and substantially increase abundance if most survived. However, fawns are extremely vulnerable to predation and a large portion die soon after birth in most years. Those that survive until their first birthday are "recruited" into the adult population which biologists report as a rate such as 30 fawns per 100 adult females or 0.30 fawns per adult female. Yellowstone pronghorn have high pregnancy rates (0.94) and an average litter size of about 1.9 fawns. Thus, the fawn to adult female ratio at birth is typically somewhere around 178 fawns per 100 adult females (or 1.78 fawns per adult female). By autumn, this ratio decreased substantially to between 18 and 94 fawns per 100 adult females annually since 1969 and an average of 27 fawns per 100 adult females since 2000 (range = 16 to 40 fawns per 100 adult females). In other words, about 85% of fawns died within six months. The recruitment rate needed to maintain a relatively stable population given current adult female survival rates (about 0.86 or more) is probably greater than 25 to 30 fawns per 100 adult females. Lower rates will likely contribute to the population size decreasing, while higher rates should contribute to an increasing population trend. (Caslick 1998, Barnowe-Meyer et al. 2011, White and Gunther 2013)




*Representative trend in the number of fawns per female in Yellowstone National Park during summer since 2000 as extensive fawn mortality occurs during the first 45 days following birth.*

## Emigration & Immigration

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

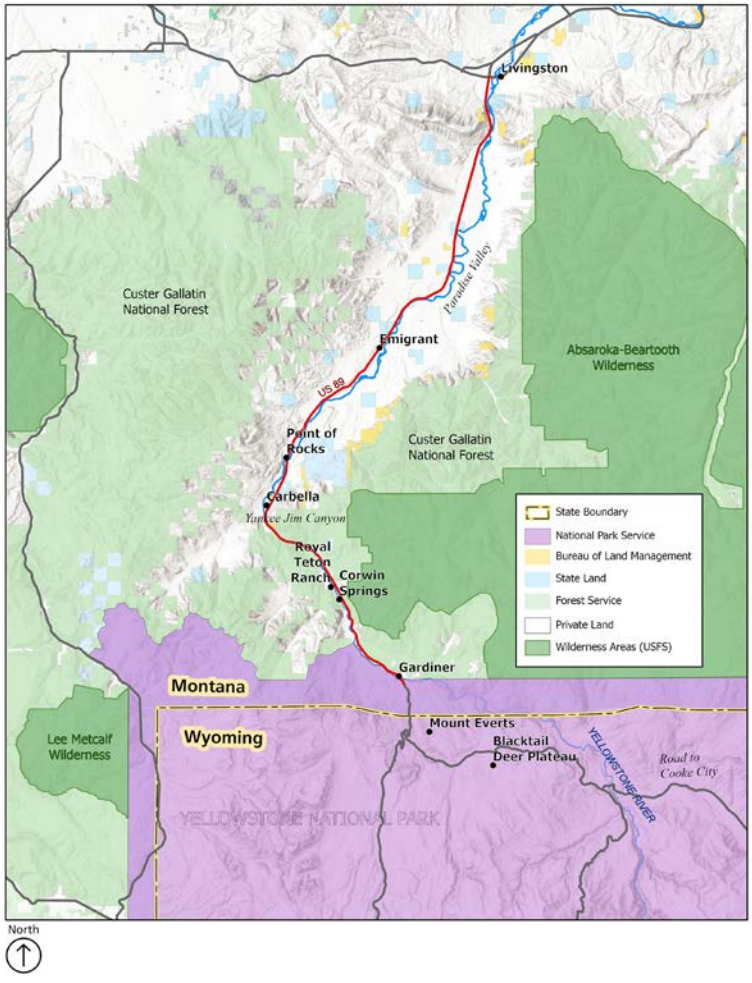
North of the Park, biologists conducted weekly surveys for pronghorn in the Paradise Valley between Carbella and Livingston, Montana, from 1988 through 1997 but only observed a few solitary animals. However, in 1998 Park staff observed 11 pronghorn about 15 miles (24 kilometers) north of Yellowstone National Park in the southern portion of the Paradise Valley near Carbella, Montana. In 2000, biologists located a group of 17 pronghorn between Carbella and Point of Rocks about 4 miles (6 kilometers) further north. This group included an adult female radio-collared in the Park during November 1999 that dispersed to the southern Paradise Valley during the summer or autumn of 2000. This doe remained in the Carbella/Point of Rocks area until April 2002 when it died. Numbers of pronghorn in this area gradually increased to about 121 in 2014 which was the first significant return of pronghorn to the southern Paradise Valley since the early 1900s. Subsequent movements by other pronghorn indicated the dispersal pathway went from the Park north through agricultural and rural developments west of the Yellowstone River and state highway 89 and then through a narrow canyon (Yankee Jim) into the southern Paradise Valley at Carbella. (Caslick 1998, Barnowe-Meyer and Byers 2008, Barnowe-Meyer 2009, Scott 2013, White et al. 2013c, White and Adams 2022)

## Conclusions

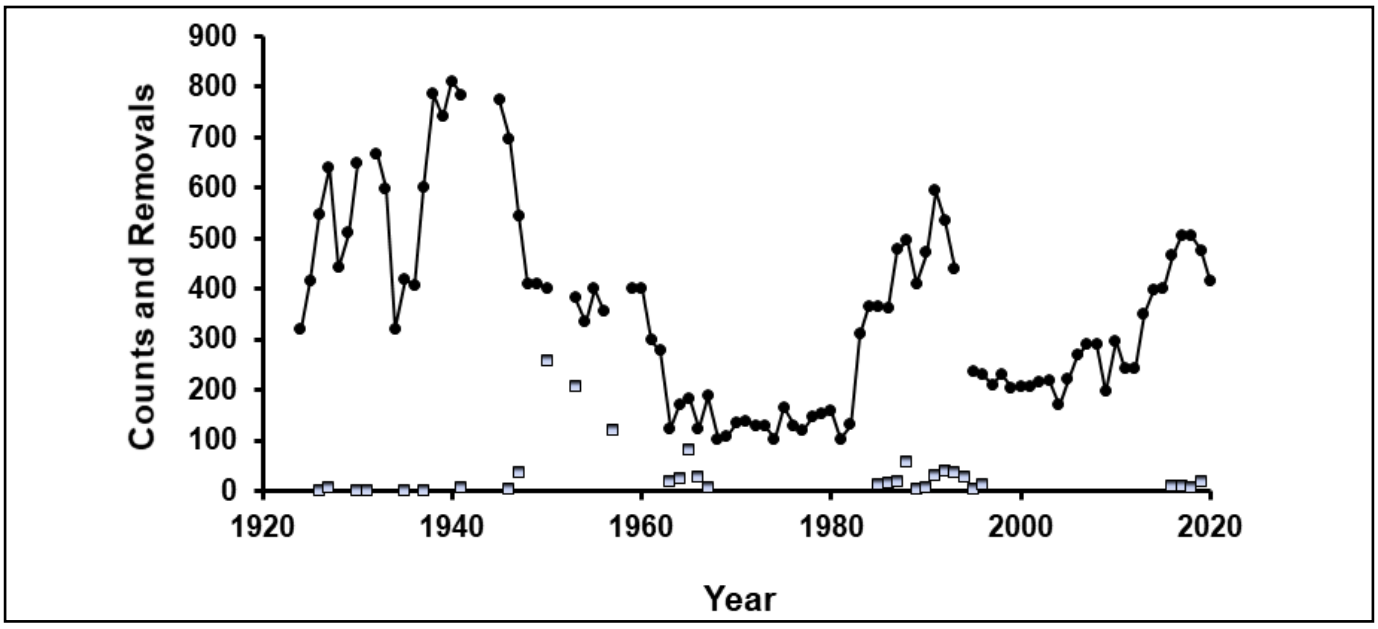
Populations of ungulates released into a new area generally increase rapidly in size due to abundant resources such as food and habitat that induce high reproduction and survival of young. As the number of animals approaches or exceeds the capacity of the range to provide food and other resources numbers

may crash to a low level as reproduction and survival decreases. After habitats recover, numbers usually increase to a level that is somewhat lower than the original peak abundance. Similar dynamics occur in populations that are substantially reduced through harvests or captures and removals and then "released" when managers cease these activities. Pronounced fluctuations in population size also occur due to changes in food availability, predation, and diseases. (Caughley 1970, 1979; Sinclair 1979, Bergerud 1983, McCullough 1997, Forsyth and Caley 2006)

Biologists used the data presented in this chapter and a suite of models to evaluate the population dynamics of Yellowstone pronghorn. Results suggested the historic curtailment of the winter range and truncated migration outside the Park following Euro-American settlement contributed to irruptive population dynamics in Yellowstone pronghorn rather than more stable or gradual fluctuations in numbers. An irruption occurred after Congress expanded the Gardiner basin winter range in 1932 and more resources were available to pronghorn. Another irruption occurred after Park managers stopped culling pronghorn from the population in 1969 and liberal hunter harvests outside the Park and predators substantially reduced the number of elk on the winter range. Crashes to relatively low numbers occurred when managers removed about 900 pronghorn from 1946 to 1967 and after the degradation of sagebrush on the winter




*Locations in the upper Yellowstone River basin referred to in the text. Figure prepared by Howard Williams, National Park Service.*




*Counts (circles) of Yellowstone pronghorn and removals (squares) by capture and harvests from 1924 to 2020.*

*Pronghorn and bison feeding on the Gardiner basin winter range of Yellowstone National Park with Electric Peak and a full moon in the background. Photo by Jacob W. Frank, National Park Service.*

range by elk during the 1990s and high predation by coyotes during the 2000s. Numbers remained low following these crashes until conditions once again promoted high recruitment and survival. Over the past 50 years, rapid increases and crashes in pronghorn numbers have been followed by 10-to-15-year periods of relative stability. This pattern is concerning because recurring population crashes can put the long-term viability of the entire population at risk. Conversely, the most recent increase in the pronghorn population appears to have encouraged dispersal and development of a neighboring population within the Paradise Valley to the north which will help buffer the effects of future crashes in either population. (Keating 2002, White et al. 2007a, 2013c)

# Chapter 4
# Habitat Use: Range Degradation Alters Selection

## *Introduction*

Sagebrush is generally a staple food for pronghorn in all seasons but especially the winter. Given concerns about the degradation of sagebrush in the Gardiner basin since the 1960s, biologists evaluated if pronghorn selection of these habitats had changed. The repeated intense use of preferred forage plants by livestock or wildlife within a habitat type can cause changes in plant composition, productivity, and soil organic matter. Such transitions also occur due to changes in environmental conditions including those influenced by humans such as climate warming. Climate is the main factor affecting forb and grass production in northern Yellowstone because variations in precipitation and temperature strongly influence soil moisture which can limit production. Animals respond to transitions in plant communities by altering their selection of habitats to sustain nutritional intake, body condition, reproduction, and survival. This chapter summarizes the history of range conditions encountered by Yellowstone pronghorn within the Gardiner basin and an investigation of pronghorn resource selection within this area from 1997 through 2001. (Werner and Anholt 1993, Yoakum 2004b, Boccadori et al. 2008, Frank et al. 2013, Geremia and Hamilton 2019)

## *Range Degradation*

Historic photographs depicted an increase in the density of big sagebrush (*Artemesia tridentata*) in the Gardiner basin in areas grazed by livestock from the late 1880s to early 1900s. After livestock were removed, the density, productivity, and survival of sagebrush declined due to intense grazing by deer, elk, and pronghorn concentrated on feed grounds and kept in the Park by fencing and intense hunting along the boundary. This overgrazing combined with sustained periods of drought substantially decreased the amount of big sagebrush on the pronghorn winter range in the Gardiner basin by the 1940s. (Murie 1940, Kittams 1950, Houston 1982, Singer and Renkin 1995, Scott and Geisser 1996, Meagher and Houston 1998, Wambolt and Sherwood 1999, Keating 2002, Wagner 2006, Boccadori et al. 2008)

Park managers responded to this reduction in sagebrush by implementing population reduction efforts from 1946 to 1967 to decrease numbers of pronghorn from about 800 to 125 and elk from about 10,000 to less than 4,000 (see Chapter 2). However, the removals did not reduce congregations of ungulates and browsing in the Gardiner basin during winter. The abundance of big sagebrush decreased by 43% and canopy cover by 29% between 1957 and 1990 as ungulate browsing reduced sagebrush heights and prevented the recruitment of seedlings. Sprouting shrubs like rabbitbrush increased in abundance because they withstood the intense browsing better than sagebrush. (Houston 1982, Singer and Renkin 1995, Scott and Geisser 1996, Keating 2002, Wagner 2006, Boccadori et al. 2008)

In addition, about 530 acres (215 hectares) in the Gardiner basin were cleared of native vegetation and planted with non-native grasses such as oats (*Avena sativa*), smooth brome (*Bromus inermis*), clover (*Trifolium repens*), and timothy (*Phleum pratense*) to grow hay for deer, elk, pronghorn, and other wildlife between 1904 and 1952. Managers also eventually planted non-native crested wheatgrass (*Agropyron cristatum*) in these hayfields. A warming climate and high nitrogen deposited in feces and urine from ungulates allowed winter annuals (including annual wheatgrass *Eremopyrum triticeum*, cheatgrass *Bromus*

*tectorum*, and desert alyssum *Alyssum desertorum*) to spread during the following decades, replacing crested wheatgrass and filling in spaces between native bunchgrasses. Annual grasses comprised more than 70% of the plants in some areas by the 2000s which adversely reduced forage productivity compared to other community types. Once these non-native annual species were introduced, climate rather than grazing was primarily responsible for the development of these annual grass communities. (Cahalane 1944, Whittlesey 1995, Geremia and Hamilton 2019, White et al. 2021a,b)

By the 1990s, the winter range for pronghorn in the Gardiner basin consisted of about 48% grassland cover, 20% sagebrush, 10% grassland-sagebrush mix, 13% old agricultural fields, 4% rabbitbrush and greasewood (*Sarcobatus vermiculatus*), and 5% riparian areas and conifer forests. Native plants in grasslands included blue bunch wheatgrass (*Pseudoroegneria spicata*), fringed sage (*Artemisia frigida*), Idaho fescue (*Festuca idahoensis*), needle and thread (*Hesperostipa comata*), prairie junegrass (*Koeleria macrantha*), Sandberg bluegrass (*Poa secunda*), sandwort (*Arenaria hookeri*), and western wheatgrass (*Pascopyrum smithii*). Sagebrush cover was mostly dominated by basin big sagebrush (*Artemesia tridentata tridentata*) and Wyoming big sagebrush (*Artemesia tridentata wyomingensis*) with an understory of primarily blue bunch wheatgrass, prairie junegrass, and Sandberg bluegrass. Grassland-sagebrush mix included big sagebrush with some rubber rabbitbrush (*Chrysothamnus nauseosus*) and green rabbitbrush (*Chrysothamnus viscidiflorus*) and an understory of prairie junegrass, Sandberg bluegrass, annual wheatgrass, and desert alyssum. Old agricultural fields included areas previously planted in hay and currently containing cheatgrass, crested wheatgrass, annual wheatgrass, and desert alyssum. Rabbitbrush and greasewood cover included an understory of Sandberg bluegrass, annual wheatgrass, crested wheatgrass, desert alyssum, dandelion (*Tarasacum officinale*), and stickseed (*Lappula redowskii*). Riparian areas and conifer forests included cottonwood (*Populus*), willow (*Salix*), and Douglas-fir (*Pseudotsuga menziesii*). (Boccadori 2002, Savage 2005, Boccadori et al. 2008, Geremia and Hamilton 2019)

*Female pronghorn in the Gardiner basin portion of Yellowstone National Park during winter. Photo by Jim Peaco, Yellowstone National Park.*

## Altered Habitat Use

Pronghorn frequently used sagebrush habitats in the Gardiner basin during winters in the 1930s, but their use decreased by the 1960s as the abundance and productivity of sagebrush decreased and other shrubs like rabbitbrush became more available. Pronghorn chose flat to rolling terrain with moderate west-facing slopes and hilltops from 1968 to 1970. They mostly fed in areas with less than 3 inches (8 centimeters) of snow and avoided areas with more than 6 inches (15 centimeters). Most feeding occurred in old agricultural fields from October to December, dry grasslands from January through April, and wet grasslands during May. Pronghorn generally did not select sagebrush habitats. Biologists noted similar habitat selection patterns from 1986 to 1988 which was surprising because sagebrush previously was a favored winter forage. (Murie 1940, Singer and Norland 1994, Singer and Renkin 1995, Wambolt and Sherwood 1999, Keating 2002, Barmore 2003, Boccadori et al. 2008)

Pronghorn were widely distributed through the Gardiner basin from the northern end of Mount Everts in Yellowstone National Park through the Royal Teton Ranch north of the Park during winters from 1988 to 1994. From 1997 to 2001, about 13% to 51% of habitat use by pronghorn in the Gardiner basin during winters occurred north of the Park in hay pastures, shrub-steppe habitats, and grass-forb communities, perhaps due to an increase of 190 acres (77 hectares) in irrigated hay fields and the reseeding of old fields adjacent to the Park. Radio-collared pronghorn continued to select lower elevations and gentle slopes during winters from 2000 to 2005. During this period, pronghorn again selected greasewood and grassland habitats more than sagebrush. This is believed to be due to the substantial decrease in sagebrush since the 1960s from intense browsing by elk and other ungulates. (Singer and Renkin 1995, Caslick and Caslick 1997-2001, Wambolt and Sherwood 1999, Keating 2002, Boccadori et al. 2008, Scott 2013, 2014)

## Conclusions

A truncated and degraded winter range within and adjacent to the Park may not support large numbers of pronghorn for sustained periods due to the substantial decrease in sagebrush habitat and the nutrition those areas provide during winter. The habitats within and adjacent to Yellowstone National Park in the Gardiner basin have low productivity and contain a relatively small percentage (10% to 38% cover) of shrubs and herbaceous plants such as forbs. Pronghorn may no longer be able to rely on sagebrush as a staple food source during some winters but instead use a variety of habitat types to meet their nutritional needs. However, pronghorn maintained relatively high reproductive and survival rates (see Chapters 3 and 6) despite the decrease in sagebrush since 1960, and there is no evidence of widespread malnutrition. A comparison of reproductive effort between pronghorn at Yellowstone and those at the National Bison Range, which are descended from Yellowstone pronghorn, suggested reproduction was only slightly affected by habitat quality. Yellowstone pronghorn subsisted on a poorer winter range in a colder drier climate, but their reproductive effort was the same as for pronghorn on the National Bison Range. (Byers 1997, Keating 2002, Scott 2004, White et al. 2007b, Boccadori et al. 2008, Renkin 2021)

*Female pronghorn traveling in the Lamar Valley of Yellowstone National Park. Photo by Neal Herbert, National Park Service.*

# Chapter 5
# Seasonal Movements: Partial Migration Strategy

## *Introduction*

Development, fencing, habitat fragmentation, and a loss of migration memory from the Yellowstone population truncated the migration of pronghorn north of Yellowstone National Park by up to 50 miles (80 kilometers) by the late 1800s. Given concerns about the curtailed and degraded winter range in and adjacent to Yellowstone National Park, biologists wanted to restore the historical movements further north into the southern Paradise Valley to provide pronghorn with access to more forage. Most ungulates in temperate environments make some type of seasonal movements or migration to obtain more nutritious food and/or reduce the risk of predation. 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. 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.(Fryxell et al. 1988, Scott 1992, Scott and Geiser 1996, Caslick 1998, Keating 2002, Scott 2004, Coughenour 2008, White et al. 2013c)

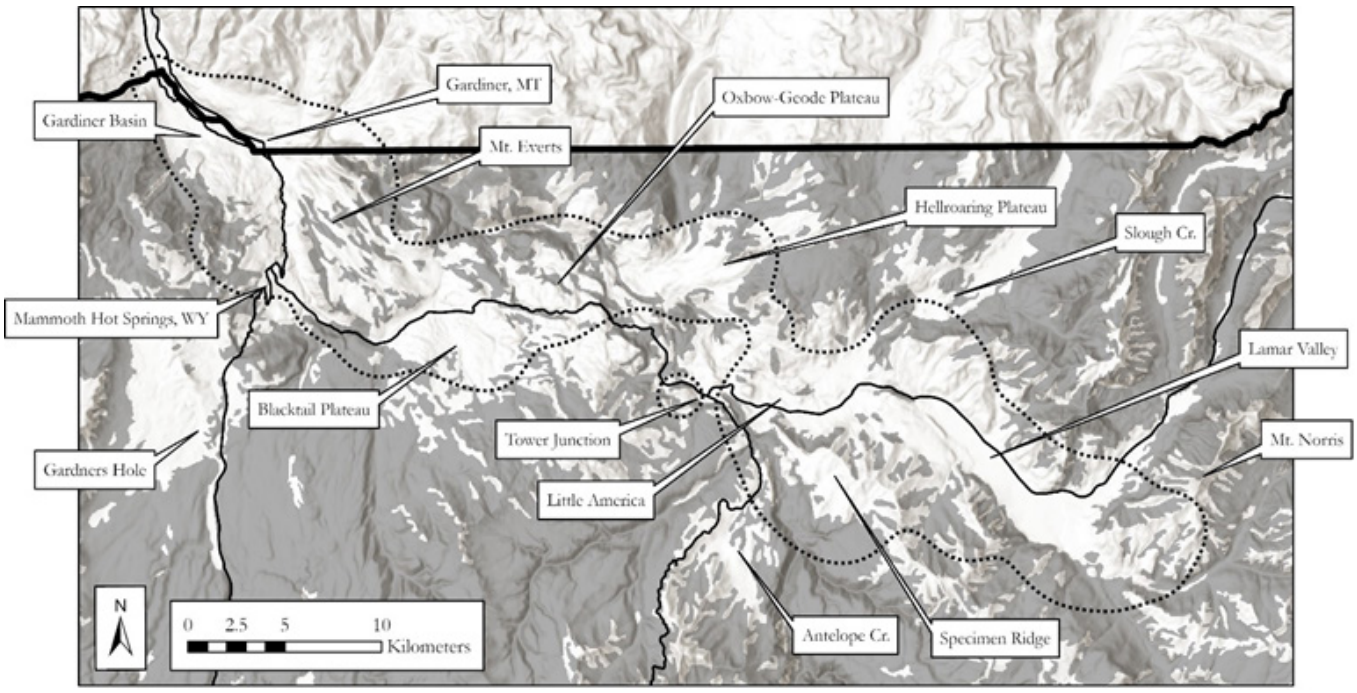
To identify migration pathways and strategies and inform protection and restoration actions, biologists assessed the movement patterns of Yellowstone pronghorn from 1999 through 2005 by fitting dozens of adult females with radio collars and tracking their seasonal movements. This chapter summarizes what we have recently learned regarding the extent of migration within the Yellowstone pronghorn population and some of the implications of that behavior with respect to predation risk.

## *Partial Migration*

During 1999 to 2005, about 70% of the pronghorn on the winter range in the Gardiner basin migrated 10 to 30 miles (16 to 48 kilometers) to higher-elevation summering areas in the interior of the Park to access newly emerging, highly nutritious food plants. About 30% of the pronghorn remained in the Gardiner basin during summer but shifted short distances up the foothills and slopes of surrounding mountains. There were migrant and non-migrant individuals from both sexes. (White et al. 2007b, Barnowe-Meyer 2009)

Migratory pronghorn gathered at the southeastern end of the Gardiner basin winter range in late March and early April on an open flat near the northwestern foot of Mount Everts. As snow receded these animals traveled southeast about 7 miles (11 kilometers) over Mount Everts which separated their winter and summer ranges. Pronghorn traveled along grassland-sagebrush passageways through gaps in surrounding conifer forests, most of which were less than 328 yards (300 meters) wide with occasional constricted areas of 22 to 66 yards (20 to 60 meters; see following figure).

Once spring migrants reached the southeastern end of Mount Everts, they dispersed somewhat to travel to their individual summer ranges. Most pronghorn generally followed the Yellowstone River to summer ranges further east. Spring migrations occurred over 1 to 2 months during mid-March to mid-May with most pronghorn reaching their summer ranges during April. Females migrated when vegetation green-up began but before giving birth in late May and June. Telemetry studies identified five main



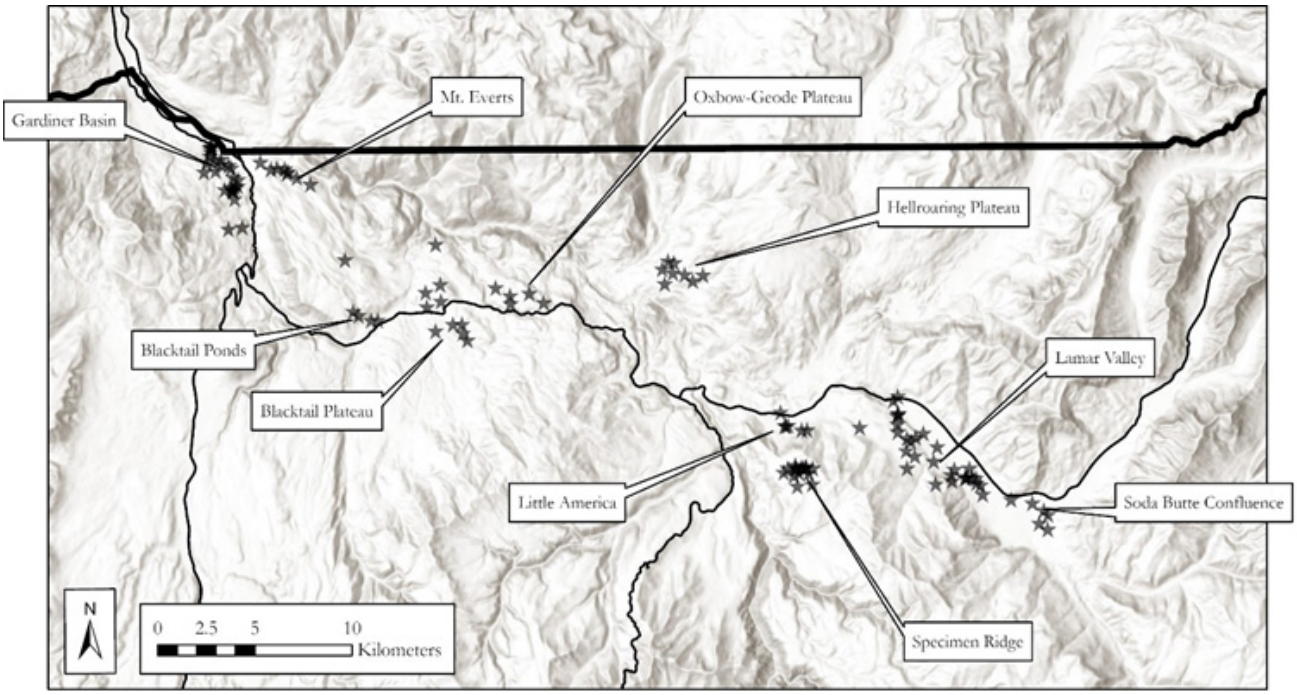

*The approximate yearly range of pronghorn (dashed line) in Yellowstone National Park with the Mount Everts migration corridor between the winter range near Gardiner, Montana (MT), and summer ranges to the east. Forested habitats are grayed, and non-forested habitat types are depicted in white. The heavy black line indicates the northern boundary of the Park, while thin black lines indicate major roads. Migrant pronghorn occupy areas from Mt. Everts east to Mt. Norris in Wyoming (WY) during the summer months, while non-migrants stay in the Gardiner area (from Barnowe-Meyer 2009).*

summering areas from west to east: 1) Gardiner basin winter range and northwestern portion of Mount Everts (non-migratory); 2) Blacktail Deer Plateau including Blacktail ponds and Oxbow/Geode creeks; 3) slopes of Hellroaring Mountain east of Hellroaring Creek; 4) Little America and Specimen Ridge; and 5) Lamar Valley and the Soda Butte area. There were 10 distinct clusters of pronghorn locations within those summering areas. (White et al. 2007b, Barnowe-Meyer 2009, Scott 2013)

Autumn migrations occurred over 1 to 2 months from mid-September to mid-November with most pronghorn reaching the Gardiner basin winter range during October. Animals mostly migrated after breeding but before snow covered their summer ranges. Most animals migrated between their seasonal ranges in less than one week by moving 3 to 9 miles (5 to 15 kilometers) each day.

## *Philopatry & Behavioral Flexibility*

Most individual pronghorn showed strong fidelity and philopatry by using the same migration strategy and summer use area each year. There was some flexibility in migratory behavior with about 20% of the animals migrating in some years but not others. This flexibility suggests migration in Yellowstone pronghorn may be a conditional strategy based on individual age and nutritional condition, environmental conditions, and the behaviors and density of other animals. Differences in reproductive success between migrants and non-migrants also could induce changes in individual behavior. Interestingly, all radio-collared pronghorn that switched strategies became non-migratory as they aged. Only one radio-collared female shifted her summering area between years from the Lamar Valley to the slopes of Hellroaring




*Summering areas for radio-collared adult female pronghorn in Yellowstone National Park from 1999 to 2005. The number of symbols in each cluster represent the number of radio-collared females using the area (from Barnowe-Meyer 2009).*

Mountain about 7 miles (11 kilometers) away. (Kaitala et al. 1993, White et al. 2007b, Barnowe-Meyer 2009)

Flexibility in migration strategies likely contributed to rapid, dynamic changes in the proportion of migrants over time which changed from 80% from 1967 to 1969 to 20% from 1988 to 1993 and back to 70% from 1999 to 2005. Research on partial migration in other species suggests differences in mortality and reproductive success among migrants and non-migrants may promote the long-term coexistence of both strategies in a population with each strategy being more favorable under different circumstances and conditions. From 1999 to 2005, the proportion of migrants was about 70% and fawns born to migrant females were in better condition and had higher survival than fawns from non-migrant females due to higher quality forage conditions for migrant mothers (see Chapter 6). (Kaitala et al. 1993, Scott and Geisser 1996, Caslick 1998, Barmore 2003, White et al. 2007b, Barnowe-Meyer et al. 2011, 2017a; Scott 2013, 2014)

## *Predation Risk*

Partial migration in ungulates may be related to costs associated with migration, such as an increase in the risk of predation, compared to benefits such as access to higher quality resources. Predation risk appeared to be a primary factor affecting the choice of habitats by females about to give birth, with mothers trying to avoid having fawns in areas of high predation risk and moving to areas where the risk of predation to themselves and their fawns was lower. (Byers 1997, Kie 1999, Barnowe-Meyer et al. 2010)

Coyotes were a significant predator of pronghorn in Yellowstone from 1999 to 2007 and contributed to substantial fawn mortality, decreased recruitment, and some adult mortality. There were abundant coyotes on the pronghorn winter range in the Gardiner basin owing to plentiful ungulate carrion from hunters just outside the park, starvation, and wolves. It may have benefited pronghorn to migrate elsewhere for fawning, but migration alone did not take them to areas devoid of coyotes. In fact, migrants had a higher risk of predation from other predators like bears, cougars, eagles, and wolves than non-migrants.

Cougars killed several radio-collared pronghorn migrating along the narrow grassland pathways through forested areas on top of Mount Everts between their winter and summer ranges. Cougars also killed some pronghorn near the edges of forests on the periphery of the Blacktail Deer Plateau and Hellroaring Mountain slopes. (O'Gara 1968, Houston 1982, Fryxell et al. 1988, Bergerud et al. 1990, Nicholson et al. 1997, Crabtree and Sheldon 1999, Scott 2004, Ruth et al. 2019)

However, the restoration of wolves to Yellowstone in the mid-1990s may have indirectly contributed to higher recruitment for migrant pronghorn by altering the behavior, distribution, and risk of predation from coyotes. Prior to wolf restoration there were many coyotes in areas used by migrant pronghorn for summer ranges in low-lying areas where snow depths were relatively low during winter. In these same areas, however, wolves killed coyotes through inter-specific aggression and excluded them from areas of intense use while only infrequently preying on pronghorn adults and fawns themselves. As a result, wolves indirectly increased the survival rates of migrant females and their fawns by excluding coyotes from areas where wolves were common. Fawns born to females using these areas had higher survival than fawns born to non-migratory pronghorn remaining on the winter range where wolf densities were relatively low. This effect was pronounced in lower-lying areas of the migrant range such as the Lamar Valley where territorial coyotes were otherwise quite numerous. (Crabtree and Sheldon 1999, Berger and Gese 2007, Berger et al. 2008, Barnowe-Meyer et al. 2009, 2010; Metz et al. 2020)

Other migratory pronghorn used a different strategy to reduce the risk of coyote predation on their fawns by shifting into higher-elevation areas near timberline where there were fewer coyotes. During winter, coyotes generally avoided these areas because deep snows limited the availability of prey (such as rodents), and ungulate carcasses from wolf kills were more abundant at lower elevations where elk and bison spent winter. Most coyotes established their territories and denning areas from December through February in these lower elevation areas. These territories were maintained through the year, including during the pronghorn birthing period. By selecting birthing areas at higher elevations, pronghorn avoided most territorial coyotes and lowered the risk of predation from this primary predator. There was one minor tradeoff with this approach: these areas had more mixed coniferous forest habitat and less visibility which placed them at greater risk of predation from cougars. (Gese et al. 1996a,b; Crabtree and Sheldon 1999, Barnowe-Meyer et al. 2010, Ruth et al. 2019)

During the telemetry studies, migrant females had higher annual survival rates (~91%) than non-migrant females (~82%) primarily due to consistently higher survival each summer (migrants: 93% to 99%; non-migrants 67% to 99%). Both migratory and non-migratory females had high survival (97% to 99%) when they shared the winter range from January through April. Non-migrants had lower survival (91% to 93%) than migrants (97% to 98%) during birthing and lactation (May to June) and autumn (October to December). Fawns born to migratory females had somewhat higher survival rates (13% to 25%) to August than fawns born to non-migrants (2% to 14%). (Byers 2001, Barnowe-Meyer et al. 2011)

## *Conclusions*

The proportion of pronghorn migrating apparently increased in the early 2000s during a severe and extended drought that reduced the quantity and quality of food on the winter range in the Gardiner basin. Biologists realized resources on the winter range were inadequate to sustain the entire population during some years and that restoring movements and gene flow between pronghorn populations in Yellowstone

National Park, the southern Paradise Valley to the north, and the Madison Valley to the west would improve the long-term viability of pronghorn in the Park. They began working with the National Parks Conservation Association, Montana Fish, Wildlife and Parks, Custer Gallatin National Forest, and private landowners to remove or modify fences in critical areas and restore portions of these migratory pathways (see Chapter 8). (Scott 2004, White et al. 2007b, Boccadori et al. 2008, Barnowe-Meyer et al. 2013, Renkin 2021)

Future infrastructure projects in and outside the Park could further restrict seasonal pronghorn movements and reduce the viability of this population. As an example, the relocation of an existing road in the Park to an area traversing the spring migration staging area and corridor over Mount Everts could inadvertently affect migratory tendencies and alter behaviors. All migrant pronghorn that spent summer in the Park traveled about 7 miles (11 kilometers) over this topographic bottleneck between winter and summer range, a route which requires crossing a two-lane road between Gardiner, Montana, and Mammoth, Wyoming. Additional barriers in this migration corridor could reduce the survival and reproductive success of migrant pronghorn which could reduce the viability of the overall population. Increased mortality and a decreasing proportion of migrants could be as important a threat to the persistence of this population as habitat fragmentation. The continued protection of the Mount Everts migration corridor is essential to ensure future infrastructure projects do not adversely affect migrant pronghorn and other migratory ungulates that seasonally travel through this area, including bighorn sheep, bison, deer, and elk. Similar issues exist for migration pathways north and west of the Park into the Paradise and Madison valleys. (White et al. 2007b, 2013c; Barnowe-Meyer 2009)

*Pronghorn buck eating a forb (probably an aster or mustard) in the Lamar Valley of Yellowstone National Park. Photo by Jacob W. Frank, National Park Service.*

# Chapter 6
# Foraging & Diet: Adaptive Benefits of Migration

## *Introduction*

The contraction and degradation of the winter range could affect the quality of pronghorn diets and their nutritional condition, reproductive success, and survival. Depending on circumstances, these changes could affect both the migratory and non-migratory segments of the population because they share the winter range in the Gardiner basin. Alternatively, they could primarily affect the non-migratory segment because residents remain year-round in the Gardiner basin whereas migratory females move to higher elevations each spring prior to parturition and lactation. Higher elevation ranges typically receive more precipitation and support higher quality forage during the summer growing season. Migratory pronghorn may therefore have access to more nutritious food when the energy demands of late gestation and lactation are high which could increase fawn birth weights, milk production, fawn growth rates, and reproductive success. (Barnowe-Meyer et al. 2009, 2010, 2011; Geremia and Hamilton 2019)

The level of nutrition in the diets of Yellowstone pronghorn depends on the quality and quantity of available food. While nitrogen-limitation can reduce plant production, precipitation is likely the most important driver of annual differences in forage production because ungulates increase soil nitrogen through grazing and the deposition of urine and feces and release forbs and grasses from nitrogen limitation. In turn, precipitation strongly influences soil moisture which can limit production. A common strategy of pronghorn is to select plants or plant parts, such as shrubs and forbs during winter and new plant growth during spring and summer, with relatively high protein content and digestibility. (Fryxell et al. 1988, Harder and Kirkpatrick 1994, Parker et al. 1999, Cook 2002, Yoakum 2004c, Frank et al. 2013, Geremia and Hamilton 2019, Geremia et al. 2019)

The amount of fat and protein stored by an animal depends on the ingestion and assimilation of enough energy and nutrients (nutrition) to meet metabolic demands and store reserves. This nutritional state (or body condition) also depends on the animal's physiological requirements and environmental conditions. The body condition of ungulates like pronghorn strongly influences the likelihood of breeding, pregnancy, recruitment of young (lactation), survival, and susceptibility to predation. Poor nutritional condition in a pregnant or lactating female can predispose fawns to predation and other causes of mortality. (Moen 1973, Cook 2002, Yoakum 2004c)

## *Winter Diets*

Sagebrush was the primary forage species for pronghorn on the Gardiner basin winter range during the 1930s, with some rabbitbrush and greasewood eaten as well. This trend continued during studies from 1962 to 1970 and 1986 to 1988 when pronghorn ate 59% to 67% sagebrush (primarily big sagebrush) and 4% to 5% rabbitbrush during winter. In a study in 2000 and 2001, however, the amount of sagebrush in pronghorn diets during winter decreased to less than 10%, while rabbitbrush increased to 60%. Pronghorn also were found to be consuming more Gardner saltbush (*Atriplex gardneri*), winterfat (*Eurotia lanata*), and Rocky Mountain juniper (*Juniperus scopulorum*). Pronghorn diets during these later winters also consistently included the forbs granite gilia (*Leptodactylon pungens*) and desert alyssum but few grasses until March. Although the causes are not fully known, perhaps pronghorn may have altered their diets due to the continued degradation of sagebrush on the winter range (see Chapter 4) or a shift

in habitat use to hay pastures and grass-forb communities north of the Park. (Murie 1940, O'Gara 1968, Singer and Norland 1994, Caslick and Caslick 1997-2001, Caslick 1998, Barmore 2003, Boccadori et al. 2008)

To learn more, biologists evaluated the composition and nutritional quality of pronghorn diets during January to April in 2006 and 2007 to determine if the winter range provided adequate nutrition for sustenance and pregnancy when migrants and non-migrants occupied the same area. Winter diets consisted of about 67% shrubs, 17% forbs, 13% grasses, and 3% sedges (*Carex*), juniper (*Juniperus*), and lichens. Pronghorn diets from January through March included about 72% sagebrush with big sagebrush being predominant (58%). Other shrubs included fringed sagebrush, rabbitbrush, saltbush, and winterfat. Forbs included desert alyssum and gilia, while grasses included Sandberg bluegrass, brome, cheatgrass, and wheatgrass. The proportion of shrubs decreased in April to 34% as new growth of forbs and grasses began to emerge. Forbs comprised about 36% of April diets, with 29% grasses, and 1% lichens, moss, and thorns. (Barnowe-Meyer et al. 2017a)

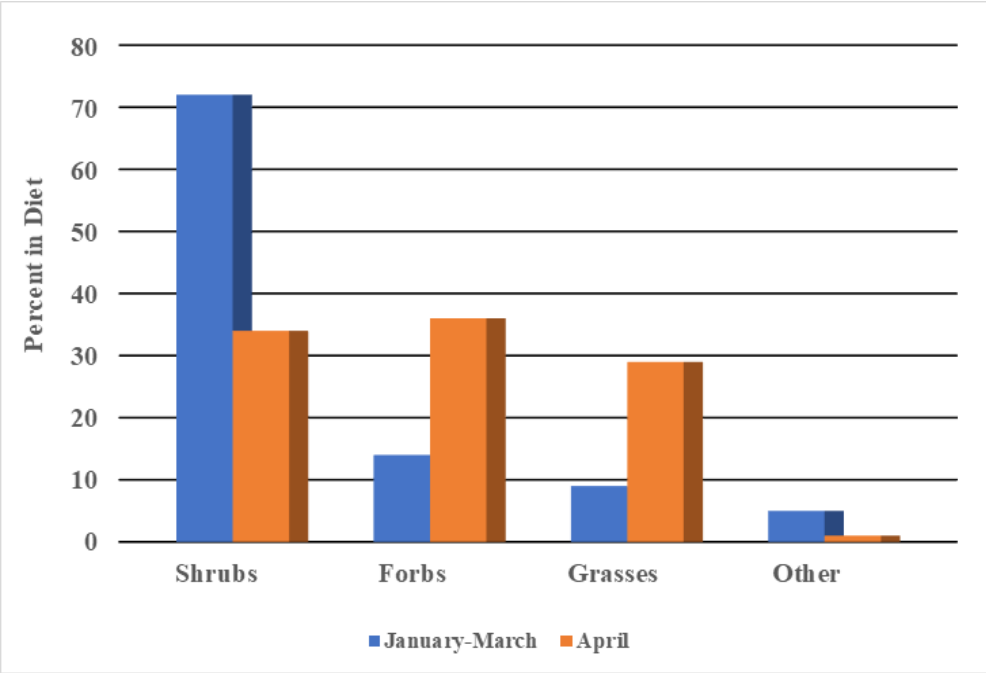
Crude protein was about 10% in shrubs and forbs during January and February but increased by April to about 17% in shrubs and 15% in forbs. Digestibility increased from about 38% in January to 53% in April for shrubs, 44 to 66% for forbs, and 43 to 56% for grasses. In response, winter diets of pronghorn contained about 12% crude protein and 50% digestible dry matter from January through March. These proportions increased in April (when new growth of forbs and grasses began to emerge) to about 17% crude protein and 66% digestible dry matter. (Barnowe-Meyer et al. 2017a)

Higher ingestion of nitrogen (protein) by ungulates like pronghorn results in more nitrogen and diaminopimelic acid (DAPA) excreted in feces. DAPA is an index of the digestible energy available in an animal's rumen. Fecal samples contained about 1.7% nitrogen and 0.51 milligrams DAPA per gram from January through March. Predictably, these values increased during April to 2.2% nitrogen and 0.59 milligrams DAPA per gram when new growth of forbs and grasses emerged. (Mould and Robbins 1981, Yoakum 2004c, Barnowe-Meyer et al. 2017a)

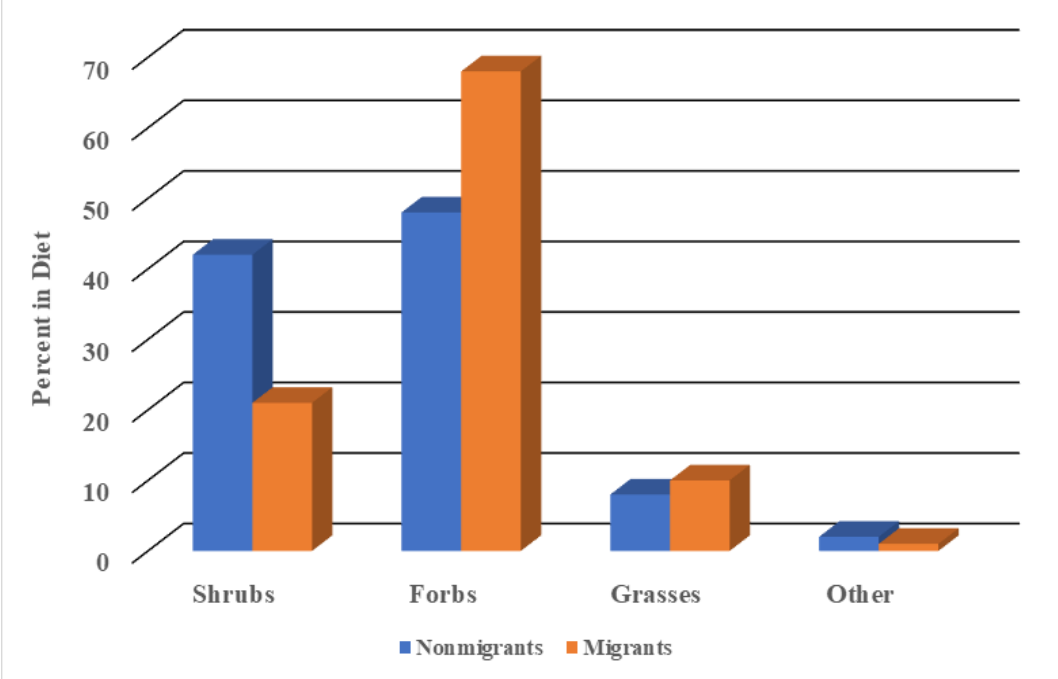
## *Summer Diets*

Biologists evaluated pronghorn diets from May to August to assess whether migratory pronghorn obtained higher nutrition during late pregnancy and lactation than non-migratory animals that remained on winter range. Summer diets of non-migratory pronghorn in the Gardiner basin were 48% forbs, 42% shrubs, 8% grasses, and 2% sedges and lichens. Summer diets of migratory pronghorn were 68% forbs, 20% shrubs, 8% grasses, and 4% sedges and lichens. Predominant shrubs in diets across both areas included big sagebrush, fringed sagebrush, and rabbitbrush; forbs included aster (*Lonactis* spp.), biscuitroot (*Lomatium* spp.), dandelion, desert alyssum, geranium (*Geranium* spp.), lupine (*Lupinus* spp.), and phlox (*Phlox* spp.); and grasses included Sandberg bluegrass, brome, and wheatgrass. However, there was wide variation in diets among migrant pronghorn using different summering areas (see Chapter 5). The percentage of shrubs in migrant pronghorn diets varied from 17% on the Blacktail Deer Plateau to 28% on Specimen Ridge to 10% in the Lamar Valley (geographic distribution west to east). The percentage of forbs in diets varied from 74% on the Blacktail Deer Plateau to 63% on Specimen Ridge to 77% in the Lamar Valley. The percentage of grasses in diets was similar among areas with 8% on the Blacktail Deer Plateau, 7% on Specimen Ridge, and 10% in the Lamar Valley. (Barnowe-Meyer et al. 2017a)

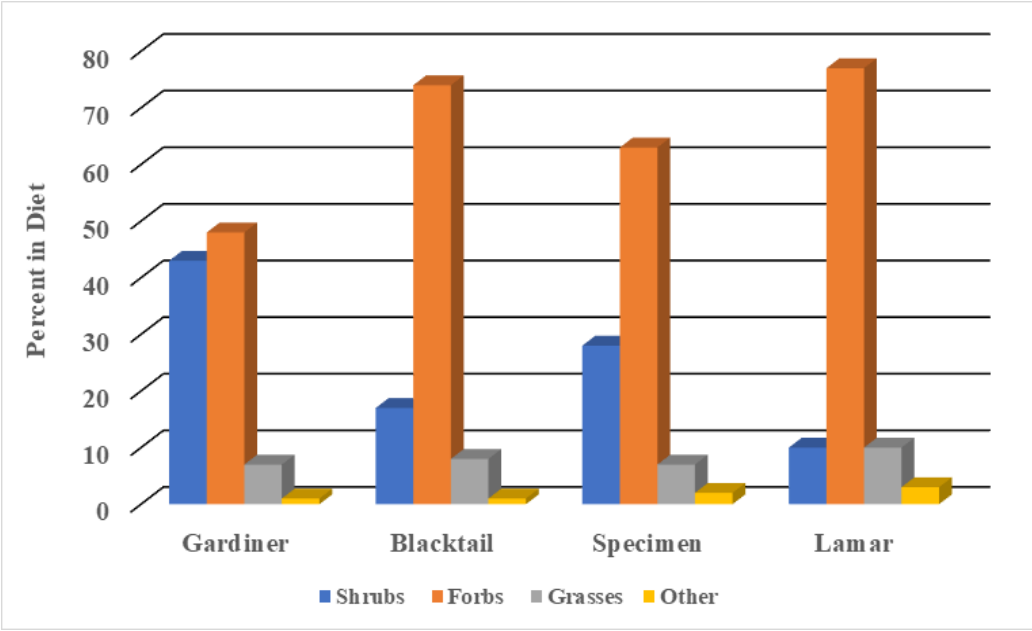
Fecal nitrogen and DAPA peaked during May and June in diets of non-migrants and migrants. Fecal samples from non-migratory pronghorn from May through August contained about 2.5% fecal nitrogen and 0.56 milligrams per gram DAPA. Diets of migratory pronghorn from June through August contained about 3.0% fecal nitrogen and 0.53 milligrams per gram DAPA. Migrants had higher values of percent fecal




*Percentages of various forages in the diets of adult female Yellowstone pronghorn in the Gardiner basin during the winters of 2006 and 2007 (from Barnowe-Meyer et al. 2017a).*




*Percentage of various forages in migrant and non-migrant adult female Yellowstone pronghorn from May through August in 2006. (from Barnowe-Meyer et al. 2017a).*




*Percentage of various forages in Yellowstone pronghorn diets in each of the main summering areas from May through August in 2006. Summering areas geographically from west to east are the Gardiner basin winter range (non-migrants), Blacktail Deer Plateau, Specimen Ridge, and Lamar Valley (from Barnowe-Meyer et al. 2017a).*

nitrogen than non-migrants in June and July but not August. (Barnowe-Meyer et al. 2017a)

## Foraging Strategies

The composition of Yellowstone pronghorn diets varied by season, from primarily shrubs in winter to forbs in summer and a mix of forbs and shrubs during spring and autumn. Shrubs have relatively low digestibility, high crude protein content, and they are readily available because they are rarely covered by snow. Forbs are high in digestibility and crude protein but less available in winter due to snow cover. Grasses have high digestibility in spring and summer but low digestibility in winter when they are dry and senescent. They are also less available during winter due to snow cover. The diets of pronghorn during winter had crude protein contents well above the minimum level of 5% to 7% required for maintenance, and fecal nitrogen and DAPA were similar or higher to levels reported for other populations. (Yoakum 2004b, Boccadori et al. 2008, Barnowe-Meyer et al. 2017a)

Migrant pronghorn grazed primarily on forbs during spring and summer, while non-migrants grazed and browsed about evenly on forbs and shrubs. Fecal nitrogen levels suggest diet quality for migrants was higher than for non-migrants from May to July. Late May and June coincide with high energy demands during late gestation and lactation when diet selection has a strong influence on the condition and survival of fawns. Females accessed more higher-quality forage for about six weeks prior to parturition and lactation in June by migrating to higher-elevation areas. (Pettorelli et al. 2005, 2007; Barnowe-Meyer et al. 2011, 2017a)

The reasons for the substantial differences in winter diet composition between studies in 2000-2001 when pronghorn ate mostly rabbitbrush and 2006-2007 when they ate mostly big sagebrush are unclear. Severe sustained drought conditions occurred from 1999 to 2007 based on the Palmer Drought Severity Index. The winters of 2001 through 2005 were relatively mild, but snow conditions in 2006 were relatively severe based on the amount of water in the snowpack and migrations of bison, deer, and elk to lower

elevations in and outside the Park. Perhaps concentrated browsing in the Gardiner basin made rabbitbrush less available by 2006-2007 and compelled pronghorn to rely on sagebrush again. The different results also could reflect some unintended bias in how biologists collected or interpreted samples between the two studies. (Palmer 1968, Farnes et al. 1999, National Oceanic and Atmospheric Administration 2015)

## *Nutritional Condition*

Biologists assessed maternal condition, investment, and fawn survival in migrant and non-migrant ranges from 1999 to 2001 to evaluate if there was an adaptive benefit to migration in terms of nutrition and body condition. Female pronghorn in Yellowstone weighed about 104 pounds (47 kilograms) during late winter, and fawns weighed about 6.8 pounds (3.1 kilograms) at birth. The litter weight of twin fawns was about 13% the mother's weight. Female weights and pregnancy rates were similar between migrant and non-migrant pronghorn and within the ranges reported for pronghorn populations elsewhere. There was no association between female condition the previous winter and fawn date of birth (which were similar for migrants and non-migrants). Degraded habitat conditions on the winter range and lower nutrition for non-migrant females during spring did not appear to substantially prolong gestation or limit reproductive rates during the study period. However, female weights were lower than reported for this population from 1965 to 1967 (110 pounds, 50 kilograms) and fawn birth weights were slightly low compared to other populations. Perhaps this indicates compromised reproductive effort due to decreased winter and spring nutrition and nutritional condition. (O'Gara 1968, Byers 2001, Barnowe-Meyer 2009, Barnowe-Meyer et al. 2011)

The condition of fawns at birth influenced their survival which was only about 15% to August. Fawns born to migrant females were in better condition, weighed more, and survived longer than fawns born to non-migrants despite all females having access to the same forages on their shared winter range in the Gardiner basin. The differences between fawns born to migrant and non-migrant females likely reflected higher spring and early summer nutrition for migrant females during late gestation and lactation. About 80% of fetal weight gain in pronghorn occurs during the last 50 days of gestation, and migrant females generally arrived on their summer ranges by mid-April to give birth around June 1st. In addition, lactation represents two-thirds of the cost of fawn production. Thus, a major benefit of migration was that females moved to habitats that offered better nutrition for lactation. The average survival rate of fawns born to migrant females was 80% greater than for fawns born to non-migrant females. About two-thirds of fawn deaths occurred within two weeks of birth with one peak during the hiding phase the first few days after birth and another when fawns began traveling with their mothers and were more visible to predators. The primary cause of death for fawns was coyote predation (79%), with other deaths due to predation by cougars, black bears, and golden eagles. (Robbins and Robbins 1979, Byers 2001, White et al. 2007b, Barnowe-Meyer 2009, Barnowe-Meyer et al. 2009, 2010, 2011)

*Female pronghorn browsing on big sagebrush in Yellowstone National Park. Photo by Neal Herbert, National Park Service.*

## Conclusions

Conditions during the 2000s promoted an adaptive advantage of migration for Yellowstone pronghorn due to the degraded condition of the winter range and lower nutrition for non-migrants during late gestation and lactation. Migrants accessed higher quality foraging areas than non-migrants which contributed to improved diets before parturition and during lactation. Fawns born to migrant females were in better condition and had higher survival than fawns born to non-migrant females. Migrant pronghorn had higher reproductive success than non-migrants despite occupying areas with more abundant and diverse predator communities (see Chapter 3). If environmental conditions continue as they existed during this study, there could be a widening gap in survival rates of fawns born to migrant and non-migrant pronghorn over time. Higher rates of fawn survival and recruitment for migrants could lead to an increasing proportion of migrants in the population if relatively few animals switch strategies. However, the extent to which migration represents an adaptive strategy is sensitive to future changes in the relative quality of spring and summer forage between migrant and non-migrant areas as well as other determinants of reproductive success in pronghorn such as predation. (Byers 2001, White et al. 2007b, Barnowe-Meyer et al. 2010, 2011, 2017)

# Chapter 7
# Social & Genetic Structure: Kin-based Associations

## *Introduction*

Yellowstone pronghorn have persisted in a relatively small population of fewer than 1,000 animals since 1910 and fewer than 600 animals since 1947 (count of 594 pronghorn in 1991). Market hunting and habitat loss from settlement and fencing reduced numbers of pronghorn from "thousands" to about 200 by the late 1880s. The population was geographically isolated in the Park on the northern boundary by 1905 and no pronghorn migrated from the Madison Valley into the western portion of the Park by 1920 (see Chapter 2). Another population reduction occurred from 1946 to 1967 when managers captured pronghorn in the Park and removed them due to concerns about overgrazing. Abundance decreased again, from about 800 to 125 by 1963, and remained less than 200 for 20 years thereafter. A third reduction in abundance occurred from 1992 to 2004 when numbers decreased from about 540 to 170 due to a degraded winter range and high predation on fawns by coyotes. (Skinner 1922, Houston 1982, Keating 2002, Boccadori et al. 2008, Barnowe-Meyer 2009)

This history of severe population reductions, persistent low numbers, and apparent lack of connectivity with neighboring populations may have resulted in substantial losses of genetic diversity and decreased the long-term viability of the population. Severe reductions in population size, termed "bottlenecks," often result in chance losses of genetic variation due to the loss of so many individuals and sub-groups. Persistent low numbers increase the potential for inbreeding (mating with close relatives) due to fewer unrelated potential mates. Inbreeding can result in the expression of harmful traits that contribute to poor reproduction and survival. A lack of connectivity and gene flow also could contribute to inbreeding and a decrease in genetic diversity. For example, pronghorn on the National Bison Range had diminished fawn survival when the parents of fawns were related at the level of first cousins or closer. (Scott 1990, Keating 2002, Dunn et al. 2011, Barnowe-Meyer et al. 2013, Flesch et al. 2021)

Yellowstone pronghorn have several behaviors that could lead to social and/or genetic structuring or subdivisions in the population. These behaviors include a polygynous mating system, partial migration strategy, and strong fidelity of adults to summer ranges and breeding areas. These behaviors can lead to local adaptations beneficial for reproductive success and survival, but genetic structuring also could make segments of the population susceptible to random events or management actions that inadvertently lead to a loss of certain migratory routes, use areas, or sub-groups. Pronghorn apparently stopped using summer areas near Swan Lake, Antelope Creek basin, and the Hayden Valley after population reductions in the 1920s and 1940s. (Skinner 1922, Scott 1990, Scott and Geisser 1996, Keating 2002, Barnowe-Meyer et al. 2013)

This chapter summarizes the results of extensive population genetic research conducted in 2006 to better understand the genetic status, diversity, and social structure of the Yellowstone pronghorn population.

## *Social Organization*

From 1999 to 2005, Yellowstone pronghorn occurred in relatively small groups averaging about 5 to 10 individuals in May and June when females dispersed to give birth and hide their newborn fawns. Adult

males were solitary or in small bachelor groups during this time. Fawns joined their mothers in nursery groups after they were 2 to 3 weeks old and capable of rapid, sustained running. Group sizes increased to about 13 to 20 individuals with females and their young during July and August when mature males began defending groups of females (harems) from other males as the rut approached. Biologists reported bucks forming territories from May through October and females moving between them during the September breeding season between 1988 and 1998, but that behavior was not observed during our studies. Pronghorn formed larger mixed-sex groups averaging about 20 to 30 individuals from November through March when they congregated on the winter range in the Gardiner basin. Non-migratory pronghorn that were year-round residents of the Gardiner basin were frequently located in groups with pronghorn that migrated to higher elevations in summer (see Chapter 5). Pronghorn became well mixed and moved freely within the population during winter with no evidence of spatial segregation or sub-grouping. (Caslick 1998, White et al. 2007b, 2012; Scott 2013)

Variations in group size were relatively small during fawning in spring and fawn rearing in summer, but there was more variability in winter when numbers of animals in groups often changed substantially within a day and could include up to 100 individuals. This suggests pronghorn were mixing and switching associations with other animals frequently rather than staying with the same group. Variations in group size appeared to be strongly influenced by reproductive and social factors because groups were smaller during parturition and the fawn rearing period. Pronghorn density and snow conditions were associated with changes in group sizes, whereas habitat type, predator numbers, and vegetation green-up were not good predictors of group sizes or stability from 1999 to 2005. (White et al. 2012)

Larger aggregations of pronghorn from autumn through winter led to decreased group cohesion with pronghorn aggregating, groups fracturing, and pronghorn re-mixing more frequently than during the fawning period and summer. This decreased cohesion was likely due to higher densities of animals and aggressive or competitive interactions among individuals. Mating behavior and the fracturing and rejoining of groups as males attempted to keep harems of females together also likely contributed to this pattern. Group cohesion increased as snow conditions became more severe at higher elevations and restricted pronghorn to a smaller area on the lower-elevation winter range where food was more available. Using areas with shallow or no snow that provide protection from the wind is typical for animals trying to conserve energy in harsh winter environments. (Moen 1973, Byers 1997, White et al. 2012)

## *Genetic Diversity*

A specific portion of DNA called microsatellites can be used to evaluate genetic diversity and movements among populations or sub-groups. DNA contains pairs of four nucleotides including adenine (A), cytosine (C), guanine (G), and thymine (T) that code for proteins making up an animal. Microsatellites consist of segments of DNA where nucleotide pairs are repeated many times such as G-C, G-C, G-C, G-C, and G-C. The number of repeats at a given location is called an allele, and many different combinations of alleles are possible. Biologists can use these patterns to assess genetic relationships among different populations or sub-groups. If neighboring populations or sub-groups have separate patterns of alleles, it is likely few movements with subsequent breeding occur between them. If they have similar patterns of alleles, movements and gene flow through breeding are probably frequent. (Flesch et al. 2021)

Geneticists from the University of Idaho used microsatellites from 18 locations on DNA to evaluate the effects of the historic population bottlenecks on genetic diversity in Yellowstone pronghorn. They also evaluated genetic structure in the population, including patterns of relatedness and differences between migratory and non-migratory individuals. Evidence for a historic genetic bottleneck in the population was strong based on differences in allele frequencies between females and males that indicated reduced allelic diversity from historic levels. However, Yellowstone pronghorn still retained substantial genetic diversity

in terms of the number of alleles (average ~7, range = 2 to 11) compared to other pronghorn populations. The relatively low portion (~30%) of non-migrants from 1999 to 2005 raised concerns about potential inbreeding within this segment of the population since fawn body condition and survival were lower for non-migrants than migrants (see Chapter 6). Inbreeding appeared to be low in both population segments, however, and there was no evidence of a recent loss of genetic diversity within either segment of the population. The lack of inbreeding in the population after more than a century of apparent isolation was surprising and suggests there may have been undetected gene flow into the population over time. (Scott 1990, Scott and Geisser 1996, Barnowe-Meyer and Byers 2008, Barnowe-Meyer 2009, Barnowe-Meyer et al. 2010, 2011, 2013)

## *Genetic Structuring*

Genetic differentiation between migrants and non-migrants in partially migratory populations can be substantial if they are entirely separate during the breeding season and few individuals change migration strategies among years. Over time, this can result in genetic structuring within the population. Conversely, there may be no or weak genetic structure if a larger portion of individuals change migration strategies or breeding areas among years.

Three genetic sub-groups were detected in the Yellowstone population. One group contained only migratory individuals, another contained only non-migratory individuals, and a third group contained both migrant and non-migrant individuals. Individuals sampled within the migratory portion of the summer range were more related to each other than to individuals in the non-migratory portion of the range and vice versa. The genetic sub-group containing both migrant and non-migrant individuals likely consisted of individuals that changed migration strategies or summer use areas among years which would tend to weaken genetic structuring in the population. Some genetic structuring was evident in both migrant and non-migrant segments of the population, with individuals sampled in each summering area being more related to each other than with individuals in separate summering areas. Relatedness among individuals decreased rapidly with increasing distance to animals in neighboring groups. (Wright 1943, Tiedemann et al. 2000, Barnowe-Meyer et al. 2013)

## *Kin-based Social Structure*

There were frequent changes in group associations and cohesion on the shared winter range, but most females in the Yellowstone population had strong year-to-year fidelity to their summering and breeding areas. There was evidence of a maternal-based social structure in pronghorn summer use areas, with females in a social group generally related at the level of first cousins. This organization was likely maintained through a polygynous mating system, fidelity to summering and breeding areas by mothers, and inheritance by mothers passing on this knowledge and behavior (fidelity) to their daughters. Harem defense of groups of females by males further increased relatedness in breeding areas because most fawns were related as paternal half-siblings or full siblings in the case of twins. Dispersal by young male pronghorn functionally elevates the importance of fidelity by mother-daughter pairs to summering areas across years. Maternal relatedness could continue to promote genetic sub-groups within the population and result in more divergent genetics between migrant and non-migrant segments over time. (White et al. 2007b, Barnowe-Meyer et al. 2013, Bracis and Mueller 2017, Jesmer et al. 2018)

*Pronghorn buck chasing an intruder away from his harem of does during the rut near Reese Creek in Yellowstone National Park. Photo by Jacob W. Frank, National Park Service.*

## Conclusions

The behavioral flexibility of pronghorn with respect to grouping and social cohesion may increase their resilience to changes in conditions such as forage or weather but complicates predicting the effects of management actions. Biologists should consider grouping tendencies when planning the timing and location of management actions to restore habitat or limit adverse effects of fences or recreational activities such as hunting on pronghorn. Yellowstone pronghorn tend to avoid areas with deep snow and aggregate during winter on lower elevations of the Gardiner basin. This winter range has degraded over decades due to decreased sagebrush and development, fencing, and other land-use practices fragmenting migration routes to historic wintering habitat outside the Park. The National Park Service implemented restoration actions in this area to reestablish native vegetation and provide more habitat for larger groups of pronghorn. Park personnel also are working with the U.S. Forest Service, State of Montana, private landowners, and the National Parks Conservation Association to improve connectivity between the Park and historic winter ranges to the north (see Chapter 8). (White et al. 2007b, 2012; Boccadori et al. 2008)

The maintenance or restoration of migratory behaviors and summer use areas in Yellowstone pronghorn may depend on the retention of experienced individuals and transmission of this knowledge to young pronghorn along maternal lines. Management actions that inadvertently remove related animals using specific areas or barriers that impede migration such as fences or roads could threaten the long-term persistence of this partially migratory population. These disturbances could occur on the winter range as well as the summer range such as the management removals that occurred during the 1940s and apparently contributed to lost migratory behavior in the population. Low population abundance and strong fidelity to summering and breeding areas may retard the recolonization of lost migratory routes and summer use areas for many decades. Pronghorn did not recolonize the area near Swan Lake for numerous decades following its abandonment, and use is now sporadic even though it is only about 6 miles (10 kilometers) through sagebrush-steppe habitat from the winter range. Migrants currently contribute much more to reproductive success (recruitment) in the Yellowstone pronghorn population than non-migrants. A reduction in this population segment could reduce productivity and recruitment in the overall population or eliminate the use of certain summering areas for many decades. (Skinner 1922, Scott and Geisser 1996, Caslick 1998, White et al. 2007b, Barnowe-Meyer et al. 2013, Scott 2013, Bracis and Mueller 2017, Jesmer et al. 2018)

*Pronghorn doe with three fawns in Yellowstone National Park. Photo by Jacob W. Frank, National Park Service.*

*Pronghorn buck bedded in a field with blue flax in the Lamar Valley of Yellowstone National Park. Photo by Neal Herbert, National Park Service.*

# Chapter 8
# Current Management: Restoring Connectivity & Population Stability

## *Introduction*

The Yellowstone pronghorn population experienced range restriction and severe reductions in population size over the past 150 years, fueling concerns about inbreeding depression and susceptibility to random catastrophic events such as severe drought, harsh winters, or a disease outbreak. Fortunately, the population has modest genetic diversity despite these demographic and genetic bottlenecks with no evidence of inbreeding depression. Abundance increased to about 500 animals during the 2000s, and some pronghorn dispersed to the southern Paradise Valley north of the Park and contributed to the establishment of a neighboring population. There is no documentation and scant indirect evidence of pronghorn from other locales dispersing into the Park, however, and there are still several threats to the viability of Yellowstone pronghorn including a degraded winter range and fragmented migration corridors north and west of the Park. (White and Treanor 2002, Barnowe-Meyer 2009)

The mission of wildlife managers in Yellowstone National Park is to preserve natural resources unharmed for the benefit and enjoyment of people. This is accomplished by conserving or restoring native species and the ecological processes that sustain them while attempting to minimize human intervention. This can be difficult because the Park is not large enough to preserve processes such as long-distance migration or dispersal—it is primarily mountainous without many of the lower-elevation valleys historically used by many ungulates to sustain themselves during winter. As animals move in and out of the Park, they pass into different jurisdictions with varying public mandates and philosophies that result in different wildlife management policies. For example, there is high visitation with habituation by wildlife to non-threatening people in the Park, while there are hunter harvests and multiple land uses outside the Park. (White et al. 2013b, White 2016)

The Secretary of the Interior issued order 3362 in 2018 which tasked federal agencies with restoring habitat for ungulates along migration pathways and on winter ranges. The Secretary emphasized working with the states to advance shared conservation goals, reduce local conflicts, enhance enjoyment by people, and avoid deleterious impacts. Agencies need to continue coordinating management and research, sharing data and expertise, and collaborating with willing landowners and conservation organizations to enhance the movements of animals across highways and through or around developments. They also must be flexible and address social and economic concerns by promptly managing human-wildlife conflicts and providing adequate funding and staff for these efforts.

Fortunately, there are relatively abundant opportunities to preserve wildlife habitat and maintain or restore migration corridors in the Greater Yellowstone Area due to extensive and relatively intact habitat on public land within the region. The various federal and state wildlife agencies have similar missions to conserve sustainable wildlife populations and their habitats for multiple uses. There is a strong ethic of wildlife conservation by private landowners and local communities that has spanned many generations. Numerous non-governmental organizations are active in habitat protection and restoring migration corridors while indigenous tribes are re-engaging in wildlife management in the Yellowstone area. The national public cares deeply about what happens in the region, and there is a growing tourism economy

and support for wildlife. These common interests have led to partnerships working across jurisdictional boundaries to conserve or restore wildlife habitat, migration corridors, and populations. (White et al. 2013b,c; White 2016, Clark 2021)

## *Restoring Regional Connectivity*

Restoring dispersal and genetic exchange between Yellowstone pronghorn and neighboring populations in the Paradise and Madison valleys would enhance the long-term viability of all these populations. This achievement will require protecting and restoring movement pathways, increasing regional abundance to facilitate pioneering dispersal and the re-establishment of migratory movements, and conservative management to allow population growth and expansion without inadvertently altering social and genetic structure through actions such as development, harvests, or removals. This is a difficult undertaking in an area where habitat degradation and fragmentation almost certainly will continue due to rural residential development and climate warming. (White et al. 2007b, Barnowe-Meyer and Byers 2008, Barnowe-Meyer et al. 2013)

A partnership of government agencies, conservation organizations, energy development companies, and private landowners in western Wyoming worked together during the 2000s to protect a 43-mile (70-kilometer) migration pathway for pronghorn between Grand Teton National Park and Pinedale in the upper Green River basin. This pathway traversed the National Elk Refuge, Bridger Teton National Forest, Teton and Sublette counties, and Bureau of Land Management and privately-owned lands with at least three constricted areas due to development and topography. Managers learned several lessons from this process to designate the first federally protected migration corridor in the United States and safeguard future migrations along this pathway. The leaders of this effort conducted research to define the pathway and public outreach through articles, media coverage, meetings, presentations, and workshops to achieve acceptance and support in this culturally diverse and politically divided area. They conducted a risk assessment, obtained funding and support from energy companies, and gained the support of local, state, and congressional officials. They realized that coalescing a broad spectrum of beliefs and values into a focus on common interests beneficial to pronghorn and the broader community was most important for gaining support and accomplishing this effort. (Sawyer and Lindsey 2000, Berger et al. 2006, Berger and Cain 2014, Clark et al. 2014, Middleton et al. 2020)

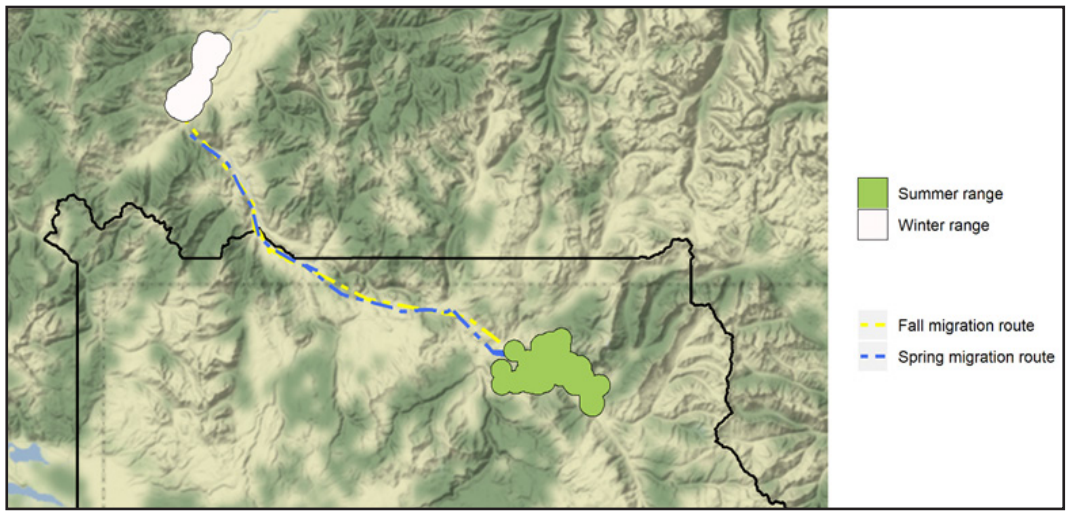
Partners are using a somewhat different and less formal approach to protect and restore migration corridors north and west of Yellowstone National Park. However, the lessons learned in western Wyoming are still applicable and valid, including the mapping of pathways, assessment of risks, agency coordination and leadership, involvement of private landowners to gain increased protection while meeting their needs, and the involvement and support of local communities, governments, and non-governmental organizations. Biologists conducted the research summarized in previous chapters to determine pronghorn demographics, genetics, and movements, and establish local and scientific credibility. They engaged social scientists from the University of Montana to conduct in-depth interviews with residents from the Gardiner and West Yellowstone, Montana, communities to understand their beliefs and values regarding migratory wildlife. People had strong favorable attitudes toward migratory wildlife which were mentioned as a primary reason for living in the area and a major benefit to the economy. Migratory wildlife provided extensive recreational opportunities as well (including fair-chase hunting, photography, and wildlife watching) and were viewed as a major component of the social character of these communities. At the same time, people wanted to reduce property damage such as vehicle strikes of animals on highways and requested fencing assistance projects. People also wanted meaningful input into agency decisions and more informal interactions with agency staff to improve communication. (Metcalf et al. 2016, Middleton et al. 2020)

Biologists from the National Park Service engaged with Montana Fish, Wildlife and Parks, U.S. Forest Service, and U.S. Geological Survey through the Northern Yellowstone Cooperative Wildlife Working Group to gain collaborative agency support and participation. The purpose of this group is to "cooperatively preserve and protect the long-term integrity of the northern Yellowstone winter range by increasing scientific knowledge of its species and habitats, promoting prudent resource management activities, and encouraging an interagency approach to data collection, answering questions, and solving problems." Federal and state biologists from this group met with the National Parks Conservation Association to solicit their advice and help in reaching out to private landowners due to a wariness of some landowners about federal involvement and possible restrictions on land use practices. (National Parks Conservation Association 2008, Northern Yellowstone Cooperative Wildlife Working Group 2015, Tilt 2020, White and Adams 2022)

The National Parks Conservation Association began working with private landowners and public land managers from the Bureau of Land Management, Custer Gallatin National Forest, and Montana Fish, Wildlife and Parks in 2008 to remove unnecessary fences and modify or rebuild other fencing to eliminate obstacles to movements by pronghorn and other wildlife while still meeting landowner needs. More than 1,000 volunteers worked with the organization to remove or modify about 20 miles (32 kilometers) of fence in critical areas between Yellowstone National Park and Emigrant, Montana, in the southern Paradise Valley. The willingness of private landowners to participate in this effort was outstanding and essential because these lands are crucial for conserving wildlife habitat and movement corridors in this area (see https://www.npca.org/advocacy/68-saving-pronghorn-at-yellowstone-national-park). These partnerships enabled pronghorn and other wildlife to access additional winter habitats, some of which had been inaccessible for decades. Many of the volunteers participating in these efforts were students from around the country. The opportunity for a student to spend a day making a fence wildlife friendly helps to foster a connection to national parks and mentor them in leadership and building partnerships. These efforts will facilitate future support for the long-term conservation of migratory wildlife and preservation of national parks. (Tilt 2020, National Parks Conservation Association 2021, White and Adams 2022)

In response to these efforts, more pronghorn are spending time outside the Park during winter and summer. All pronghorn observed by biologists during pre-migration, late-winter counts in the Gardiner basin from 2002 to 2008 were inside the Park. Since 2009, however, biologists have observed groups of pronghorn outside the Park from Beattie Gulch through the Royal Teton Ranch approximately 9 miles (14 kilometers) north to Yankee Jim Canyon. Observations of dispersing or migrating female pronghorn, including a few radio-collared animals, also indicate some gene flow is continuing to the Carbella/Point of Rocks population approximately 12 to 18 miles (19 to 29 kilometers) north of the Park in the southern Paradise Valley. Geneticists from the University of Idaho used microsatellites from 18 locations on DNA to evaluate gene flow between the Yellowstone and Carbella/Point of Rocks populations. There was significant evidence of recent dispersal and gene flow from Yellowstone to Carbella/Point of Rocks but not vice versa, even though evidence for inbreeding in the Yellowstone population was low. Evidence for inbreeding in the newly established population in the Carbella/Point of Rocks area was relatively high with somewhat low genetic diversity, which is not surprising for a herd founded by a small number of individuals. (Barnowe-Meyer and Byers 2008, White et al. 2013c, Flesch et al. 2021)

In 2019, a doe wearing a collar that collected Global Positioning System (GPS) locations left her summer range in the Lamar Valley of Yellowstone on October 5th and traveled for 11 days and 50 miles (81 kilometers) along this pathway to the Carbella/Point of Rocks area in the southern Paradise Valley, where she remained until April 20, 2020. She then retraced the pathway back to the Lamar Valley over 9 days travelling 55 miles (89 kilometers). It is unknown how many pronghorn accompanied this doe on this journey to and from the Paradise Valley. Pronghorn generally migrate in small groups, and such




*The pathway used by an adult female pronghorn to migrate from its summer range in the Lamar Valley of Yellowstone National Park to its winter range in the Carbella/Point of Rocks area of the southern Paradise Valley in Montana in 2019. The same pathway is used by dispersing females. Figure by Lauren McGarvey and data from Chris Geremia, National Park Service.*

movements could lead to migratory knowledge, dispersal, and gene flow to and from the Park that could provide increased resiliency and stability to both the Yellowstone and Carbella/Point of Rocks populations.

In 2020 and 2021, the State of Montana fitted 46 pronghorn in the Gardiner basin and Paradise Valley with collars that recorded GPS coordinates of movements as part of efforts to protect migration corridors and winter ranges for elk, pronghorn, and mule deer in collaboration with the Department of the Interior (Secretarial order 3362). Many of the pronghorn radio-collared in the Gardiner basin spent winter between Gardiner, Montana, and Yankee Jim Canyon on national park, national forest, and private lands. Some of these pronghorn were year-round residents in this area, while others migrated into the Park as far as the slopes of Hellroaring Mountain and the Lamar Valley. At least one pronghorn moved from the Gardiner basin north through Yankee Jim Canyon to the Carbella/Point of Rocks area during spring. (Montana Fish, Wildlife and Parks 2021)

Building on this success, the National Parks Conservation Association, private landowners, the Custer Gallatin National Forest, and Montana Fish, Wildlife and Parks removed and modified fences in critical areas in the Madison River Valley west of Yellowstone National Park. Volunteers have now removed or modified an additional 30 miles (48 kilometers) of fencing north and west of the Park to assist in restoring the historical migratory pathways of Yellowstone pronghorn in this area as well. They initiated a remote camera program with citizen scientists and the U.S. Forest Service that documented pronghorn near West Yellowstone, Montana, for the first time in decades. People also observed small groups of females and young along the Madison River in the Hebgen Lake basin near the western Park boundary. These pronghorn may be dispersing or migrating from the Madison Valley population via Henrys Lake, Idaho. The National Parks Conservation Association has begun working with agencies, landowners, and community members on projects west of Yellowstone in Idaho to help restore pronghorn migration over Targhee Pass. (National Parks Conservation Association 2021, White and Adams 2022)

People have also observed male pronghorn in the area near Mount Washburn (Antelope Creek) and in the Swan Lake area of northern Yellowstone, possibly animals dispersing or migrating from the Gardiner basin winter range. These sightings suggest management assistance could lead to the restoration of the historic migration pathways into these summer use areas that disappeared during the first half of the last

*Pronghorn fawn in sagebrush habitat in Yellowstone National Park. Photo by Jane Olson, National Park Service.*

century. Restoration of these migration pathways for pronghorn also benefit bighorn sheep, bison, deer, elk, and moose, thereby facilitating migration, dispersal, gene flow, and range expansion for the entire guild of migrating ungulates and other wildlife in this portion of the Greater Yellowstone Area. (Skinner 1922, Scott and Giesser 1996, Caslick 1998, Scott 2013, White et al. 2013b,c)

## *Restoring the Northern Winter Range*

Restoring native bunchgrass, forb, and sagebrush habitat for pronghorn in the Gardiner basin winter range will be difficult. The desert-like, windswept basin only receives about 10 inches (25 centimeters) of precipitation annually, and the climate has warmed and dried substantially over the past 40 years. A drier, warmer climate in the future could exacerbate the spread of winter annual weeds and the loss of remaining native species that cannot tolerate dry conditions. Cheatgrass and other winter annuals often outcompete native plants by germinating in autumn and growing earlier and rapidly in the spring. As a result, a pragmatic goal given current conditions is to restore previously cultivated areas to a mix of native forbs and grasses, regionally native species that are efficient in hot dry climates, and less than 50% winter annuals. (Tercek et al. 2015, Geremia and Hamilton 2019, Renkin 2021, Yellowstone Center for Resources 2021)

The National Park Service, U.S. Forest Service, and Center for Invasive Plant Management at Montana State University convened a group of about 20 agency staff and 10 restoration specialists in 2005 to develop

recommendations for restoring native plant associations on about 1,200 acres (485 hectares) of former agricultural fields in the Gardiner basin portion of Yellowstone National Park and nearby areas of the Gallatin National Forest. The specialists concluded low precipitation, weeds, high winds, low native seed availability, and browsing by ungulates would make restoration challenging but possible using intensive site preparation, farm machinery, herbicide treatment of weeds, and perseverance. The Gallatin National Forest implemented weed treatments, barley (Hordeum vulgare) planting, prescribed burning, and native grass seeding in the Beattie Gulch and Cutler Meadow areas north of the Park from 2006 to 2013. Cutler Meadow was plowed and seeded, but much of the native seed did not grow and the field was mostly cheatgrass by 2013. Fencing was erected at Beattie Gulch to exclude wild ungulates, but it was ineffective and removed in autumn 2013. Staff from the Custer Gallatin National Forest then partnered with the Animal and Range Sciences Department at Montana State University from 2014 to 2019 to conduct a baseline inventory in portions of the Gardiner and Hebgen basins north and west of Yellowstone National Park. Rangeland managers developed ecological descriptions for grassland communities and evaluated their status. (Yellowstone National Park et al. 2005, Canfield et al. 2013, Marlow et al. 2019, Renkin 2021)

The National Park Service initiated native vegetation restoration projects on about 50 acres (20 hectares) of the Gardiner basin in the Stephens Creek area during 2008 and 2009. Plots were fenced to exclude ungulates, sprayed with an herbicide to kill non-native plants, and then seeded via no-till drilling with a preparatory cover crop of barley or winter wheat (Triticum aestivum) to develop soil organic matter, increase water holding capacity, loosen compacted surface layers, and stimulate microbial activity. The cover crop was mowed or burned each year before it went to seed. Native grass seed collected and grown from local sources was planted in October 2013 on 30 acres (12 hectares) using a no-till drill. The seed mix included bluebunch wheatgrass (Pseudoroegneria spicata, 50%), Sandberg bluegrass (30%), slender wheatgrass (Elymus trachycaulus, 15%), and green needlegrass (Nassella viridula, 5%), with smaller amounts of needle-and-thread grass and prairie junegrass. In addition, botanists broadcast seeds from local shrub species such as basin big sagebrush, Wyoming big sagebrush, rabbitbrush, and greasewood on these areas during early winter. They seeded another 20 acres (8 hectares) in autumn 2014. Botanists then used a variety of chemical, mechanical, and reseeding techniques in these areas to promote the establishment and growth of native grasses within these areas. They successfully completed restoration efforts in three areas and removed the fences during 2019 and 2021. Efforts in the other area will be completed during 2022. (Renkin 2021, Yellowstone Center for Resources 2021)

Botanists also initiated restoration efforts within two unfenced areas totaling 20 to 30 acres (8 to 12 hectares) during 2018 and 2019. They successfully restored one field using autumn and spring chemical treatments to reduce the winter annual seedbank followed by reseeding. The second field experienced secondary invasions of winter annuals with limited establishment of native vegetation. Botanists will repeat the treatment and reseeding of this area during 2021 and 2022.

In summary, after much trial-and-error, botanists have succeeded in restoring native grasses in some relatively small areas of the Gardiner basin. However, it is unclear if these restored communities will persist without intensive management such as spraying weeds or be outcompeted once again by invasive non-native plants. In addition, these restored plant communities do not yet include a sagebrush or other shrub component. Thus, more focused efforts to restore sagebrush are needed. (Geremia and Hamilton 2019, Renkin 2021, Yellowstone Center for Resources 2021)

The purchase of lands or conservation incentives for the benefit of wild animals has been effective at protecting habitat for decades. Conservation groups and government agencies have successfully used this strategy with willing landowners to increase the permeability of ungulate movements across the Park boundary through the Custer Gallatin National Forest and private lands north of the Park. In 1999, the

Rocky Mountain Elk Foundation facilitated an agreement to transfer 1,508 acres (610 hectares) of lands on the Royal Teton Ranch just north of the Park boundary to the Gallatin National Forest for administration and monitoring. Funds appropriated to the Department of the Interior were used for the acquisition of this conservation easement which was intended to "facilitate the use, movement, or migration of the surface estate by bison, elk, bighorn sheep, pronghorns, grizzly bear, black bear or mule deer, and to avoid destruction or impairment of the natural habitat." Montana Fish, Wildlife and Parks purchased the grazing rights on the Royal Teton Ranch for a 30-year period in 2008. The lease agreement provided for wildlife movements through the ranch to Yankee Jim Canyon and the National Park Service and Montana Fish, Wildlife and Parks provided funds to implement the agreement.

The establishment of more long-term conservation agreements and incentives with landowners along the Yellowstone River valley from the Park to the southern Paradise Valley, including protection and restoration of vegetation such as sagebrush, would add much needed winter range for pronghorn and other wildlife and protect migration and dispersal pathways. Efforts are ongoing to identify additional habitat and conservation areas for pronghorn, develop fencing strategies with landowners, and identify opportunities for conservation incentives and the enhancement of habitat. The newly formed pronghorn population in the Carbella/Point of Rocks area of the southern Paradise Valley, founded in part by pronghorn dispersing from the Yellowstone population, often feed in irrigated hay fields on private ranches. It is unlikely these areas will be available in the long-term if rapid amenity and rural residential development continue in the valley unless efforts are made to keep farming and ranching financially sustainable and benefit wildlife conservation. Long-term partnerships for conservation efforts are needed in this area. (Scott 2004, Barnowe-Meyer et al. 2017b, Tilt 2020)

## *Other Management Considerations*

Coyote Predation—Intense predation on fawns by coyotes across the summer range severely limited pronghorn recruitment and population growth during several periods from the 1960s to the 2000s (see Chapter 3). From 1999 to 2007, this predation appeared to be higher in the Gardiner basin area of the pronghorn range. One possible explanation is coyotes concentrated in this area to scavenge on gut piles from bison left by hunters outside the boundary and at a carcass dumping site near Stephens Creek used by the National Park Service to dispose of animals killed along roads from vehicle strikes. (Houston 1982, Keating 2002, White et al. 2007a, Barnowe-Meyer 2009, Barnowe-Meyer et al. 2010)

Several biologists have recommended control actions to limit the number of coyotes and improve fawn survival and recruitment within the non-migratory segment of the population. The Lacey Act passed by Congress in 1894 prohibits hunting and the harassment, possession, or removal of birds and animals from Yellowstone National Park (16 USC 26). Even though the Superintendent has discretion to transfer or dispose of "surplus" animals (16 USC 36; 54 USC 100101, 100752), the National Park Service's policies for managing biological resources indicate "[t]he Service does not engage in activities to reduce the numbers of native species for the purpose of increasing the numbers of harvested species (i.e., predator control), nor does the Service permit others to do so on lands managed by the National Park Service." (Houston 1982, Keating 2002, National Park Service 2006, Barnowe-Meyer 2009, White et al. 2013b, White 2016)

As mentioned previously, high numbers of bison carcasses can accumulate in Beattie Gulch adjacent to the northern Park boundary during winters when large numbers of bison migrate out of the Park and are harvested by primarily tribal hunters with long-standing treaty rights to hunt on these lands. In July 2019, a group of residents called the Bear Creek Council recommended requiring bison hunters to remove carcasses and expanding an existing zone where no carcasses are allowed. The federal, state, and tribal agencies involved with bison management are considering these recommendations and have instructed hunters to spread stomach contents on the ground to lessen attractions to scavengers. The agencies also

are considering measures such as having hunters place remains in a dumpster for incineration or transport to local landfills or composting areas based on options developed by the Greater Yellowstone Coalition.

Since 2000, wolves from the Swan Lake, Quadrant, and 8-Mile packs have maintained territories encompassing the Stephens Creek carcass dump and bison hunt area within or adjacent to the pronghorn winter range where gut piles and other parts from tribal subsistence hunts are scavenged. About 75% of coyote-wolf interactions in Yellowstone occur at or near carcass sites, with 7% of these interactions resulting in the death of a coyote. Wolves have killed at least 116 coyotes in the Park since their reintroduction in 1995. Consistent wolf presence in the Gardiner basin may reduce coyote effects on pronghorn somewhat but further study is needed to clarify the timing and extent of these effects. (Barnowe-Meyer 2009, Merkle et al. 2009, Cassidy et al. 2020, Stahler et al. 2020)

Wildfire and Prescribed Burns—In addition to the influence of uncontrolled wildfires preceding Euro-American settlement, indigenous hunting parties in the Yellowstone area historically lit fires to influence the movements of pronghorn and other ungulates and regenerate habitat. Park managers suppressed fires which reduced the regenerating effects of wildfires and allowed conifers to invade some grassland habitats used by pronghorn (see Chapter 2). Grazing by bison and other ungulates alters the composition of grasslands by promoting a variety of plants and more variation across the landscape. Fire can enhance and maintain these effects. Yellowstone pronghorn increased exploratory movements after the extensive wildfires in 1988 burned forest canopies and about 30% of upland summer range in northern Yellowstone which resulted in more nutritious forbs and grasses. (Norris 1881a,b; Wear 1885, Harris 1889, Scott and Geisser 1996, Caslick 1998, Meagher and Houston 1998, Knapp et al. 1999, Fuhlendorf and Engle 2004, Confederated Salish and Kootenai Tribes 2005, Fuhlendorf et al. 2012)

Dr. Starker Leopold and colleagues suggested in 1963 that national parks should protect representative examples of wildland systems by maintaining ecological processes such as wildfire and other disturbances and using active management when necessary to prevent potentially serious and unacceptable changes. In response, the National Park Service placed more emphasis on science and research to support decision-making and transboundary partnerships to manage ecosystems that included public and private lands and social and economic concerns outside parks. The agency issued policies allowing ecological processes such as wildfire and predation to naturally modify ecosystems when feasible while lessening human interventions and manipulations. This management approach was reiterated in 2012 with recommendations to preserve ecological integrity, provide visitors with inspiring experiences, and manage park units as the core of a national conservation system. (Leopold et al. 1963, Keiter and Boyce 1991, Sellars 1997, Boyce 1998, du Toit et al. 2004, Gordon et al. 2004, National Park Service 2006, National Park System Advisory Board Science Committee 2012, White et al. 2013a,b)

Park managers currently allow natural disturbance processes such as fire, flooding, landslides, native insect outbreaks, and other natural disturbances to occur in wilderness areas. An average of 26 fires per year burned an average of 5,936 acres (2,402 hectares) in Yellowstone National Park during the last 45 years, excluding the massive fires during 1988. Park managers also could implement prescribed burns to prevent the encroachment of conifers and winter annuals into grasslands. However, this is an uncertain endeavor because such fires could inadvertently increase the spread of non-native plants in drier areas. A drying, warming climate would substantially increase the frequency of wildfires and area burned during coming decades and adversely impact soil moisture deficits and nutrient cycling. This could make grassland communities more vulnerable to the spread of non-native grasses. (Scott and Geisser 1996, Westerling et al. 2011, Canfield et al. 2013, Yellowstone Center for Resources 2018, 2021)

Tribal Subsistence Hunts—Bison migrations follow the same corridor used by pronghorn in the Gardiner basin and north towards Yankee Jim Canyon in Montana. In 2006, tribes of indigenous people resumed

hunting Yellowstone bison that migrated north and west of the park during winter onto national forest lands pursuant to long-standing treaties with the United States government. These traditional subsistence hunts often involve concentrations of hunters trying to shoot many bison at once near the park boundary to obtain large amounts of meat, hides, and other resources. The number of tribes and tribal members hunting near the park boundary increased over time and by 2013 issues such as "firing lines" and "flock shooting" prevented bison from distributing across the larger landscape and induced surviving bison to return to the park where hunting is prohibited. Tribal members began shooting more elk and a few pronghorn in the Gardiner basin outside the park in 2021 due to mild winter conditions and a relatively small bison migration. Many of these animals attempted to avoid hunters by returning to the park which limited their access to low-elevation winter range and migration further north into the Gardiner basin and Paradise Valley. The Custer Gallatin National Forest, Montana Fish, Wildlife and Parks, and treaty hunting tribes have taken actions to address public safety and natural resource concerns associated with these hunts on public lands. Park managers will continue to consult with the tribes and other agencies to facilitate the migrations of bison, deer, elk, pronghorn, and other ungulates north and west of the park. (White et al. 2015)

*Pronghorn buck in the Lamar Valley of Yellowstone National Park. Photo by Jacob W. Frank, National Park Service.*

# Conclusions

The management and research efforts described in this book greatly improved our knowledge about Yellowstone pronghorn, the viability of the population, and the connectivity of movement corridors essential for the population's persistence. However, population size is still relatively small and persistent threats such as habitat degradation and long-term connectivity to neighboring populations remain worrisome. Continued diligence, management, and partnerships are needed to further improve the situation. The following management actions will improve efforts to conserve Yellowstone pronghorn:

- Work with federal and state agencies and non-governmental organizations to pursue long-term conservation agreements and incentives with willing landowners along the Yellowstone River from the Park to the southern Paradise Valley to protect and restore migration and dispersal pathways and seasonal ranges for pronghorn and other wildlife.
- Protect the landscape between the Gardiner basin and the Lamar Valley as a wildlife migration corridor where no infrastructure development will occur outside of existing road corridors and developed areas.
- Initiate specific sagebrush restoration projects in the Gardiner basin to increase the density and canopy cover of this staple food during winter and the nutritional condition of non-migratory pronghorn during late pregnancy and early lactation.

In addition, the following research projects will eventually help inform new or improved management actions to directly impact the restoration of pronghorn, their habitats, and movement pathways:

- Continue collecting data on migration and dispersal pathways to identify impediments such as fences and take remedial actions with landowners to minimize obstacles and promote connectivity to historic use areas and neighboring populations.
- Assess the fidelity of maternal lineages to summer use areas by tagging fawns and following their movements over many years.
- Conduct a regional assessment of genetic diversity and gene flow among populations to determine if Yellowstone pronghorn are isolated and unique compared to neighboring populations.
- Evaluate the composition and nutritive quality of pronghorn diets in all use areas through the year and assess variations in the phenology, quality, and quantity of forbs among non-migrant and migrant use areas.
- Determine the distribution and density of coyotes across northern Yellowstone including high-elevation areas and evaluate whether wolves decrease the density of coyotes in various pronghorn summer use areas by competitively excluding them.
- Determine the age structure of migrant and non-migrant segments of the population and assess the impacts of climate warming and annual differences in weather conditions such as precipitation, soil moisture, and snow severity on forage production and availability and the demographics of this population. (White et al. 2007a,b; Barnowe-Meyer and Byers 2008, Boccadori et al. 2008, Barnowe-Meyer 2009, Barnowe-Meyer et al. 2009, 2010, 2013, 2017a; White 2021)

The authors hope the next generation of biologists in the Yellowstone area will learn from our experiences and continue to collaboratively conserve and restore long-distance migrants like pronghorn across the vast landscapes of the region. This will be a difficult but critical endeavor requiring creativity to advance novel ideas, trust to develop strong partnerships, confidence to take bold actions that benefit common interests, courage to withstand criticism, and determination to adapt and overcome. We wish you Godspeed.

# Appendix
## *Chronology of Conservation & Management*

***1870:*** Narrative accounts indicate there were thousands of pronghorn in the Yellowstone area, widely distributed in the upper Yellowstone River drainage and migrating to lower elevation areas during winter (Whittlesey et al. 2018, Whittlesey and Bone 2020).

***1872:*** Congress established Yellowstone National Park.

***1872-1883:*** Market hunters and poachers killed thousands of pronghorn in and near Yellowstone National Park each year.

***1883-1884:*** The Secretary of the Interior prohibited the hunting of wildlife in Yellowstone National Park and the legislature of the Territory of Wyoming passed an act to protect fish and game within the Park. However, poaching continued due to a lack of enforcement.

***1886:*** A detachment of First Cavalry, U.S. Army, arrived to manage Yellowstone National Park, enforce regulations, and prevent poaching. They implemented predator control such as poisoning, shooting, and trapping until 1934-1935.

***1886-1912:*** Soldiers herded pronghorn back into the Park to prevent them from being killed.

***1887:*** Human settlement and market hunting reduced pronghorn numbers to about 200 animals.

***1889-1890:*** Congress admitted the states of Idaho, Montana, and Wyoming into the Union.

***1891:*** Congress passed the Forest Reserve Act and presidential orders over the next 12 years designated more than 6.5 million acres (26,300 square kilometers) around Yellowstone National Park as public forest lands.

***1894:*** Congress passed the Lacey Act (16 USC 26) to prohibit hunting and the harassment, possession, or removal of wildlife from Yellowstone National Park.

***1894-1903:*** Pronghorn numbers varied between 500 and 1,000 animals.

***1902:*** The U.S. Army began feeding pronghorn during winter in the northern portion of Yellowstone National Park.

***1903:*** 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. This fence was not entirely effective, however, and some cattle continued to graze some areas in the Park.

***1904:*** The U.S. Army began cultivating and irrigating hay on at least 50 acres (20 hectares) within the Park near Gardiner, Montana, to produce about 100 tons (91 metric tons) of hay each year for feeding pronghorn and other ungulates during winter. These cultivated fields induced some pronghorn to remain on the winter range year-round rather than migrating.

***1908:*** Pronghorn abundance increased to about 2,000 animals due to feeding, protection, and predator control.

***1916:*** Congress created the National Park Service.

***1917:*** Pronghorn numbers decreased to about 200 to 300 following a series of severe winters, starvation, and dispersal.

***1918:*** The National Park Service assumed management of Yellowstone National Park from the U.S. Army.

***1918-1946:*** The population increased with the growth rate slowing after counts exceeded 600 pronghorn.

***1919:*** The National Park Service issued the Graves Nelson Report which recommended the acquisition of many private lands between Gardiner, Montana, and Yankee Jim Canyon at the southern end of the Paradise Valley.

***1920:*** Human settlement, fencing, and unregulated hunting eliminated the pronghorn migration from Yellowstone National Park to the north sometime before this year.

***1922:*** Pronghorn use of the Hayden Valley and Swan Lake areas ended prior to this year for unknown reasons.

***1922-1930:*** The Game Preservation Company purchased thousands of acres in the Gardiner basin and continued irrigation and hay production on many acres to produce forage for wildlife.

***1931-1932:*** Congress added about 7,609 acres (3,079 hectares) of lands near Gardiner, Montana, to Yellowstone National Park and adjacent Absaroka and Gallatin national forests which increased the winter range for pronghorn.

***1931-1934:*** Park staff cultivated about 300 acres (121 hectares) of the Gardiner basin to produce hay for feeding pronghorn and other wildlife during winter. The plowing, irrigation, haying, and feeding program ended in 1934.

***1934-1935:*** Counts of pronghorn increased to more than 600 and Park staff removed the boundary fence and discontinued predator control.

***1936-1946:*** Pronghorn counts increased to a high of 811 and pronghorn expanded their distribution.

***1946:*** Park managers decided to reduce the size of the pronghorn population to 400 animals.

***1946-1967:*** Park managers conducted at least eight culls totaling a minimum of 1,144 pronghorn to reduce abundance due to concerns about over-browsing of sagebrush in the Gardiner basin. Pronghorn counts decreased to about 200.

***1947:*** Pronghorn use of the Antelope Creek basin ended; they have not consistently migrated to this basin since.

***1953:*** Park managers decided to maintain pronghorn numbers between 100 and 125 animals.

***1957-1990:*** Intense browsing in the Gardiner basin by congregated elk decreased sagebrush by about 43% and cover by 29% (Singer and Renkin 1995).

***1962-1970:*** Sagebrush comprised 59% to 67% of pronghorn diets during winter (Singer and Norland 1994).

***1963:*** A special advisory board on wildlife management in national parks (Leopold Report) recommended allowing natural processes to function with minimal human influence.

***1967-1969:*** Research indicated about 80% of the pronghorn population migrated to higher elevation summering areas while 20% remained year-round on the winter range in the Gardiner basin (Barmore 2003).

***1968:*** Managers ceased culling pronghorn and subsequently allowed numbers to fluctuate in response to predators, resource limitations, and weather.

***1969-1981:*** Counts remained between 100 and 190 pronghorn. Migration still terminated at the Park boundary and raised concerns about the long-term viability of the population.

***1974:*** The Northern Yellowstone Cooperative Wildlife Working Group formed to cooperatively preserve and protect the long-term integrity of the northern Yellowstone winter range for wildlife species by increasing scientific knowledge of the species and their habitats, promoting prudent land management activities, and encouraging an interagency approach to answering questions and solving problems. Members are Yellowstone National Park, Custer Gallatin National Forest, Montana Fish, Wildlife and Parks, and the Northern Rocky Mountain Science Center (U.S. Geological Survey).

***1982:*** Park biologist D. B. Houston speculated culling had reduced pronghorn abundance from levels limited by food resources to lower levels maintained by coyote predation, vehicle strikes, and dispersal.

***1982-1991:*** Pronghorn numbers increased rapidly to almost 600 due to high recruitment, but the growth rate slowed after counts exceeded 500 pronghorn.

***1985-1988:*** Sagebrush comprised about 70% of pronghorn diets in the Gardiner basin during winter.

***1985-1997:*** Montana Fish, Wildlife and Parks permitted hunts of pronghorn in the Gardiner basin north of Yellowstone National Park (district 313) with harvests of 2 to 58 per year.

***1987-1988:*** The Royal Teton Ranch constructed about 2 miles (3.2 kilometers) of buck-and-pole fence along the boundary of Yellowstone National Park near Reese Creek that hindered but did not stop movements by pronghorn (Scott 1992).

***1988-1993:*** Research indicated about 20% of the pronghorn population migrated to higher elevation summering areas while 80% remained year-round on the winter range in the Gardiner basin (Scott and Geisser 1996, Caslick 1998, Scott 2013, 2014).

***1989:*** Park managers convened a panel of pronghorn experts to assess the viability of the population. They concluded the winter range was degraded and insufficient to support the population.

***1992-1995:*** Population growth slowed as pronghorn counts exceeded 500, followed by a rapid decrease in recruitment and counts from 536 to 235. The causes of this crash are unknown.

***1996-2011:*** Pronghorn numbers remained between 200 and 300 following the crash in abundance.

***1998:*** The U.S. House Appropriations Committee directed the National Park Service to initiate a National Academy of Sciences review of ungulate management and the ecological effects of ungulates on the rangeland in Yellowstone National Park and provide recommendations.

***1999:*** The Rocky Mountain Elk Foundation assigned 1,508 acres (610 hectares) from the Royal Teton Ranch just north of the Yellowstone National Park boundary to the Gallatin National Forest for administration. Funds appropriated to the Department of the Interior were used for the acquisition of this conservation easement.

***1999-2001:*** Research indicated fawn condition and survival were greater for migrants occupying higher-elevation summering areas than for non-migrants remaining on the winter range year-round. Winter habitat conditions did not appear to limit reproductive rates (Barnowe-Meyer et al. 2011).

***1999-2005:*** Research indicated about 70% of the pronghorn population migrated 10 to 30 miles (15 to 50 kilometers) to four contiguous summering areas and 30% remained year-round in the Gardiner basin (White et al. 2007b).

***1999-2006:*** Research indicated coyotes accounted for 56% of predation on adult pronghorn and up to 79% of fawn predation (Barnowe-Meyer et al. 2009).

***2000:*** A small herd of about 17 pronghorn was detected approximately 12 to 18 miles (19 to 29 kilometers) north of Yellowstone National Park in the southern portion of the Paradise Valley using the area from Carbella to Point of Rocks, Montana. This began the first sustained return of pronghorn to the southern Paradise Valley since the early 1900s.

***2000-2001:*** Research during these winters indicated sagebrush comprised less than 10% of pronghorn diets in the Gardiner basin, while rabbitbrush increased to approximately 60% of diets (Boccadori et al. 2008).

***2002:*** Montana Fish, Wildlife and Parks closed pronghorn hunting in district 313 due to low abundance.

***2002:*** A Committee on Ungulate Management in Yellowstone National Park convened by the National Research Council in 1998 released its findings in a book entitled Ecological Dynamics on Yellowstone's Northern Range. The Committee concluded "Yellowstone's pronghorn population is small, isolated, and at severe risk of extirpation."

***2002:*** Yellowstone National Park convened a Yellowstone Pronghorn Conservation Assessment Workshop to assess the status of the population and provide management and research recommendations.

***2005:*** The National Park Service, U.S. Forest Service, and Center for Invasive Plant Management convened a group of restoration specialists to develop recommendations for restoring native plant associations to about 1,200 acres (485 hectares) of former agricultural fields in Yellowstone National Park and nearby areas of the Custer Gallatin National Forest. The U.S. Forest Service implemented weed treatments, barley planting, prescribed burning, and native grass seeding in the Beattie Gulch and Cutler Meadow areas until 2013.

***2006-2007:*** Research during these winters indicated sagebrush comprised 66% of pronghorn diets in the Gardiner basin (Barnowe-Meyer et al. 2017a).

***2008:*** Montana Fish, Wildlife and Parks purchased the grazing rights on the Royal Teton Ranch for a 30-year period. The lease agreement provided a movement corridor for bison and other wildlife through the ranch. The National Park Service provided funds for the initial payment.

***2008:*** The National Park Service initiated native vegetation restoration projects on about 100 acres (40 hectares) between Landslide and Reese creeks in the Gardiner basin of Yellowstone National Park.

***2010-2015:*** The National Parks Conservation Association worked with landowners and federal and state agencies to remove and modify fences in critical migration pathways north of Yellowstone National Park (see https://www.npca.org/advocacy/68-saving-pronghorn-at-yellowstone-national-park).

***2010-2019:*** Botanists erected four 8- to 20-acre (3- to 8-hectare) fenced enclosures in the Gardiner basin near the northern Park boundary and used a variety of chemical, mechanical, and reseeding techniques to reduce the winter annual seedbank, restore areas infested with winter annual monocultures to a mix with native species, and improve nutrient and water cycling and energy transfer.

***2013:*** Genetic and telemetry data indicated the Carbella/Point of Rocks population in the southern Paradise Valley was started or supplemented by Yellowstone pronghorn with ongoing dispersal from the Park (Barnowe-Meyer et al. 2013, 2017b).

***2013-2017:*** Counts of Yellowstone pronghorn increased rapidly with 506 in the spring of 2017 (the highest count since 1992).

***2014:*** One hundred and twenty-one pronghorn were counted in the Carbella/Point of Rocks population in the southern Paradise Valley.

***2016:*** Montana Fish, Wildlife and Parks resumed pronghorn hunting in district 313 with 10 permits (licenses) each autumn which they increased to 11 permits in 2018 and 21 permits in 2019 before decreasing the number of permits to 10 in 2020.

***2016:*** The National Parks Conservation Association began working with landowners and agencies to remove and modify fences in critical pathways in the Madison River Valley west of Yellowstone National Park to enable pronghorn to reestablish their historic migration pattern into the Hayden Valley.

***2016-2017:*** Yellowstone National Park provided data to the University of Wyoming and participated in public workshops on the Wyoming Migration Initiative to advance the understanding, appreciation, and conservation of Wyoming's migratory ungulates by conducting innovative research and sharing scientific information through public outreach (http://migrationinitiative.org/).

***2018:*** The Secretary of the Interior signed order 3362 (Improving Habitat Quality in Western Big-Game Winter Range and Migration Corridors) which directed the National Park Service and other bureaus to work with Western states to "enhance and improve the quality of big-game winter range and migration corridor habitat … in a way that recognizes state authority to conserve and manage big-game species and respects private property rights."

***2018-2021:*** Botanists initiated native vegetation restoration efforts in the Gardiner basin on two unfenced areas totaling 20 to 30 acres (8 to 12 hectares) using autumn and spring chemical treatments to reduce the winter annual seedbank followed by reseeding.

***2020-2021:*** A biologist counted 416 pronghorn while surveying from the ground between Yankee Jim Canyon in Montana and Mammoth Hot Springs in Yellowstone National Park. Biologists did not conduct aerial surveys with a pilot and observer during these years due to health concerns related to the COVID-19 pandemic.

*Pronghorn fawn hiding in Yellowstone National Park. Photo by W. L. Miller, National Park Service.*

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*Pronghorn buck in the Gardiner basin of Yellowstone National Park. Photo by Jim Peaco, National Park Service.*

# Index

## G



## H



## I



## L



## M

## *N*



## *P*



## *R*



## *S*

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