Climate Adaptation Science Center and Land Change Science Program

Ungulate Migration in a Changing Climate—An Initial Assessment of Climate Impacts, Management Priorities, and Science Needs

Circular 1493

U.S. Department of the Interior
U.S. Geological Survey

Elk on their winter home at the National Elk Refuge. Photograph by Gannon Castle, U.S. Fish and Wildlife Service.

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By Katherine C. Malpeli

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Conversion Factors

International System of Units to U.S. customary units

Multiply	By	To obtain
	Length	
centimeter (cm)	0.3937	inch (in.)
meter (m)	3.281	foot (ft)
kilometer (km)	0.6214	mile (mi)
kilometer (km)	0.5400	mile, nautical (nmi)
meter (m)	1.094	yard (yd)
	Area	
square kilometer (km^2)	247.1	acre
square kilometer (km^2)	0.3861	square mile (mi^2)

U.S. customary units to International System of Units

Multiply	By	To obtain
	Length	
inch (in.)	2.54	centimeter (cm)
inch (in.)	25.4	millimeter (mm)
	Area	
acre	4,047	square meter (m^2)
acre	0.4047	hectare (ha)
acre	0.4047	square hectometer (hm^2)
acre	0.004047	square kilometer (km^2)

Temperature in degrees Celsius (°C) may be converted to degrees Fahrenheit (°F) as follows: °F = (1.8 × °C) + 32.

Abbreviations

AGFD	Arizona Game and Fish Department
BLM	Bureau of Land Management
°C	degree Celsius
CASC	Climate Adaptation Science Center
cm	centimeter
DOI	Department of the Interior
ECC	ecological carrying capacity
FWS	U.S. Fish and Wildlife Service
GPS	Global Positioning System
IDFG	Idaho Department of Fish and Game
in.	inch
IRG	instantaneous rate of green-up
km	kilometer
m	meter
NDVI	Normalized Difference Vegetation Index
NOROCK	Northern Rocky Mountain Science Center
NPS	National Park Service
SO3356	U.S. Department of the Interior Secretarial Order 3356
SO3362	U.S. Department of the Interior Secretarial Order 3362
USGS	U.S. Geological Survey
WAFWA	Western Association of Fish and Wildlife Agencies

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Executive Summary

Migratory behavior among ungulates in the Western United States occurs in response to changing forage quality and quantity, weather patterns, and predation risk. As snow melts and vegetation green-up begins in late spring and early summer, many migratory ungulates leave their winter range and move to higher elevation summer ranges to access high-quality forage and areas with vegetative cover for protection during fawning. Ungulates remain on these ranges until the fall when increasing snowfall and decreasing temperatures trigger them to migrate back to their lower elevation winter ranges. While researchers have begun to assess the effects of physical barriers such as roads and energy infrastructure on migration, less attention has been paid to understanding how changing climate conditions might affect ungulate movements and range habitats. Does earlier spring green-up make ungulates leave their winter ranges sooner? Do persistent drought conditions reduce the carrying capacity of seasonal range habitats or lead to shifts in migration pathways? These and other questions remain largely unanswered but could have cascading effects on ungulate population dynamics and migratory behavior.

In February 2018, the Secretary of the Interior signed Department of the Interior Secretarial Order 3362 (SO3362), “Improving Habitat Quality in Western Big-Game Winter Range and Migration Corridors.” The order, which focuses on elk, mule deer, and pronghorn in 11 Western States, directs the Bureau of Land Management (BLM), the U.S. Fish and Wildlife Service (FWS), the National Park Service (NPS), and the U.S. Geological Survey (USGS) to partner with State wildlife agencies on their priorities and objectives for identifying and conserving ungulate migration corridors and winter-range habitat. The USGS Climate Adaptation Science Centers (CASCs) were established to help managers of the Nation’s fish, wildlife, waters, and lands understand the effects of climate change and adapt to changing conditions. To support the recent Department of the Interior (DOI) emphasis on ungulate migration corridors and winter-range habitat, this report assesses current information on how climate change could affect elk, mule deer, and pronghorn migration. The report synthesizes the drivers of migration, outlines what is known about how climate change might affect these drivers, and summarizes management priorities and science needs related to ungulate migration corridors and range habitat.

A review of the literature on ungulate migration shows that the core drivers of spring migration are the timing of spring green-up and snowmelt, and the core driver of fall migration is winter severity. After exploring what is known about how these drivers affect or could be affected by climate change, several pathways through which ungulate migration could be altered were identified: (1) ungulates alter migration timing to better track plant phenology or in response to changes in winter conditions; (2) ungulates change their migration route or distance traveled during migration to accommodate changes in environmental conditions; and (3) ungulate populations that are currently migratory may begin to demonstrate interannual variability in whether they migrate, depending on environmental conditions and density-dependence, and may remain resident for sets of consecutive years.

Through discussions with managers, physical barriers to movement such as roads and fences were identified as a core concern. In addition, the primary research needs of States are the acquisition and analysis of data on ungulate movements, to refine delineation of winter range, summer range, and corridors, and to support a better understanding of how ungulates use these habitats. When it comes to understanding climate effects, managers were more concerned with understanding the vulnerability of winter- and summer-range habitats than the vulnerability of migration corridors because of the influence of summer and winter forage on ungulate condition and reproductive success. Managers were also concerned about how forage quality and quantity might change because of stressors such as drought, wildfire, and invasive species and how they might need to alter habitat-treatment strategies as a result.

More baseline data are needed before effective projections of ungulate migration, at a West-wide scale under climate change, can be made. These data needs include (1) more clearly defined corridors and seasonal range habitats; (2) a comprehensive understanding of the ecological drivers of migration across ungulate species and populations; and (3) the identification of environmental thresholds for key variables that influence migration, above which ungulates alter migratory behavior.

The CASCs have several opportunities to play a role in addressing these needs. The CASCs could initiate projects to identify past and potential future changes and trends in key variables known to affect ungulate migration, such as plant phenology, forage quality, or winter severity. However, it would be difficult to use this information to determine what those trends mean for ungulate migration due to the lack of knowledge about environmental thresholds for ungulates. Additional projects would be required to compare multiple years of movement data with key variables to define thresholds. Once available, information on environmental thresholds could be integrated with projections of key variables to forecast the likelihood that the migration routes or the distance traveled could change—another area in which the CASCs could contribute.

A more immediate role for the CASCs would be to carry out synthesis projects. One such project could summarize the "state of the science" on the drivers of ungulate migration. Although there are dozens of population- and location-specific studies on this topic, collating this information could help highlight trends in migration drivers that span species and geographies: a necessary first step toward determining the extent to which migration drivers could be affected by climate change. A second project could focus on what is known about how climate variability and change affect ungulate life-histories, population dynamics, and migration in the Western United States. The goal of this effort could be to identify knowledge clusters and information gaps that require further investigation. Together, these synthesized products could focus future scientific activities on the most pressing issues of ungulate migration and climate change in the Western United States.

Introduction

The seasonal migration of wildlife, from songbirds to wildebeest, is a biological phenomenon that enables animals to gain access to favorable resources and avoid adverse environmental conditions. Among migratory animals, ungulates demonstrate some of the most dramatic examples of migration. Blue wildebeest (*Connochaetes taurinus*) in Africa, Mongolian gazelles (*Procapra gutturosa*), and the pronghorn (*Antilocapra americana*) of North America can migrate more than 450 kilometers (km) roundtrip, and barren-ground caribou (*Rangifer tarandus groenlandicus*) migrate more than 1,600 km across the Arctic (Berger and others, 2014).

Today, many historical, long-distance migrations of herd-bound mammals have changed or been lost altogether as human populations expand and habitat fragments or disappears. For example, black wildebeest (*Connochaetes gnou*) in southern Africa and hartebeest (*Alcelaphus buselaphus*) in East Africa are no longer migratory (Harris and others, 2009). As their migration routes have been disrupted, some populations declined or became locally extinct. Wildebeest, hartebeest, and gemsbok (*Oryx gazella*) populations in East Africa's Tarangire Ecosystem declined by 88–95 percent as their migration routes were constricted by agricultural development (Bolger and others, 2008). In the Western United States, approximately 75 percent of the migration routes for elk (*Cervus elaphus*), bison (*Bison bison*), and pronghorn have been lost, yet the region still contains some of the greatest examples of long-distance migration in the Western Hemisphere (Berger, 2004). For example, archeological records show that pronghorn have used the same 150-km route linking their summer range in Grand Teton National Park to their winter range in the upper Green River Basin for the last 5,800 years (Berger and others, 2006).

Purpose and Goals

Physical barriers to movement, such as roads, oil and gas infrastructure, and residential development, are a major threat to ungulate migration in the Western United States and are a priority management concern. Researchers are assessing the effects of barriers on ungulate migration, particularly oil and gas development, as the economy of the West shifts from a focus on livestock production to energy extraction. In an era of global change, it is prudent for the research and natural resource management communities to consider how changing climate conditions might affect ungulates and their movements between seasonal ranges.

Our understanding of whether ungulates can respond to changing landscapes, and, if so, how quickly, is still rudimentary (Bolger and others, 2008; Jesmer and others, 2018). Research exploring the effects of changing climate conditions on ungulate populations and migration patterns is sparse. Will earlier spring green-up cause ungulates to leave their winter ranges sooner? Will persistent drought conditions reduce the carrying capacity of seasonal range habitats or lead to shifts in where animals migrate? How will the cheatgrass fire-cycle affect the conditions of forage on the winter range? These and other questions remain largely unanswered but could have cascading effects on ungulate population dynamics and migratory behavior, particularly if changing climate conditions alter forage quality, quantity, and seasonal or spatial distribution.

The USGS CASCs were established to help managers of the Nation's fish, wildlife, waters, and lands understand the effects of climate change and adapt to changing conditions. The goal of this report is to provide an initial assessment of the potential ways climate change could affect ungulate migration and seasonal range habitats and identify climate-related science needs that, if addressed, could support forward-looking ungulate management. This assessment focuses specifically on the three species—elk (fig. 1), pronghorn (fig. 2), and mule deer (fig. 3)—that were the subject of SO3362. Hereafter, where the term "ungulate" is used, it only references these three species.

The first phase of this assessment was a literature review to determine (1) what is known about the drivers of migration for elk, pronghorn, and mule deer in the Western United States and the importance of access to quality summer and winter ranges, and (2) the anthropogenic and environmental threats facing these species to determine how climate change and variability fit into the broader scope of threats. Based on this phase of the assessment, several potential pathways by which changes in climate might affect ungulate migration are outlined.

The second phase aimed to identify key management priorities, knowledge gaps, and science needs related to the effects of climate change on ungulate migration. This was achieved through conversations with State and Federal managers and a review of the action plans prepared by State wildlife management agencies, after the signing of SO3362, that highlight ungulate-migration management challenges and research needs. Based on the results of this assessment, paths for advancing the science and practice of ungulate management in a changing climate are outlined, with a focus on the role of the CASCs.

Figure 1. Photograph of elk in Rocky Mountain National Park, Colorado. Photograph courtesy of M. Reed, National Park Service.

Figure 2. Photograph of pronghorn in the Lamar Valley, Yellowstone National Park. Photograph courtesy of Neal Herbert.

Figure 3. Photograph of mule deer on the National Elk Refuge, Wyoming. Photograph courtesy of Kari Cieszkiewicz, U.S. Fish and Wildlife Service.

Ungulate Migration: Seasonal Ranges and Movement Patterns

Migratory behavior among ungulates is thought to occur in response to dynamic patterns of forage quality and quantity (Hebblewhite and others, 2008), weather patterns (Bruns 1977), and predation risk (Fryxell and Sinclair, 1988). Large herbivore migration is a learned behavior rather than genetically determined (Jesmer and others, 2018). Merkle and others (2019) found that spatial memory plays an important role in determining where mule deer migrate to and which routes they use, whereas the tracking of seasonal changes in, and accessibility to, forage resources influences the timing of migration.

Many studies have documented flexibility in migratory behavior within populations and that migration can be an individually variable trait (for example, Mysterud [2013] and Eggeman and others [2016]). Many populations are partially migratory, consisting of individuals that migrate seasonally, and year-round residents. Among partially migratory populations, seasonal movements are thought to be driven by a density-dependent demography (as in Eggeman and others [2016]). Further, not all populations or individuals migrate annually with consistency (as in Collins [2016]).

Spring Migration

The spring migration of ungulates from a low elevation winter range to a higher elevation summer range is a relatively well-studied phenomenon. By the end of winter, ungulates tend to be in poor condition nutritionally relative to other seasons (Parker and others, 2009). As snow melts and vegetation green-up begins in late spring and early summer, migratory ungulates in temperate climates move to summer-range habitats to access higher quality forage and areas with vegetative cover that provides protection for them during fawning (Wasserman and Friggens, 2017). Spring migration typically begins in late March or early April, depending on winter severity and elevation (Messmer and Klimack, 1999; Kolar and others, 2011; Monteith and others, 2011; Collins, 2016), and is initiated by decreasing snow depth and increasing plant growth. Hoskinson and Tester (1980) found that the start of spring migration among pronghorn in southeastern Idaho coincided with the breakup of snow cover, and Monteith and others (2011) found that later snowfall events delayed the mean date of mule deer migration by several weeks. Similarly, Garrott and others (1987) found that mule deer migrated to the summer range earlier after relatively mild winters and later after more severe winters. By moving to summer ranges as soon as the snow cover disappears, animals can take advantage of improved forage and space resources.

Plant phenology is a critical factor that shapes the resource landscape for ungulates. Because plant growth is delayed at high elevations and latitudes in the spring, the onset of spring green-up occurs as a resource wave known as “the green wave.” Some populations track, or “surf,” the green wave during spring migration, timing their movements to maximize access to optimal forage conditions (Monteith and others, 2011; Merkle and others, 2016). Forage quality is highest in new plant growth due to the high cell-soluble content (for example, crude protein, sugars, and starches) at that time. Cell solubles are easily digestible but decline as plants mature and accumulate fiber; therefore, although forage quantity increases as plants mature and biomass increases, the quality decreases. According to the forage maturation hypothesis, ungulates balance forage quantity and quality by selecting for intermediate forage biomass (Fryxell, 1991).

By timing spring migration with the emergence of vegetation, animals can take advantage of highly digestible forage for a prolonged period, leading to improved nutritional condition, survival, and reproductive success (Fryxell and Sinclair, 1988). For example, Hebblewhite and others (2008) found that migratory elk achieved an average of 6.5 percent higher forage-quality exposure compared with resident elk. Other studies found that some ungulates “jump” rather than “surf” the green wave, moving quicker along their migration routes and arrive on the summer range before the peak productivity of forage occurs (Lendrum and others, 2014). Even in these cases, migrating ungulates could access more favorable forage conditions than if they remained on the winter range.

Summer Range

Female ungulates require adequate summer forage to meet the nutritional demands of lactation and build fat reserves to survive and maintain pregnancy during the winter months (Cook and others, 2004). Fawning occurs on the summer range, typically from May to August (Messmer and Klimack, 1999), and access to high-quality forage during lactation improves the condition of female mule deer and has a positive effect on fawn survival (Monteith and others, 2014). The lactation period is energetically intensive for pronghorn, which have the highest proportion of neonate to adult female mass of North America’s ungulate species (Byers and Moodie, 1990).

Summer nutrition conditions can limit elk pregnancy rates and calf production. Proffitt and others (2016) found that elk exposed to lower summer-range nutrition entered winter in a poor nutritional condition, which resulted in lower pregnancy rates (72 percent) compared with elk that experienced higher summer-range quality (89 percent). Similarly, the summer and autumn nutrition of calves influences a female’s probability of becoming pregnant as a yearling. The probability of pregnancy among yearling elk can approach 100 percent for those that have access to high summer through autumn nutrition in their first year (Cook and others, 2004). These results highlight the important role of summer nutrition in maintaining healthy ungulate populations, as ungulate population dynamics are driven by a combination of adult female survival and juvenile recruitment (Gaillard and others, 2000).

Autumn Migration

In October, migratory ungulates depart their summer ranges for lower elevation winter ranges. Autumn migration among ungulates is less well-studied compared with spring migration. Autumn migration can be less synchronous among individuals than spring migration (Monteith and others, 2011), suggesting that autumn migration triggers may be more complex than those driving spring migration. One of the known drivers of autumn migration is the combination of increasing snowfall and decreasing temperatures. Increased snow depth and colder temperatures result in increased energy expenditures associated with movement and thermoregulation. Deep snow also directly reduces the availability of forage, which affects the nutritional condition of individuals and winter survival rates. Kucera (1992) found that major fall snowstorms caused a migration pulse in which mule deer rapidly and simultaneously left their Sierra Nevada summer ranges.

Similarly, Monteith and others (2011) found that during a year with early snowfall and cold temperatures, mule deer completed their migration 1 month earlier than during a year with mild autumn conditions. However, in the absence of cold temperatures, the authors only found a modest increase in the daily probability of mule deer migration after an early snowfall. Other mule deer herds have migrated in advance of the first snow (Garrott and others, 1987; Monteith and others, 2011), suggesting that local conditions may influence autumn migration.

As with the timing of migration, the distances traveled by ungulates between summer and winter ranges can vary among populations and between years. For example, during autumn migration, more severe winters are associated with longer pronghorn migrations, and milder winters are associated with shorter migrations (Bruns, 1977; Hoskinson and Tester, 1980; Collins, 2016). Winter severity may also determine whether individuals choose to migrate to their summer range or remain on their winter range. Collins (2016) found that 65 percent of pronghorn monitored in the northern Great Basin migrated during a year with milder winter conditions, while 100 percent migrated during a year with harsher winter conditions.

Another potential driver of autumn migration is the senescence of plants on the summer range, as autumn nutrition is a known driver of overwinter survival and fecundity (Cook and others, 2004; Tollefson and others, 2010; Proffitt and others, 2016). As plants age, their cell walls increase in thickness and fiber, making them less digestible. However, several studies found that ungulates migrate before the senescence of plants on their summer range (Monteith and others, 2011; Rivrud and others, 2016; Mikle and others, 2019). These findings suggest that animals make a tradeoff by leaving their summer range before peak rates of forage senescence to avoid becoming trapped at higher elevations by severe weather.

Land management activities, such as hunting, can also drive autumn migration. Ungulates perceive human disturbance as a predation risk and can respond to hunting by altering resource selection or moving into areas where hunting is prohibited (White and others, 2010). Changes in behavior during migration, such as reduced foraging or displacement from high-quality habitats, can affect individual fitness (Paton and others, 2017). For example, Mikle and others (2019) compared the timing of autumn migration among two subpopulations of elk in southwestern Wyoming—one that migrates to winter range located on a protected area where hunting is prohibited, and one that migrates between lands accessible to hunters. They found that 67 percent of elk that used the protected winter range left their unprotected summer range before the start of archery season (September 1), prior to frost or snow, while no elk from the second subpopulation migrated before September 1. Departing the summer range earlier to avoid hunting had tradeoffs, with early migrants leaving two months before vegetation senescence and potentially decreasing foraging efficiency (Mikle and others, 2019).

Winter Range

Autumn migration is complete when animals arrive on their winter range. Winter range habitat is often composed of grasses, forbs, and shrubs such as sagebrush (Wasserman and Friggens, 2017) and is typically much smaller in area and lower in elevation than the summer range. By moving to lower elevations, ungulates can escape deeper snow and colder temperatures. Snow conditions directly affect the ability of ungulates to access forage (Fancy and White, 1985), which in turn has consequences for their nutritional condition and winter survival. In fact, in northern climates, most annual mortality for ungulates occurs during winter (White and others, 1996).

The quality of winter-range habitat can be a limiting factor, affecting ungulate population dynamics (Bishop and others, 2009). Nutrition during winter is vital for minimizing fat loss. Winter severity thus interacts with body condition to affect the overwinter survival of juveniles and adults (Cook and others, 2004). For example, Singer and others (1997) found that winter severity had an additive effect on elk calf mortality by contributing to malnutrition. Winter nutrition can also affect calf birth weight, an essential predictor of neonate calf survival (Griffin and others, 2011). However, it is important to note that the traditional view of the winter range as the most critical and limiting factor for ungulates has begun to shift, as the importance of summer and spring or fall nutrition has been documented (Copeland and others, 2014). For example, in Nevada, summer drought and extreme temperatures can affect forage quality during those months, leading to a delayed mortality among mule deer during the winter months (Wasley, 2004).

Stopover Sites

While migrating between seasonal ranges, animals require access to adequate forage to maintain and renew energy reserves. As a result, many long-distance migrants spend part of their migration period in habitat patches along movement routes known as “stopovers,” where animals can rest and forage (Dingle and Drake, 2007). This phenomenon is well-studied among flying avian migrants but not among land migrants (Sawyer and Kauffman, 2011).

The emerging literature on the use of stopovers by ungulates demonstrates that these sites play a crucial role in their migration strategies. Most notably, Sawyer and Kauffman (2011) found that mule deer in Wyoming spent 95 percent of spring and autumn migration in stopover sites. Seidler and others (2015) found that pronghorn in Wyoming spent a significant portion of the spring migration period (78 percent) in stopovers. These sites had higher forage quality than movement corridors, and deer used the same stopover sites for years. During their spring migration, deer used stopover sites 44 days before peak green-up (Seidler and others, 2015), enabling them to exploit vegetation during the period of growth when plants are more easily digestible. Had deer not used these sites, they would have arrived on their summer ranges several weeks before optimal forage conditions. These results suggest that ungulates can reduce the amount of time they need to spend on the winter range by using stopover sites, allowing them to recover their body condition earlier in the spring and maintain a good condition longer into the autumn. More recently, Jachowski and others (2018) found that that the availability of stopover sites dampened the physiological stress response induced by human disturbances on the landscape among migratory mule deer in western Wyoming. The results of these and other studies led to a growing awareness about the importance of conservation strategies that prioritize stopover locations and the maintenance of connectivity between those locations.

Migratory Bottlenecks

Bottlenecks are features of migration routes that can influence ungulate movements. Bottlenecks are narrow areas along migration routes where landscape features such as vegetation, topography, or human development restrict the width of the corridor and, therefore, animal movements (Sawyer and others, 2005). Bottlenecks are often less than 1 km wide and can be as narrow as 100 meters (m) (Berger and others, 2006). Because of their small area, minor changes to the habitat in these corridors can completely sever established migration routes. One of the best-known bottlenecks is Trapper's Point, Wyoming, which is used by an estimated 2,500–3,500 mule deer and 1,500–2,000 pronghorn as they migrate between the Upper Green River Basin and Grand Teton National Park. This narrow sagebrush ridge was once 2 km wide, restricted by the Green River to the west and the New Fork River's riparian zone to the east; today, it has been reduced to 0.8 km by housing development and transportation infrastructure (Sawyer and others, 2005; Berger and others, 2006).

Anthropogenic Threats to Migration and Seasonal Ranges

The anthropogenic threats facing migratory ungulates in the Western United States are numerous but can be grouped into two broad categories: (1) threats that affect habitat quality on seasonal ranges and migration routes and (2) threats that affect movement during migration. Environmental conditions drive some threats; others are the result of human disturbance. Anthropogenic threats to ungulates include urbanization, residential development, transportation infrastructure, fences, energy development, and the conversion of natural land cover to agriculture (Christie and others, 2015), and can result in both habitat loss and the disruption of migration. While some anthropogenic features represent impermeable barriers that sever the connectivity of migration routes, such as certain types of fencing, most of these features are semipermeable. The effects of these types of barriers on migratory movements are less clear (Sawyer and others, 2013).

Residential Development

The effects of residential-scale development on ungulates have received less attention. Exurban development, which is characterized by low-density, vehicle-dependent communities outside of cities and towns, can be particularly detrimental to wildlife. This type of dispersed development can fragment habitat, alter animal movement patterns and behavior, cause species' home ranges to overlap, and reduce fitness (Riley, 2006). In the Rocky Mountain West, areas targeted for residential development, such as valley bottoms and low-elevation foothills, frequently intersect with ungulate winter ranges (Polfus and Krausman, 2012).

Research shows that ungulates can exhibit short-term behavioral responses to human disturbance, although responses vary by species. For example, Goad and others (2014) found that elk demonstrated decreased occupancy of high-density exurban areas, while mule deer showed relatively less avoidance behavior. In areas of human activity within protected areas, there is documentation of elk and pronghorn exhibiting behavior consistent with reduced predatory threat, such as higher levels of feeding, suggesting that they use more-developed spaces as refugia from predators (Shannon and others, 2014). Few studies tested whether population-level consequences result from these behavioral shifts, which would likely require long-term (>5 years) studies to detect (Polfus and Krausman, 2012). While some research exists on how energy development can alter migration behavior, similar studies have not explored the effects of residential development on ungulate migration.

Transportation Infrastructure

Roads and highways represent a direct source of mortality for ungulates due to the risk of wildlife-vehicle collisions (Bolger and others, 2008) and are a top concern among western big-game managers. These collisions can result in human injury and fatalities and lead to costly property damage. For example, in 2007, the average cost associated with deer-vehicle collisions was $6,617, while the average cost associated with elk-vehicle collisions was $17,483 (Huijser and others, 2009). Coe and others (2015) found that 10 percent of mule deer mortalities were due to vehicle collisions, which was roughly equivalent to the mortality caused by legal (11 percent) and illegal (13 percent) hunting.

In addition to the threat of collisions, transportation infrastructure can affect ungulates by reducing habitat connectivity and impeding migratory movements. Dodd and others (2010) found that a paved highway with fenced right-of-ways represented a near-total barrier to pronghorn passage. Similarly, Seidler and others (2015) found that a highway with high traffic volume and non-wildlife-friendly fencing represented a complete barrier to pronghorn movement: no animals were able to cross the highway. However, a highway with lower traffic levels and wildlife-friendly fencing remained permeable, and all pronghorn were able to successfully cross. Gavin and Komers (2006) identified behavioral changes in response to transportation infrastructure, with pronghorn demonstrating increased vigilance and decreased time foraging along high-traffic roads. Meanwhile, mule deer are able to search for less busy portions of highways to cross during migration (Coe and others, 2015). Lendrum and others (2012) found that in areas with high road-density, mule deer did not substantially deviate from their migration route but increased their movement rate. This finding suggests that deer avoid roads if they can do so without significantly altering their migration route. In highly developed areas, deer might not have this option, and fidelity to their migration route wins out (Lendrum and others, 2012). A lack of avoidance behavior could put migrating mule deer populations at increased risk if their movements crossing roads increased mortality.

Some States have installed—or are exploring the feasibility of installing—wildlife crossings over or under highways to reduce wildlife-vehicle collisions and support safe passage across transportation infrastructure. In Wyoming, the construction of seven underpasses, plus game-proof fencing on Wyoming Highway 30, which intersects a migration route used by thousands of mule deer, reduced deer-vehicle collisions by 81 percent (Sawyer and others, 2012). Detailed information on the location of migration corridors and where animals tend to cross roads is critical to ensuring the effective placement of crossing structures (Sawyer and others, 2012; Coe and others, 2015).

Railroads are another type of transportation infrastructure that can be a direct source of mortality for ungulates. In Canada's Yoho National Park in British Columbia and Banff National Park in Alberta, train strikes are the second-largest source of mortality for deer, elk, and moose (Dorsey and others, 2017). Railroads are travel corridors for some ungulates, such as elk, and deep snow can make an escape from oncoming trains difficult (Popp and others, 2018). Despite substantial documentation of ungulate-train collisions, our understanding of the effects of this type of transportation infrastructure on ungulates is limited compared with the effects of roads (Popp and others, 2018).

Fences

Fencing can prevent ungulates from crossing roads and being involved in collisions. Game-proof fencing may be necessary for guiding ungulates to underpasses or overpasses, improving the effectiveness of these structures (Sawyer and others, 2012). In northern Arizona, the installation of fencing along roadways designed to guide animals to existing crossing structures resulted in a 97 percent reduction in elk-vehicle collisions along a 9.17-km stretch of road (Gagnon and others, 2015).

Fencing not friendly to wildlife, including that associated with roads, livestock, or property, can be a source of direct mortality and a complete barrier to movement. Ungulates can snare their legs in fences if they attempt to jump over them. For example, wire fences in Colorado and Utah killed an annual average of one ungulate per 4 km of wire fence, with juveniles being eight times more likely to die in fences than adults (Harrington and Conover, 2006). Pronghorn more often attempt to crawl under fences when they cross, whereas deer jump (Jones, 2014). There are several solutions for making fences wildlife friendly. These solutions include limiting fence heights to 42 inches (in.), which adult deer and elk can jump, and leaving an 18-in. clearance under the bottom wire or rail for animals such as pronghorn that prefer to crawl under, rather than jump over, fences. Gates, dropdowns, and other mechanisms that allow wildlife passage can also be installed in areas where wildlife concentrate or where livestock is not present (Paige, 2012).

Energy Development

Over the last decade, researchers started to explore how the expanding scale and intensity of oil and gas development in the Western United States could affect migratory ungulates (Beckmann and others, 2012; Sawyer and others, 2013; Christie and others, 2015; Seidler and others, 2015). Two of the largest natural gas fields in the contiguous United States partially occupy the southern reaches of the Greater Yellowstone Ecosystem, an area of Wyoming that is home to more than 100,000 wintering ungulates (Beckmann and others, 2012).

Studies suggest that ungulates alter their migratory behavior in response to energy development. For example, Sawyer and others (2013) found that mule deer can migrate through moderate levels of energy development, but in areas of intense development, behavioral changes were identified, including detouring from traditional migration routes, increasing the rate of movement, reducing the use of stopover sites, and reducing the use of migration routes. Mule deer have also increased their rate of movement during spring migration in areas high in natural gas development, resulting in earlier arrivals on their summer range (Lendrum and others, 2013). Among pronghorn, Seidler and others (2015) found that animals reduced their use of stopover sites in the most intensively developed areas of two natural gas fields. Beckmann and others (2012) found that pronghorn avoided habitat patches with the highest level of disturbance from energy activities. In addition to the density of energy development, the level of human activity at these sites may also influence ungulate habitat selection. For example, Sawyer and others (2009a) found that mule deer avoided all natural-gas infrastructure and selected areas farther from well pads with higher levels of vehicular traffic.

These changes in migratory behavior and habitat use can affect the fitness of individuals, as when animals migrate more quickly and reduce the time spent at stopover sites with high-quality forage (Christie and others, 2015). Behavioral changes may be precursors to demographic responses, such as lower reproduction and survival rates in subsequent years (Beckmann and others, 2012). Christie and others (2015) identified a demographic cost to pronghorn caused by energy development, determining that 8 percent of an observed 73 percent decline in abundance was likely attributed to oil and gas development. One potential reason is that this type of infrastructure reduces the net primary productivity of forage plants because of the removal of vegetation to build oil pads, roads, and other infrastructure (Allred and others, 2015). Oil and gas development are also associated with increased road-density and vehicular traffic, representing an additional source of mortality and habitat fragmentation (Christie and others, 2015).

Climate Impacts, Vulnerability, and Adaptive Capacity

To date, most research on climate change and migration focused on identifying the effects of changing conditions on long-distance bird migrations. These studies focus on "trophic mismatch," which occurs when migratory birds fail to advance their breeding phenology to track earlier insect emergence (Both and others, 2009). This growing body of literature shows evidence that some bird populations can adjust their migration behavior, thereby avoiding mismatch and suggesting that the timing of migration is more flexible than previously thought. Understanding the plasticity of migration behavior across populations and species is central to understanding their vulnerability to current and future climate change (Beever and others, 2017; Rickbeil and others, 2019).

Among ungulates and other large herbivores, a trophic mismatch occurs if individuals fail to adjust the timing of migration to track earlier spring green-up, which could ultimately affect their nutritional condition and minimize the benefits that migration traditionally affords. As changes in forage conditions become increasingly common, it is critical to understand the impacts of these changes on ungulate migration. Aikens and others (2017) demonstrated that mule deer adjusted migration timing to track changes in spring green-up. More studies are needed to identify whether there is evidence of these behavioral changes across populations, species, and geographies. An impediment is the lack of long-term, large-scale datasets needed to understand the plasticity of ungulate migratory behavior and disentangle the influence of large-scale climatic changes from individual life-history patterns (Monteith and others, 2011; Rickbeil and others, 2019). Further, the responses of ungulate populations to climate change are likely complex and mediated by local processes. For example, populations in hotter, drier ecoregions could be more adversely affected by climate change because of diminished forage conditions, while populations in regions that experience extreme winters may undergo short-term positive impacts to forage conditions as temperatures increase (DeVos and McKinney, 2007).

When considering climate change, it is important to recall that migration behaviors have persisted for millions of years and evolved to let animals cope with extreme environmental variability (Lennox and others, 2016). However, a critical question remains about whether the rate of change might be too rapid for ungulates to adequately adjust the timing of their movements. This question becomes more critical if the rate of change outpaces the ability of ungulates to adapt evolutionarily by altering their reproductive phenology (Loe and others, 2016). Changing average temperatures and precipitation, and the corresponding variability in plant phenology, winter severity and snowpack, drought frequency and severity, wildfire size and frequency, and invasive species distributions in the Western United States can directly or indirectly impact ungulate populations. The potential and documented effects of these changes on ungulate population dynamics and migration behavior are outlined below.

Warming Temperatures and Plant Phenology

Plant phenology, a central determinant of ungulate habitat use (Fryxell, 1991), is sensitive to climatic variation because of the role of temperature in plant development. Large-scale climate variability plays an important role in shifting spring onset on interannual and multidecadal time scales (Ault and others, 2015), and shifts have been observed at both the individual plant and landscape levels (Cleland and others, 2007). The observed changes in plant phenology appear to vary with altitude and are affected by changes in both temperature and precipitation phases. While there is increasing evidence of longer growing seasons at low altitudes, there is less evidence of shifts at higher altitudes (Inouye and others, 2000). This difference is likely due to variations in snow accumulation across altitudinal zones. For example, in the Colorado Rocky Mountains, at an elevation of 2,945 m, snowfall increased over a 25-year period; therefore, spring green-up did not shift significantly despite warming temperatures (Inouye and others, 2000).

In a study of phenological shifts across the elk range in Wyoming (1,315–3,066 m), Christianson and others (2013) found that snow cover influenced the timing and rate of green-up. The authors found that years with extended periods of snow cover tended to result in later but more rapid spring green-up, while winters with snow cover that receded early resulted in an earlier spring onset but slower green-up. Therefore, shifts in plant phenology can vary both latitudinally and altitudinally. The extent to which ungulates are affected depends on the location and altitude of their winter and summer ranges.

Impacts on Population Demographics

Identifying the effects of warming temperatures and changing plant phenology on ungulate population dynamics is an evolving area of research. Hurley and others (2014) examined the effects of spring and autumn phenology on mule deer in Idaho and found that fawn overwinter survival was higher when the autumn growing season was longer because of its effects on body mass. There is also mounting evidence that the timing and rate of spring green-up can impact several aspects of ungulate life history (Searle and others, 2015). For example, Middleton and others (2013) found that rapid spring green-up correlated with declines in recruitment and pregnancy rates among migratory elk in Yellowstone National Park. Searle and others (2015) found that among mule deer in Colorado, individuals inhabiting summer ranges with an earlier vegetation onset had a better winter body-condition than those inhabiting ranges with later vegetation onset, likely due to their prolonged access to peak-quality forage.

More research on this topic was carried out on Arctic ungulates, where warming rates have been higher. Most notably, Post and Forchhammer (2008) found that the timing of caribou (*Rangifer tarandus*) calving in West Greenland has not kept pace with the advancement of spring green-up; as a result, population dynamics have been negatively affected. Average spring temperatures increased by more than 4 °C (degrees Celsius) since 1993, and the resulting rate of vegetation green-up has advanced more rapidly than female caribou have advanced their parturition date. As a result, there has been a rise in calf mortality and a fourfold reduction in calf production (Post and Forchhammer, 2008). However, studies exploring phenological mismatches for caribou in Alaska and Norway—specifically northern Norway and Svalbard—found no evidence of a mismatch between the onset of spring green-up and reproductive success and note instead that parturition commonly occurs well before the spring green-up (Tveraa and others, 2013; Gustine and others, 2017; Veiberg and others, 2017). This result is likely because caribou are capital breeders, and maternal, winter body-condition plays a more important role in reproductive success than spring phenology (Taillon and others, 2013). Additionally, caribou could benefit from increases in growing-season length and primary productivity in the Arctic leading to increased body mass (Albon and others, 2017).

These results suggest that changes in plant phenology can positively affect ungulates by prolonging their access to peak-quality forage. Further, while trophic mismatch is a possibility and is documented, this phenomenon is not widely observed. The current understanding of the effects of trophic mismatch on ungulates, particularly in milder temperate zones, remains limited.

Climate change, particularly temperature changes, can also impact the spatial and temporal distribution of pathogens and the emergence of disease conditions among ungulates in North America (Hoberg and others, 2008). Warming temperatures have contributed to changes in the geographic location of disease vectors and parasitic diseases and the abundance of certain parasites (Hofmeister and others, 2010). For many macroparasites that affect ungulates, even small temperature changes can substantially affect transmission dynamics (Hoberg and others, 2008). For example, *Parelaphostrongylus tenuis*, a parasite that causes neurological disease in moose, may increase in abundance as temperatures warm, while *Parelaphostrongylus odocoilei*, a lung parasite of caribou, has shifted its range northward, since 1995, from the Pacific Coastal Range into Alaska and the Yukon and Northwest Territories of Canada (Hofmeister and others, 2010). These changes in disease vectors and parasitic diseases can significantly affect ungulate population dynamics. However, information on the effects of disease on ungulate migration is unavailable, and, as a result, conducting a comprehensive review of how climate change affects ungulate disease is beyond the scope of this report.

Impacts on Migration

Several studies linked changes in the timing of ungulate migration to changes in plant phenology. For example, spring migrations of elk in northern Yellowstone occurred earlier in years with earlier spring green-up (White and others, 2010), and elk in the Greater Yellowstone Ecosystem delayed their departure from the winter range when spring green-up occurred later (Rickbeil and others, 2019). Monteith and others (2011) found that a combination of green-up and snow depth influenced spring migration timing. In years with low snow depth and early increases in Normalized Difference Vegetation Index (NDVI), they found that mule deer in the Sierra Nevada initiated spring migration sooner. In years with substantial snowfall and later green-up, deer delayed spring migration. Mule deer in western Wyoming also demonstrated that they match their movements to peaks in green-up (Aikens and others, 2017). Sawyer and Kauffman (2011) hypothesize that stopover sites may provide ungulates with the information they need to continue to track shifting phenological conditions and appropriately adjust the timing of their migrations, such that trophic mismatch can be avoided. The authors found that mule deer occupied stopover sites 44 days before peak green-up, when forage quality was highest, demonstrating that stopovers were used to track spring green-up.

These studies demonstrate plasticity in the timing of migration among multiple ungulate populations. The ability of ungulate populations to shift migration patterns to align with changes in green-up suggests that they can avoid trophic mismatch. Because the migration of temperate ungulates is cued by forage conditions, ungulates may be less susceptible to trophic mismatches than migratory birds. Bird migrations are often tied to cues such as photoperiod, which may not be a reliable means of assessing phenological conditions at the destination site (Sawyer and Kauffman, 2011).

Winter Precipitation and Severity

Warming winter and spring temperatures across the Western United States has contributed to more winter precipitation falling as rain than snow and earlier spring snowmelt (Knowles and others, 2006). As a result of warming temperatures, snowpack has declined across much of western North American since the 1950s and is projected to continue to decrease throughout the 21st century (Pederson and others, 2011). Precipitation is projected to become more variable, with more precipitation generally occurring from October to April and less expected during the summer months (DeVos and McKinney, 2007). In higher elevation areas, the projected increase in winter precipitation could result in deeper snowpack, unless warming temperatures push the rain-snow line farther upslope and precipitation falls instead as rain (Pettorelli and others, 2007).

Across many Western State mountain ranges, climate-model projections suggest the length of consistent snowfall-conducive temperatures will decrease from approximately five months (November–March) to three months (December–February) by the mid-21st century (2036–2065) (Klos and others, 2014). The Western United States could see a 30-percent average monthly reduction in the amount of land area that can remain within a wintertime snowfall regime by the mid-21st century (Klos and others, 2014). However, changes to the rain-snow transition line are influenced by elevation, latitude, and topographic relief. Areas of the Western United States with lower relief, mid-elevation mountains, such as the Northern Rocky Mountains and Northern Cascade Mountains, are projected to shift more quickly into new precipitation-phase regimes. Areas with steeper elevational gradients, such as the Sierra Nevada, Middle Rocky Mountains, and Southern Rocky Mountains, are likely to transition less quickly (Klos and others, 2014). Despite these projected changes, colder and higher areas in the intermountain West are expected to continue receiving winter snow at the highest elevations (Gonzalez and others, 2018). Climate extremes, including winter storms, are also expected to increase in frequency and magnitude. Whether or not these storms produce heavy snowfall depends on winter temperatures (Kunkel and others, 2013). However, mild and wet conditions can lead to heavy rain-on-snow events, which can result in a layer of ice forming above forage that prevents wildlife from accessing vegetation (Hansen and others, 2011).

Overall, the projections of future winter conditions suggest that warming temperatures and shifting precipitation phase regimes could, on average, lead to reductions in snowpack and less severe winters in the Western United States. However, interannual variability in winter conditions is expected to continue or increase, and severe winters could still occur if intense winter precipitation events become more frequent and coincide with temperatures that are snow-conducive, particularly in high-elevation areas.

Impacts on Population Demographics

Several studies identified correlations between winter severity and ungulate nutritional condition, survival, and abundance. When reviewing these studies, it is important to know that the indices used to quantify winter severity are inconsistent across studies. For example, Christie and others (2015) used the number of days in which snow depth is ≥35 centimeters (cm) and the number of days with a minimum temperature <7 °C; Singer and others (1997) used minimum daily temperature and snow water equivalent; and Collins (2016) used average daily temperature and snow depth.

Several studies identified links between winter conditions and ungulate population dynamics. Severe winters can cause nutritional stress, high fawn mortality, and low fawn recruitment among mule deer. Severe winters and deep snow limit the ability of mule deer to forage, which can result in die-offs and high mortality (Western Association of Fish and Wildlife Agencies [WAFWA] Mule Deer Working Group, 2003). For example, a marked decrease in mule deer populations in Utah was observed in 1965 due to harsh winter conditions (Messmer and Klimack, 1999). Studies of elk have found that colder winter temperatures, increased snowfall, and more frequent winter storms resulted in population reductions (Hebblewhite, 2005). Snow depth can also influence wolf predation to negatively affect ungulate population growth rates. In a study of elk population dynamics in Banff National Park, Hebblewhite (2005) found that increasing winter severity reduced the elk population growth rate, and this decline was steeper in areas with wolf predation. This result is likely due to increased wolf predation rates in deeper snow.

The effects of winter severity on elk may be more potent when populations are at or near the ecological carrying capacity (ECC). For example, Singer and others (1997) found no effect of winter severity on elk populations during a 21-year period when populations were below ECC, but they found that winter severity negatively affected elk-calf survival during a 4-year period when populations were at or near ECC. Severe winter conditions, with low temperatures and frequent blizzards, are associated with pronghorn mass-mortality events, in which mortalities were attributed to the loss of access to shrubs and an inability to move to more hospitable areas because of fences and roads (O’Gara, 2004). In addition, a 73-percent decrease in pronghorn abundance from 2008 to 2012 in western North Dakota corresponded to winters with heavy snowfall and low temperatures (Christie and others, 2015). Snow depths of 25–30 cm are known to impede movement for both mule deer (Wasserman and Friggens, 2017) and pronghorn (Collins, 2016).

Icing can also contribute to ungulate mortality. Mild spells that lead to rain-on-snow events can cause ice that traps forage, and these events are associated with starvation-related die-offs and reduced fecundity (Hansen and others, 2011). Icy conditions can also result in mass mortality events when ungulates slip and fall. For example, four mule deer mass-mortality events occurred during an autumn migration in the Sierra Nevada. Dozens of migrating deer slipped on ice that persisted through the summer and fell to their deaths. Each event followed winters of exceptionally high snowfall that resulted in ice-covered terrain persisting on the mountain passes traversed by deer during migration (Bleich, 2018).

In temperate environments, ungulate population growth rates are often mediated by winter severity and its effects on survival and recruitment (Wang and others, 2002). Considering what is known about the impacts of severe winters on ungulate population dynamics, populations may experience increased survival and abundance. This could happen if the trend toward warmer winters and shifts in precipitation from snow to rain result in a greater availability of forage and lower requirements for temperature regulation in the winter months. For example, in Rocky Mountain National Park, model projections suggest that increased summer precipitation could increase calf survival, and higher average-minimum winter temperatures could increase the recruitment of juvenile elk (Wang and others, 2002). A future with warmer winters and wetter summers could double elk population sizes, while warmer winters combined with drier summers could increase populations by 50 percent. Population increases of this scale could lead to overabundance exceeding the ECC (Wang and others, 2002).

Impacts on Migration

Winter severity and snowpack conditions play an essential role in the timing of fall and spring migration, the distance traveled during migration, and whether individuals migrate or remain resident. Snow depth and cold temperatures are the drivers of autumn migration (Mikle and others, 2019). For example, Monteith and others (2011) found that the daily probability of mule deer migration in autumn increased as daily snowfall and snow depth increased and as the daily temperature and the range of temperature change decreased. Spring migration can also be delayed after winters with increased snowpack (White and others 2010) or initiated earlier in years with lower snow depth (Monteith and others, 2011). During years with late spring snowstorms, ungulates may be forced to migrate when snows are deeper, making migration more taxing (Monteith and others, 2011).

Winter conditions can affect the distance traveled and the types of movements made during migration. During a winter with deeper snow and colder temperatures, pronghorn in the northern Great Basin exhibited longer average autumn-migration distances (nearly double), fewer exploratory movements, larger winter ranges (mean = 460 km^2, compared with 253 km^2), lower elevational use (mean = 1,566 m, compared with 1,778 m), and a shift in winter range location (Collins, 2016). During prolonged winters in Nevada, mule deer altered their migration patterns and occupied nontraditional winter ranges to access open areas with southern exposures (Cox and others, 2017). In contrast, during milder winters, mule deer in the Colorado Plateau used mid-elevation transitional ranges for extended periods. These areas can provide more abundant, high-quality forage for deer than drier, low-elevation, traditional winter ranges (Watkins and others, 2007).

If winter conditions become milder, as anticipated, these studies suggest that the average date of departure for the winter range could be delayed, ungulates might make more use of mid-elevation zones during winter months, and spring migration could begin sooner. These responses could all improve ungulate nutritional condition. By delaying autumn migration and initiating spring migration sooner, ungulates would have access to higher quality forage on the summer range for a prolonged period. The ability to use mid-elevation zones would likely confer similar benefits. However, migration could become less common if a decreasing trend in winter snow cover continues and migration ceases to afford the demographic benefits that it once did. Changes in climate that influence ungulate seasonal ranges can alter the ecological basis of migration (Mysterud, 2013). If more individuals become resident and ungulate abundance increases because of less severe winters and a lack of predation, overabundance and crowding on ranges becomes more likely.

Drought, Wildfire, and Invasive Species

Warming temperatures and more variable precipitation patterns are resulting in more frequent and intense droughts in the Western United States. In the Southwest, increasing temperatures amplify the severity and effect of droughts and increase the likelihood of decadal and multidecadal megadroughts. Decreasing snowpack and early peak snowmelt in the region further exacerbate drought conditions (Gonzalez and others, 2018). In the northern Great Plains, fluctuations between heavy rainfall events and severe drought suggest that the region's climate is becoming more variable as temperatures warm (Conant and others, 2018).

Fire activity also increased across the Western United States in recent decades. Warming spring and summer temperatures and earlier spring snowmelt resulted in increased fuel aridity and more favorable fire conditions in western forests (Abatzoglou and Williams, 2016). The occurrence of large wildfires increased dramatically in the mid-1980s, with a spike in large-wildfire frequency (nearly four times the average), longer wildfire durations (increased from 1 to 5 weeks), and longer wildfire seasons (increased by 78 days) (Westerling and others, 2006). The most notable increases occurred in the Northern Rocky Mountains, where spring and summer temperatures increased, and spring snowmelt occurs earlier in the season (Westerling and others, 2006).

Climate change and historical fire suppression also aid the spread of invasive plant species that degrade western rangelands and perpetuate the wildfire cycle. Cheatgrass and other invasive plants were brought into the region with crop seeds in the early 1900s and have since led to dramatic changes in rangeland vegetation structure and composition (WAFWA Mule Deer Working Group, 2003). Invasive species such as cheatgrass compete with native species for resources and can increase erosion and the frequency and intensity of wildfires (Watkins and others, 2007). More frequent and intense wildfires on mid- and low-elevation winter ranges destroy the native shrublands that ungulates use for forage and cover (Watkins and others, 2007).

Impacts on Population Demographics

Decreased precipitation reduces the availability and quality of important plants, and ungulates are forced to eat forage with less nutritional value (WAFWA Mule Deer Working Group, 2003). In arid regions, the impacts of drought on forage are likely to be more limiting than those on water availability; high-moisture forage is a critical source of water for ungulates (Watkins and others, 2007). During an extreme drought in Arizona, Sonoran pronghorn (*Antilocapra americana sonoriensis*) were forced to switch from nutritious forbs to chain fruit and cholla fruits. These fruits provide pronghorn with water but are less nutritious (DeVos and Miller, 2005). Summer drought also affects Sonoran pronghorn mortality through malnutrition, starvation, and dehydration (Brown and others, 2006). In 2002, a severe drought in southern Arizona killed 80 percent of a small Sonoran pronghorn population, resulting in their near extirpation (U.S. Fish and Wildlife Service, 2016).

Similarly, in northwestern Nevada, mule deer numbers have trended downward since a long-term drought began in 2007 (Cox and others, 2017). Severe drought also likely contributed to a decline in mule deer abundance in New Mexico: during a year when precipitation was 73 percent of normal, adult female survival was the lowest recorded among contemporary mule deer studies, with malnutrition being the primary cause of mortality (Bender and others, 2007). In this example, the spring rainy season did not occur, resulting in a spring mortality pulse. When precipitation returned to normal, adult survival increased.

The effects of wildfire and invasive species on ungulate population dynamics are less well-documented than those of drought. In Nevada, large wildfires resulted in significant losses of cover and forage for pronghorn. However, elk in some locations benefited from the vegetation succession in recently burned areas (Cox and others, 2017). In Yellowstone National Park, the winter survival rate of elk calves was reduced during a year that included severe drought, several large wildfires on winter and summer ranges, and severe winter weather (Singer and others, 1997). Wildfires appear to increase the vulnerability of calves to predation due to the loss of shrub cover. Predation rates more than doubled (30 percent compared with 13 percent) after fires (Singer and others, 1997). Meanwhile, invasive species can affect ungulate population dynamics because they replace high-quality forage with plants that are of little or no forage value. The cheatgrass invasion and the associated risk of wildfires on low elevation shrublands are the primary factors threatening mule deer winter range in eastern Utah, southwestern Colorado, southern Wyoming, northern New Mexico, and parts of northern Arizona (Watkins and others, 2007).

Impacts on Migration

Little is known about how drought, wildfire, and invasive species shape ungulate migration. One way these stressors could affect migration is through vegetation and forage conditions. Drought, for example, can diminish the quality of the greenscape. In western Wyoming, Aikens and others (2020) found that the spring green-up period lasted 120 days during wet years and 60 days during dry years and occurred less sequentially during drought years. They found that mule deer could follow the altered waves of green-up and did not experience trophic mismatch but were constrained in their ability to accrue forage resources during spring, likely decreasing the benefits of migration. Middleton and others (2013) identified lower pregnancy rates in migratory elk after drought, suggesting that drought can reduce the nutritional benefits that migration affords. In California, wildlife managers are concerned that persistent drought conditions could reduce the nutritional carrying capacity of the landscape and lead to shifts in migration strategies that condense mule deer on summer ranges (State of California and U.S. Department of the Interior, 2018).

Extreme events such as drought and wildfire could exacerbate the changes in vegetation phenology already occurring because of long-term warming trends and increase the risk for an invasion of non-native plants. For example, even if ungulates alter the timing of their migration to track earlier spring green-up, the nutritional benefits gained could still be inadequate if droughts or wildfires decreased the availability of quality forage. Whether this could shift when ungulates migrate or where they migrate remains unclear.

Ungulate Adaptive Capacity

Ungulates could adapt to changing climate conditions through behavioral plasticity, such as altering the timing of migration to better track spring green-up, or through evolutionary adaptations, such as altering the timing of parturition. Behavioral plasticity by ungulates is documented in several studies and may prove important for the long-term persistence of migratory ungulates under rapidly changing climate conditions, particularly if the rate of change outpaces evolutionary adaptations (Loe and others, 2016). Although evolutionary adaptations to climate change are observed among other taxa, ungulates have long generation times, and the pace of evolutionary change might be too slow compared with the rate of climate change. For example, caribou in West Greenland were unable to advance their reproductive phenology to coincide with the fast rate of warming temperatures and advancing spring green-up, and therefore experienced significant reductions in reproductive success (Post and Forchhammer, 2008).

The ability of ungulates to advance or delay the timing of migration could directly affect the ability of populations to persist in the face of changing climate conditions (Monteith and others, 2011). Large herbivores can adjust migration timing in response to environmental conditions, suggesting that they can buffer the adverse effects of climate change by using flexible migration strategies (Monteith and others, 2011). For example, observed interannual variation in elk migration timing, particularly the winter range departure date and the summer range arrival date, demonstrates the ability of elk to shift migration timing based on changing environmental conditions. It is possible that elk could continue to access high-quality forage as climate change alters forage conditions, assuming quality forage is available in the region and elk can locate it (Rickbeil and others, 2019). Similarly, migratory caribou on the northern Quebec-Labrador Peninsula demonstrate interannual variation in habitat use based on the climatic and habitat conditions available each year (Sharma and others, 2009).

The use of stopover sites has served as a mechanism for helping migrating ungulates better track forage conditions (Sawyer and Kauffman, 2011). Ungulate migration is cued mainly by forage conditions. As they arrive at stopover sites along migration routes, ungulates can delay or advance their movements based on the cues received at these sites. In effect, ungulates use stopover sites to ensure they arrive on their winter or summer range at the appropriate time, avoiding trophic mismatch (Sawyer and Kauffman, 2011).

Alternatively, migratory ungulates could adapt to climate change by switching to nonmigratory behaviors. For example, the partially migratory Ya Ha Tinda elk population in Alberta, Canada, demonstrated that migratory behavior is an individually variable trait that can respond to external drivers, including environmental forces (Eggeman and others, 2016). If more individuals become nonmigratory, overcrowding on ranges could become an issue (Wang and others, 2002), particularly if warming temperatures and less severe winters lead to increased population growth. However, Eggeman and others (2016) found that high elk abundance caused individuals in a partially migratory population to switch to a migrant strategy. Therefore, if climate change results in more interannual variability for factors such as winter severity, snowpack, and drought occurrence, ungulate populations that migrate every year may become partially migratory, selecting their strategy each year based on current environmental conditions and population abundance.

Data Gaps and Science Needs

A literature review on ungulate migration identified an initial set of potential “pathways” by which ungulates could alter migration behavior in response to changing climate conditions and the corresponding effects on habitat. These response scenarios do not incorporate future changes in land use and land cover, such as residential and energy development, which could intersect with climate change to restrict these pathways. This type of information is beyond the scope of this assessment but would help further refine the scenarios outlined below.

The scenarios listed here are labeled as follows: “altered migration timing,” “altered migration route,” and “behavioral switching—from migratory to resident.” Each adaptation response scenario includes the following components:

- Scenario: A description of how ungulate migration would change under the specific scenario.
- Documentation: A description of whether this response is already documented in the literature and, if so, information on the species and population for which this response was documented.
- Data needs: A description of the datasets needed to investigate the likelihood of the scenario occurring.
- Future research directions: Building on the identified data needs, this section describes potential research projects that could help understand the likelihood of the scenario occurring.

Response Scenario One: Altered Migration Timing

- Scenario: Under this scenario, individuals initiate spring migration earlier or autumn migration later to better track plant phenology or in response to increases or decreases in snow conditions.
- Documentation: This response is documented among mule deer in the Sierra Nevada (Monteith and others, 2011) and Wyoming (Aikens and others, 2017; Sawyer and Kauffman, 2011) and among elk in the Greater Yellowstone Ecosystem (Rickbeil and others, 2019; White and others, 2010). No studies were identified during the literature review that document shifts in the timing of pronghorn migration in response to changes in plant phenology or snow conditions.
- Data needs:
    - Monitor ongoing changes in forage quality. Bischof and others (2012) and Merkle and others (2016) suggest using the instantaneous rate of green-up (IRG), which measures the rate of change in NDVI data over time to identify high-quality forage at intermediate biomass.
    - Project changes in future plant phenology and how those changes vary spatially (by latitude and altitude). Predicting phenological trends requires species-specific phenological models, as the effects of temperature, precipitation, and soil moisture vary among plant species (Chuine and others, 2000).
    - Collect data on the rate of change in plant phenology and how the rate of change varies among different forage types vital to ungulates, such as forbs versus grasses. For example, Cleland and others (2007) found that warming temperatures accelerated flowering in forbs but delayed it in grasses.
    - Forecast changes in daily temperature, daily snowfall, snow depth or snowpack in autumn and spring, and seasonal snow dynamics (such as rain-on-snow events and freeze-thaw cycles).
- Future research directions:
    - Integrate the most recent phenological modeling techniques to identify potential changes in the timing of green-up and the distribution of forbs, grasses, and shrubs within elk, mule deer, and pronghorn

priority migration corridors and seasonal ranges. This includes integrating remotely sensed data with observational datasets to provide a landscape-level understanding of changes in the phenological timing, abundance, and distribution of forage.

- Add pronghorn collaring and collaring-data analysis to determine if there are examples of populations demonstrating phenotypic plasticity in migration timing in response to phenology or snow conditions.
- Continue to monitor elk and mule deer populations in the Sierra Nevada and Wyoming ecosystems and the Greater Yellowstone Ecosystem, as well as additional populations to determine the extent of phenotypic plasticity in migration timing across populations and geographies.

Response Scenario Two: Altered Migration Route

- Scenario: Individuals exhibit changes in their migration route or distance traveled based on changes in environmental conditions.
- Documentation: Changes in migration routes and distances traveled were observed in response to inter-annual variations in climate, especially winter severity and snow conditions. For example, among pronghorn in the Great Basin, Collins (2016) found that autumn migration distances doubled when winters were more severe. Hoskinson and Tester (1980) suggest that snowfall influences autumn migration distance. In Nevada, during a long winter in which snow covered the valleys and flats, mule deer moved beyond traditional winter ranges to locate open areas and southern exposures (Cox and others, 2017).
- Data needs:
    - Forecast snow depth, snow water equivalent, winter temperatures, freeze-thaw cycles, rain-on-snow events, and the frequency of extreme winter weather events.
    - Project changes in the spatial location of high-quality forage, incorporating the potential effects of disturbances such as wildfire, drought, and invasive plants, as well as variables such as snow water equivalent, freeze-thaw cycles, and rain-on-snow events. Is the location of high-quality forage shifting latitudinally or altitudinally? Are conditions projected to reach thresholds such that state-transitions occur and the quantity of high-quality forage changes?
    - Obtain additional baseline data on ungulate migration spatial patterns, with a focus on identifying drivers of change in migration routes and distances traveled. These data are needed to better understand the extent to which migratory ungulates alter their migration patterns in response to weather or forage availability.
    - Collect data on environmental thresholds for ungulates. Are there particular snow depth, snow hardness, or cold-temperature thresholds at which ungulates must alter their migration route or distance traveled? Snow depths of 25–30 cm are documented as impeding the movements of pronghorn (Collins, 2016) and mule deer (Aikens and others, 2017). Is this true across populations? Do elk have a higher threshold? What about temperature thresholds?
- Future research directions:
    - Analyze historical records of drought, precipitation, temperature, and phenology data to assess whether and how the spatial location of high-quality forage has changed to help inform projections of shifts in forage location.
    - Compare ungulate movement data (for populations with multiple years of data) and records of drought, wildfire, and invasive species occurrences to assess whether these stressors altered ungulate migration patterns in the past.
    - Integrate projections of future snow depth, winter temperatures, and the frequency of extreme winter weather events with information on environmental thresholds. These actions can help researchers forecast the likelihood that migration routes and distances traveled vary from year to year; how often ungulates are able to follow their traditional routes; or whether long-term climate trends suggest that nontraditional routes become normal routes over time.
    - Analyze ungulate movement data to determine if migration routes or seasonal range locations change based on forage conditions. Studies have found that shifts in the timing of migration can occur in response to changes in the timing of spring green-up. However, are ungulates using nontraditional migration routes in response to changes in the location of quality forage?

Response Scenario Three: Behavioral Switching—From Migratory to Resident

- Scenario: Some studies documented the declining productivity of migratory ungulates in response to factors such as changes in plant phenology and predation pressure (for example, Middleton and others [2013]). Should migration no longer afford benefits to fitness, migratory ungulates may switch to being resident or demonstrate interannual variability in whether they migrate or remain resident for sets of consecutive years.
- Documentation: Partial migration, in which part of a population migrates and the other part does not, is a common strategy among ungulates. Within partially migratory populations, some individuals are permanent residents and other individuals switch between strategies as a result of density-dependent mechanisms (as in Eggeman and others [2016]), environmental conditions (as in Brown [1992] and Jacques and others [2009]), and predation pressure (Eggeman and others, 2016).
- Data needs:
    - Gather long-term collaring data from partially migratory populations to identify the extent to which weather conditions, population density, predation risk, and other variables influence whether ungulates migrate during a given year.
    - Gather long-term collaring data to determine if there are trends in migratory populations becoming conditional migrants or long-term residents or trends in the number of partially migratory populations becoming residents.
- Future research directions:
    - Carry out research to differentiate the effects of population density, environmental conditions (such as winter severity and shifting plant phenology), predation risk, and other variables on the decision to migrate. For example, warming temperatures and milder winters could increase population abundance. As a result, while the part of a population that migrates might initially decrease in response, that part might later increase if the density on the summer range becomes too high. Once the strength of the effects of population density, winter conditions, predation pressure, and other variables on the decision to migrate are better defined, projections of future climate conditions could be integrated with this ecological data to project changes in migration.

Secretarial Order 3362

Large sections of ungulate range and corridor habitat occur on lands under the management jurisdiction of the Department of the Interior’s (DOI) three land management agencies: the Bureau of Land Management (BLM), the U.S. Fish and Wildlife Service (FWS), and the National Park Service (NPS). On February 9, 2018, the DOI formally committed to protecting winter-range habitat and migration corridors for ungulates in the West. The Secretary of the Interior signed U.S. Department of the Interior Secretaria l Order 3362 (SO3362), which focuses on elk, mule deer, and pronghorn in 11 Western States (fig. 4). These three species contribute billions of dollars, through hunting and tourism revenue, to these States. By improving ungulate habitat, SO3362 aims to increase and maintain sustainable big-game populations, which can expand opportunities for big-game hunting.

The signing of SO3362 advances the intent and purpose of U.S. Department of the Interior Secretarial Order 3356, “Hunting, Fishing, Recreational Shooting, and Wildlife Conservation Opportunities and Coordination with States, Tribes, and Territories” (SO3356), which focuses on physical access to managed lands for recreational activities and directs DOI bureaus to work closely with States. In the same spirit, SO3362 directs DOI’s three land management agencies and the USGS to partner with Western State wildlife agencies on priorities and objectives related to ungulate winter ranges and migration corridors on DOI-managed lands. State agencies have priority management authority over big-game species, and SO3362 respects this authority.

Implementation

A national coordinator oversees all implementation activities related to SO3362. States were grouped into five “unified regions” for the implementation of SO3362, and each region was assigned a Federal liaison from either the BLM, FWS, or NPS. The primary role of the liaisons is to work with the States to implement SO3362. Within 60 days of SO3362 being signed, each State was asked to identify their top three to five migration corridor, winter range, and stopover habitat priorities and their top two or three research priorities. This information was summarized in a State action plan for each State. Each plan describes the State-defined priority areas and research needs, as well as relevant, ongoing State and Federal management and research activities. The State action plans, set to be updated on an annual basis, guide the allocation of Federal funds that can protect and enhance both winter range and corridor habitat. The DOI acted immediately after the completion of these plans and provided up to $300,000 in funding for each State to support priority research needs. Table 1 lists additional funding activities related to SO3362.

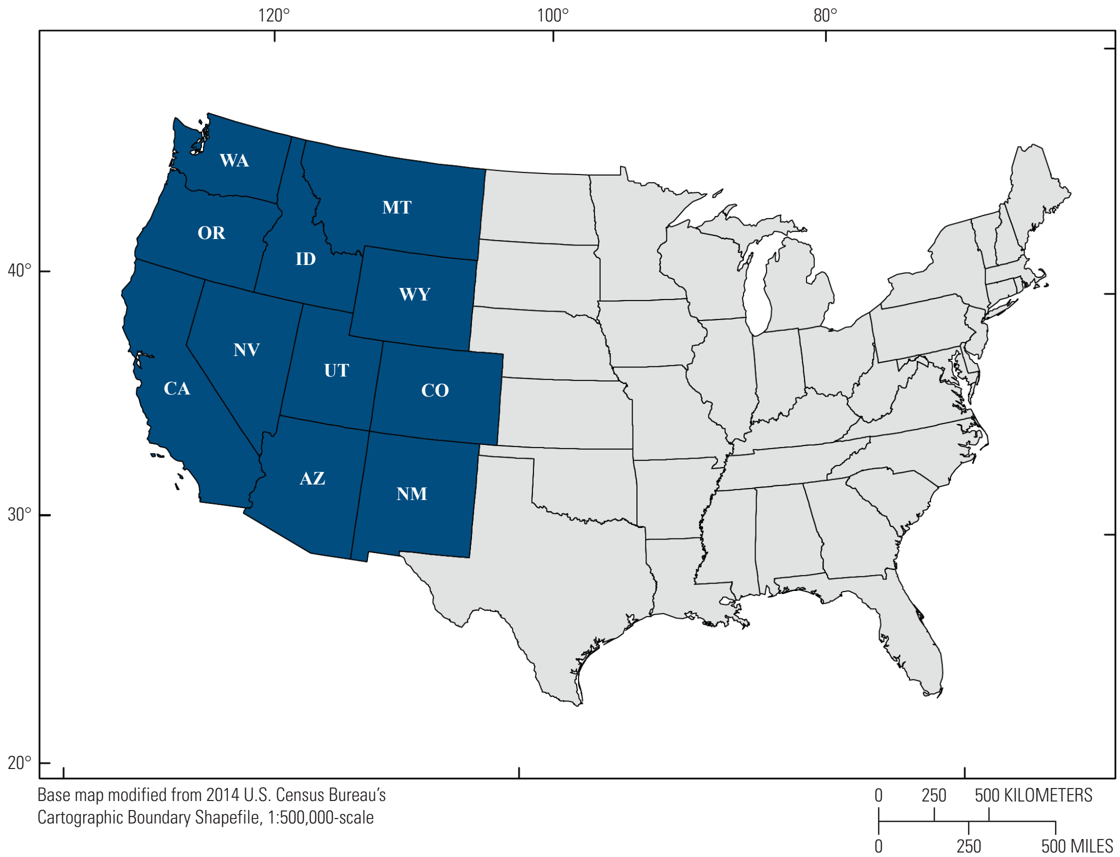

Figure 4. Map showing the 11 States included in U.S. Department of the Interior Secretarial Order 3362.

Table 1. Funding activities related to Department of the Interior Secretarial Order 3362.

Organization	Project	Effective date	Funding amount
Department of the Interior bureaus	Projects that address State-identified research priorities (maximum of $300,000 per State). Many States elected to spend this money on collaring activities.	October 2018	$2.8 million
National Fish and Wildlife Foundation in partnership with the U.S. Fish and Wildlife Service, the Bureau of Land Management, and the ConocoPhillips Company	"Improving Habitat Quality in Western Big-Game Winter Range and Migration Corridors." Projects that address State-identified research priorities	October 2018 (awarded in May 2019)	$2.65 million
U.S. Fish and Wildlife Service	Private land habitat projects, including fencing, invasive species control, and restoration projects.	March 2019	$1.5 million

U.S. Geological Survey Roles and Activities

Concerning science and research activities, SO3362 directs the USGS to work closely with States to develop maps and mapping tools related to ungulate movement or land use, evaluate the effectiveness of habitat treatments in the sagebrush ecosystem, and develop a greater understanding of the locations used by ungulates as winter range and migration corridors.

Corridor Mapping Team

One way in which the USGS responded to SO3362 was by supporting State-led corridor mapping efforts. Matt Kauffman, Wyoming Cooperative Fish and Wildlife Research Unit leader, set up the USGS-led Corridor Mapping Team based at the University of Wyoming, Wyoming Cooperative Fish and Wildlife Research Unit to provide technical assistance to States as they map ungulate migration corridors using Global Positioning System (GPS) collar data. Mapping the location of known corridors is the first step in understanding how to protect and sustain corridors. While many States have thousands of data points from GPS collars, synthesizing these data into corridor polygons is challenging.

The Corridor Mapping Team held workshops for State managers across the Western United States beginning in 2017, before SO3362 was signed, to help State wildlife agencies overcome this barrier. The workshops trained managers to use a free application, Migration Mapper, developed by the Wyoming Migration Initiative. The application applies the Brownian Bridge Movement Model, which measures the time animals spend in a defined area and their rate of movement, enabling the identification of stopover sites (areas where animals spend the most time and move slowly) and corridors (areas between stopover sites, through which animals move quickly) (Sawyer and others, 2009b). These workshops were hosted through a partnership among the Western Association of Fish and Wildlife Agencies (WAFWA) Mule Deer Working Group, the Sagebrush Science Initiative (a joint effort of the FWS and WAFWA), the U.S. Geological Survey, the Wyoming Migration Initiative, the Mule Deer Foundation, and The Pew Charitable Trusts. Through these workshops, 260 people from 13 Western States were trained.

In addition to workshops, the Corridor Mapping Team also assisted States in other ways:

- A full-time research scientist was hired at the Idaho Department of Fish and Game (IDFG) to analyze Idaho's movement data. This position is 50-percent funded by IDFG and 50-percent funded by the USGS.
- A full-time cooperative mule-deer biologist, based out of the Arizona Game and Fish Department (AGFD), was hired to work on connectivity corridor mapping and modeling for the State. This position is jointly funded by the Mule Deer Foundation, the USGS, and the AGFD.
- Work was done with Colorado Parks and Wildlife to develop an infographic primer on big-game migrations in Colorado that highlights key corridors, threats, and conservation actions in the State.
- Technical assistance was provided for analyzing movement data to assist the Utah Wildlife Migration Initiative, an effort initiated by the Utah Division of Wildlife Resources in 2017 to identify, preserve, and enhance essential movement corridors for terrestrial and aquatic wildlife species in the State.
- Analysis was provided for a half-dozen migration corridors and winter ranges for mule deer in Nevada to support the Nevada Department of Wildlife.
- Analysis was provided for several mule deer and pronghorn migration corridors prioritized by the Wyoming Game and Fish Department.
- A webinar was hosted and attended by approximately 70 State wildlife managers to provide troubleshooting tips for using the Migration Mapper application.
- New methods were developed to analyze corridors based on 12-hour GPS collar data, which many State wildlife agencies commonly collect.

U.S. Geological Survey Sagebrush Research

Department of the Interior Secretarial Order 3362 directs the USGS to "prioritize evaluations of the effectiveness of habitat treatments in sagebrush communities, as requested by States or land management bureaus, and identified needs related to developing a greater understanding of locations used as winter range or migration corridors" (U.S. Department of the Interior, 2018, sec. 4c). Many ungulate populations rely on intact sagebrush habitat for their winter range and migration routes (Copeland and others, 2014). Once encompassing up to 150 million acres, the sagebrush ecosystem currently faces a range of threats, including the spread of invasive species, overgrazing, altered fire regimes, climate change, and energy development (Thompson, 2007).

In fiscal year 2018, the USGS funded 111 projects related to sage-grouse and the sagebrush ecosystem that were carried out by the Ecosystems Mission Area, Land Resources Mission Area, and Energy and Minerals Mission Area. This research can be categorized into six topics: fire, invasive species, restoration, sagebrush, sage-grouse and sagebrush-associated species, and weather and climate (Hanser, 2018). In terms of sagebrush-obligate species, USGS research focused mainly on sage-grouse. However, much of the research on understanding changes to the sagebrush ecosystem and strategies for restoration and improving rangeland health could help inform ungulate management. Several of the many active, related projects are listed here:

- "Improving Local Scale and Resistance and Resilience Projections with Simulation of Soil Moisture Budgets in the Sagebrush Ecosystem" (Daniel Manier and Michael O'Donnell, USGS Fort Collins Science Center),
- "Assessing the Future of Sagebrush Ecosystems" (John Bradford, USGS Southwest Biological Science Center),
- "Response of Sagebrush Ecosystems to Precipitation Shifts" (Matthew Germino, USGS Forest and Rangeland Ecosystem Science Center),
- "Understanding Changes in Sagebrush Distribution and Abundance Under Climate Change" (Cameron Aldridge, Colorado State University, in cooperation with the USGS Fort Collins Science Center),
- "Evaluating Biodiversity of Sagebrush-Dependent Species Within Sage-Grouse Habitat" (Cameron Aldridge, Colorado State University, in cooperation with the USGS Fort Collins Science Center).

U.S. Geological Survey Ungulate Research

USGS scientists are also researching ungulate winter ranges, population dynamics, and migration patterns. These activities are relevant to SO3362 because they improve the understanding of ungulate population dynamics and movements. These activities are led by scientists from the Northern Rocky Mountain Science Center (NOROCK) and the Wyoming Cooperative Fish and Wildlife Research Unit. Projects include—

- "Predicting Future Forage Conditions for Elk and Mule Deer in Montana and Wyoming" (Tabitha Graves, NOROCK; North Central CASC-funded): The goal of this project is to (1) provide baseline information about the direction, degree, and certainty of change in the quality and timing of forage, and (2) develop maps of future forage based on scenarios that reflect the probabilities of important weather patterns, the distribution of cheatgrass, and the expected effects of planned habitat treatments. To date, researchers have assessed past forage conditions across the West, looking at 10 metrics of phenology and productivity, and they used the PhenoCam Network to ground-truth the results. Researchers are assessing whether there is alignment with the metrics for forage amounts (such as net primary productivity) to determine how useful these metrics are for forecasting. Researchers plan to use a scenario-planning approach to evaluate proposed habitat treatments that incorporates what is known about deer and elk response to productivity and forage.
- "Use of Sagebrush-Reduction Treatments by Mule Deer in Wyoming" (Aaron Johnston, NOROCK): The goal of this project is to assess the effects of habitat treatments on mule deer habitat-use and the habitat characteristics of migration corridors in southwest Wyoming for the Wyoming Landscape Conservation Initiative. This work may be expanded to include elk and pronghorn and might also include an assessment of the resilience of corridors to climate change to improve predictions of corridor locations over time.
- "Ecology of Elk on Department of the Interior Lands in Southwest Wyoming" (Tabitha Graves, NOROCK): Researchers are examining the relative influence that weather events, land cover, and phenology have on the location of calving areas and summer habitat-use in this sage-dominated system.
- "Assessing Drivers and Metrics of Density in Winter Range on the National Elk Refuge in Wyoming" (Tabitha Graves, NOROCK): Researchers are evaluating the relative roles of snow, temperature, hunting, and supplemental feeding on the National Elk Refuge. They are also assessing the best approaches for measuring local density and aggregation across GPS collar, satellite, and unmanned aerial system data-types. This project aims to give managers the tools for mitigating and adaptively managing the risk of diseases, including chronic wasting disease.
- "Identifying Ungulate Crossing Locations Along Highways in and Near Glacier National Park" (Tabitha Graves, NOROCK): Researchers are using multiple techniques to locate wildlife trails and identify the ungulates using them along U.S. Route 2 on the southern border of Glacier National Park in Montana and on Montana Highway 83 on the adjacent Blackfeet Indian Reservation. This project is part of a prioritization of highway mitigation efforts.
- "Impacts of Climate Change on Habitat Quality: Plant Phenology Interactions with Animal Use and Fitness" (NOROCK): Researchers are developing new methods to collect and analyze plant phenology data that can help managers understand the variability in habitat quality over space and time, to identify land-use and habitat treatments that maximize benefits and limit harm to wildlife and their habitat.
- "Phenology Tracking by Migratory Mule Deer" (Kevin Monteith and Matthew Kauffman, Wyoming Cooperative Fish and Wildlife Research Unit; funded in part by the USGS): Researchers are examining whether mule deer that accurately surf the green wave benefit from an enhanced nutritional condition and reproductive success. Researchers are also exploring how changing climate conditions, particularly drought, may alter habitat quality along migratory routes.
- "Ungulate Migrations of the Wind River Indian Reservation" (Wyoming Cooperative Fish and Wildlife Research Unit; funded in part by the USGS): The goal

of this project is to understand the location and use of migration corridors and stopover areas used by elk and mule deer on the Wind River Indian Reservation, and to examine herd demography and disease impacts.

- "Improving Connectivity Across Interstate–80: Pronghorn Movement Along a Statewide Barrier" (Benjamin Robb, Wyoming Cooperative Fish and Wildlife Research Unit; funded in part by the USGS): Researchers are working to identify optimal locations for restoring movement for pronghorn across Interstate–80 in southern Wyoming.

Management Priorities

In order to better understand current management priorities related to ungulate migration, the 11 State action plans developed in 2018 after the signing of SO3362 were reviewed. These plans identify key research priorities and threats facing priority migration corridors and range habitats. Informal discussions were also held with stakeholders in the region who represented State wildlife agencies, Federal land management agencies, and Federal scientists working on ungulate migration.

State Action Plans

Across all State action plans, acquiring better data on ungulate movement patterns through GPS collaring was listed as a priority. Data that can help States understand the location of winter range, summer range, corridors, and stopover sites, as well as how ungulates use these habitats, was a common theme. In many of the plans, these needs were identified for specific herds. Table 2 lists the research priorities identified by each State.

In each State action plan (see table 2 for the State action plan citations for each State), States identified three to five priority corridors or ranges and listed the risks and threats to each priority area. Many States identified similar threats and risks. All States identified either wildlife-vehicle collisions or transportation infrastructure as a threat. Different barriers to movement were identified as threats by almost every State. These barriers include fencing, transportation infrastructure, energy development, and irrigation infrastructure.

The threats can be grouped into 23 categories. Of these, 14 threats were identified by 2 or more States. Table 3 lists the categories of threats identified by two or more States.

The additional threat categories, which were identified by only one State, include barriers to movement (irrigation), insufficient understory, lack of early seral conditions, low genetic diversity, predation, recreation (type not specified), vegetation changes (not specified), and weather (not specified).

Arizona, California, and Washington each mention climate change in their State action plans (State of Arizona and U.S. Department of the Interior, 2018; State of California and U.S. Department of the Interior, 2018; State of Washington and U.S. Department of the Interior, 2018). Arizona mentions that an "altering climate regime" is responsible for shifts in vegetation and available resources, while the California plan states that addressing several of their outlined research needs will help understand "effects from climate change." The Washington plan identifies climate change as affecting the State's wildlife and biodiversity more broadly. The plan also identifies the need to prioritize habitat work to "protect climate refugia and buffer migratory corridor changes driven by climate" and identifies the need for "explicit [F]ederal support for global reduction in greenhouse gas emissions" (State of Washington and U.S. Department of the Interior, 2018). Protecting climate refugia and reducing greenhouse gases are listed as actions that should be taken in response to the increasing incidence of extreme weather events, such as drought and low winter snowpack, that reduce the nutritional carrying capacity of the landscape and the body condition of mule deer during migration periods.

Although climate change is not mentioned explicitly in the other plans, several of the threats identified by States are affected by changing climate conditions. These threats include drought, wildfire, habitat conversion due to invasive species, and pinyon-juniper encroachment. Understanding how the distribution, frequency, or severity of these threats might change is important for long-term planning.

Stakeholder Meetings

For this report, three State wildlife agencies in the Western United States, three Federal land management agencies (BLM, NPS, FWS), and three scientists from the USGS involved in ungulate-related research activities were consulted to assess information needs related to ungulate migration. Of the climate-related information needs identified by stakeholders, a common need was information that can help agencies prioritize the application of habitat treatments and restoration efforts. State agencies want to ensure that they are strategic in the use of limited resources. If information is available to help managers identify how different parts of the landscape may be altered by changing climate conditions, managers could more effectively place habitat treatments by focusing efforts on those areas. Understanding the resistance and resilience of the landscape first requires an understanding of how the landscape responded to past climate changes. Projections of wildfire activity, drought frequency and severity, invasive species distributions, and other climate-related stressors can then be incorporated to provide forward-looking assessments of how the landscape might change.

Additionally, the vulnerability of winter and summer ranges was of more interest than the vulnerability of migration-corridor habitat because of the influence of summer- and winter-range foraging on ungulate condition and reproductive success. State stakeholders were most interested in short-term outlooks of approximately 2–3 years than in long-term outlooks.

Climate Adaptation Science Center Role

The Climate Adaptation Science Centers (CASCs) were established in 2008 to help managers of the Nation's fish, wildlife, waters, and lands understand the impacts of climate change and adapt to changing conditions. The network comprises one national and nine regional centers covering the contiguous United States, Alaska, Hawaii, the U.S. Affiliated Pacific Islands, Puerto Rico, and the U.S. Virgin Islands. The CASCs strive to ensure that their science is strategic and actionable and meets the needs of the natural resource management community. As a result, the CASCs fund projects that address management-defined science needs and priorities. In a similar vein, SO3362 directs DOI agencies to partner with State wildlife agencies to accomplish State management objectives for ungulate winter range and migration corridors.

Our understanding of how ungulate migration could change either spatially or temporally because of changing climate conditions is rudimentary. For understanding future conditions, managers express concerns about how forage quality and quantity might change as a result of stressors such as drought, wildfire, and the spread of invasive species, or how they might need to alter current habitat-treatment strategies. Many States are still defining the locations of core ungulate corridors and seasonal ranges, and their current primary research need is to collect and analyze ungulate movement data. Better refinement of the boundaries of ungulate corridors and range habitats is the first step toward identifying changes in movement patterns and determining what defines typical versus atypical movements.

While these baseline ungulate movement data are still being collected and analyzed, it may be valuable for the CASCs to initiate one or more projects that work to identify past and potential changes and trends in variables that affect ungulates, including plant phenology, forage quality, and winter severity. However, it would be difficult to take this information to the next step and determine what those trends mean for ungulate migration at this time due to a lack of knowledge about environmental thresholds for ungulates. Therefore, an additional project would be required to compare multiple years of movement data with these key variables and start defining snow depth, cold-temperature, and other key thresholds. Ideally, this work would be carried out for numerous populations of elk, mule deer, and pronghorn to develop an understanding of these thresholds across species, populations, and geographies. This type of project could be carried out by the CASC network in partnership with other USGS programs currently invested in ungulate research—such as the Wyoming Cooperative Fish and Wildlife Research Unit, NOROCK, and Federal, tribal, and State agencies—that collect collaring data. Once these environmental thresholds are better defined, the next step would be to integrate this information with projections of crucial climate and ecological variables to forecast the likelihood that the migration routes or distances traveled could change.

A more immediate role for the CASC network is to synthesize the existing literature on ungulates to help determine the potential effects of climate change and more narrowly define knowledge gaps and future research directions. Although a review of the literature on ungulate migration was completed as part of this assessment, it was neither comprehensive nor truly systematic. This initial review focused on the academic literature and left out most gray and white literature, such as State agency reports, due to time constraints. Completing a comprehensive literature review that incorporates gray and white literature and follows standard protocols to ensure that all relevant studies are reviewed during the research process would be valuable. Several potential efforts—two synthesis papers and a workshop—are outlined here.

Potential Projects to Support Ungulate Migration Research

Synthesis Paper: Drivers of Ungulate Migration in the Western United States

- What: This paper could synthesize the state of the science on the ecological drivers of migration among elk, mule deer, and pronghorn in the Western United States.
- Why: Dozens of studies looked at migration drivers within elk, mule deer, and pronghorn populations. Each of these studies is population- and location-specific, and collating this information could help identify trends in migration drivers that span species and geographies. Understanding the range of factors influencing ungulate migratory movements is the first step toward understanding how climate change might affect the timing and spatial patterns of migration more broadly. Variables such as forage quality and quantity, snow conditions and temperature, predator avoidance, competition avoidance, and anthropogenic disturbances such as hunter access are all identified as influencing ungulate migration. To identify the potential impacts of climate change on migration, it is necessary to determine the extent to which migratory behavior is driven by variables controlled by, or sensitive to, climate conditions.

Table 2. Research priorities as defined in 11 State action plans.

State	Research Priorities	Citation
Arizona	● Collar mule deer to identify detailed movements and help better plan for accommodating movements of deer and other wildlife in consideration of the construction of Interstate 11. ● Evaluate how mule deer use the corridor after the installation of an overpass between the Santa Catalina Mountains and the Tortolita Mountains. ● Identify movement corridors for mule deer that summer on the San Francisco Peaks. ● Better understand the spatial and temporal distribution of mule deer in Game Management Units 1 and 27.	State of Arizona and U.S. Department of the Interior, 2018
California	● Produce the project implementation document for the Caltrans District 9 Wildlife Vehicle Collision Reduction Project. ● Collect high-resolution, long-term movement data for mule deer to identify high-use corridors and stopovers in the Sierra Nevada ecoregion. ● Collect long-term habitat use and movement data for elk in the northern California Coast ecoregion to identify locations for roadway modifications and encourage range expansion for elk, as appropriate. ● Analyze existing movement data for Tule Elk to assess barriers, habitat use, and population estimates.	State of California and U.S. Department of the Interior, 2018
Colorado	● Collect fine-scale telemetry data to understand changes in mule deer wintering distributions, the percentage of deer that migrate out of herd units, corridor use, the timing of migration relative to hunting seasons, and out-of-area winter ranges for the North Park mule deer herd. ● Collect fine-scale telemetry data to understand changes in mule deer and elk wintering distributions, the proportion of both species migrating to New Mexico, corridor use, the timing of migration relative to hunting seasons, and out-of-area winter ranges used by the San Juan Basin mule deer and elk herds.	State of Colorado and U.S. Department of the Interior, 2018
Idaho	● Statewide mapping of elk and mule deer winter ranges, movement routes, and stopover sites. ● Collar white-tailed deer, elk, and moose in northern Idaho between the Selkirk and Cabinet mountain ranges to better understand animal movements. ● Collar pronghorn populations lacking migratory information to estimate winter range, movement routes, and stopover sites.	State of Idaho and U.S. Department of the Interior, 2018
Montana	● Map seasonal ranges and migratory corridors of Madison Valley pronghorn. ● Identify gaps in statewide knowledge of pronghorn, elk, and mule deer seasonal core-use areas and migration corridors.	State of Montana and U.S. Department of the Interior, 2018
Nevada	● Map migration corridors and stopover sites for two pronghorn herds in northwestern and northeastern Nevada and quantify the amount of time spent in crucial winter habitats.	State of Nevada and U.S. Department of the Interior, 2018
New Mexico	● Collect data on mule deer, elk, and pronghorn seasonal movement pathways in north-central New Mexico, including the timing and magnitude of movements; if movements are weather dependent; and if distances moved, routes travelled, and stopover areas are consistent across years.	State of New Mexico and U.S. Department of the Interior, 2018
Oregon	● Collect movement data for pronghorn in southeastern Oregon to identify seasonal distribution and ranges, location and timing of migration corridors, and potential barriers to migration.	State of Oregon and U.S. Department of the Interior, 2018
Utah	● Map the Lake Mountains migration corridor in central Utah to define mule deer summer and winter ranges and migratory movements and corridors. ● Map corridors for the Zion mule deer herd. ● Collect data to understand movements and use of critical habitats in the Chalk Creek and Kamas units in northern Utah.	State of Utah and U.S. Department of the Interior, 2018

Table 2. Research priorities as defined in 11 State action plans.—Continued

State	Research Priorities	Citation
Washington	• Collect high-resolution, long-term movement data for mule deer in Chelan and Kittitas Counties in the East Slope Cascades to identify habitats and important land ownerships within the highest use corridors and stopover locations.	State of Washington and U.S. Department of the Interior, 2018
Wyoming	• Map corridors and identify barriers for the Carter Mountain pronghorn herd. • Understand movement patterns of the Powder River mule deer herd and the Pumpkin Buttes mule deer herd. • Additional analysis of pronghorn within the Sublette herd unit to identify migration corridors.	State of Wyoming and U.S. Department of the Interior, 2018

Table 3. Threats identified in two or more State action plans.

[Information was derived from State action plans. See table 2 for the State action plan citations for each State]

Threat	Number of States
Development and fragmentation	11
Wildlife-vehicle collisions	10
Barriers to movement (transportation infrastructure)	7
Barriers to movement (energy development)	7
Barriers to movement (fencing)	7
Habitat conversion (invasive species)	7
Pinyon-juniper encroachment	6
Increasing traffic	6
Wildfires	6
Drought	6
Recreation (off-road vehicles)	5
Disease	4
Noxious weeds	4
Overgrazing (feral horses)	4

Synthesis Paper: Climate Change Effects on Ungulates in the Western United States

- What: This paper could synthesize what is known about how climate change has already affected ungulates in the Western United States. The synthesis could include research on what is known about how climate influences individual life-histories, population dynamics, and migratory behavior. Expanding the review beyond elk, mule deer, and pronghorn to include other western ungulates, such as bighorn sheep, moose, and mountain goats, could be beneficial. Including additional ungulate species would help identify a broader spectrum of potential climate impacts and enable cross-species comparisons to determine which species appear vulnerable and which species may require more information for analysis.
- Why: Much of the existing literature on western ungulates and climate change focuses on how abundance, population growth, survival, and other population dynamics are affected, while few studies assessed the effects of climate on migration. The goal of the paper would be to identify the range of climate-related effects across ungulate species, populations, and geographies, and highlight knowledge gaps and clusters that can support management decision making and inform research directions.

Workshop: The Response of Big Game to Climate Change in the Western United States

- What: This project could convene a USGS–WAFWA sponsored working group and workshop to discuss what is known about how big-game herds have responded to climate change. Temperatures in the West have increased for 30 years. What changes have State wildlife managers noticed in ungulate demographics, behavior, forage conditions, and similar categories? What impacts are documented in the literature? This workshop could leverage the existing relationships that the Wyoming Migration Initiative, led by Matt Kauffman of the Wyoming Cooperative Fish and Wildlife Research Unit, has developed with big-game managers through their corridor mapping work.
- Why: The goal of this workshop would be to bring together all stakeholders—including big-game managers and scientists from Federal agencies and academia—to produce a baseline "state of the science" product on big-game responses to climate change. Additionally, the synthesis papers outlined in this section could help structure the workshop. Building this baseline knowledge of climate-change impacts on big game is important for developing effective, forward-looking projections that span a range of plausible future scenarios and help managers prepare for changes to ungulates and their habitat.

Conclusion

This initial assessment articulates the importance of ungulate range habitats; the drivers of seasonal migrations; the anthropogenic, non-climate-related threats facing ungulates; the potential effects of climate variability and change on ungulate population dynamics and migratory behavior; and a number of climate and non-climate-related ungulate management priorities. By examining the science on the drivers of migration and population productivity among elk, pronghorn, and mule deer, several pathways by which ungulate populations and migratory behavior might be affected by changing climate conditions were identified. The results of this effort suggest that more baseline data are needed before effective, forward-looking projections of future ungulate movements or population dynamics can be made at West-wide scales. These data needs include (1) clearly defined corridors and seasonal range habitats, on which the analyses of future changes could be focused; (2) a comprehensive understanding of ecological migration drivers across ungulate species and populations; and (3) the identification of environmental thresholds for key variables that influence migration, above which ungulates begin to alter their migratory behavior. Small-scale pilot projects focused on well-studied ungulate populations could also be initiated to develop methods for integrating information on climate trends, projected changes in migration drivers, and environmental thresholds to assess potential effects on migration.

Additional activities could build upon this initial assessment and better refine research needs. First, as part of the management-needs assessment, it would be ideal to meet with managers from all 11 States represented in Secretarial Order 3362. Although managers from three States were engaged as part of this assessment, meeting with managers from the remaining eight States would enable a more complete understanding of ungulate management research needs and priorities. Second, incorporating information on projected changes in land use and land cover, and information on how these changes could interact with shifting climate conditions to affect ungulate migration, is necessary. These actions would help define potential ungulate-migration response scenarios and guide the development of potential conservation strategies to manage ungulates in an uncertain future. Lastly, developing the literature review presented here into comprehensive, "state of the science" syntheses on the drivers of ungulate migration and the impacts of climate change on migration, population dynamics, and individual life-histories could provide the baseline information. This information is needed to identify science gaps and inform future research directions.

Climate changes occur across spatial and temporal scales, and the response of ungulate populations is not uniform and likely mediated by local processes and species-specific traits (DeVos and McKinney, 2007). Enhancing understanding of the potential effects of climate variability and change on ungulate population dynamics and migration, across species and geographies, could help managers prepare for changes to ungulates and their habitat. Incorporating this information with projections of changes in land use and land cover, and other key threats, such as barriers to movement, could guide comprehensive, forward-looking management planning for ungulates in the Western United States.

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