



Potential Impacts of Global Climate Change on Abundance and Distribution of Elk and Mule Deer in Western North America

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Executive Summary

Global climate change is a natural phenomenon and has occurred throughout Earth's history. Glaciation affected significant portions of the Earth's surface many times in the past, and the Pleistocene Ice Age in North America ended only about 12,000 years ago. Until about 10,000 years ago, extreme cold, low levels of carbon dioxide (CO_2), and great climatic variability persisted. Since the end of the Pleistocene Ice Age and especially in the last 200 years, atmospheric concentrations of greenhouse gases were the primary factors affecting global temperatures. Greenhouse gases are rare in the atmosphere. They trap heat from the sun near the Earth's surface and are key to maintaining thermal regulation of the planet. Carbon dioxide comprises up to 60% of the 30 greenhouse gases that exist. Scientists believe that atmospheric concentrations of CO_2 are important because of their role in both regulating the Earth's climate and contributing to global warming. Burning of fossil fuels by humans has greatly changed the concentration of key greenhouse gases and is thought to be the initiating factor of the current episode of rapid global warming.

Compared to between 10,000 and 20,000 years ago, the present rate of global warming has increased 30-fold. Since about 1950, global warming corresponds with widespread changes in distribution and trends of biotic communities. Included in these changes is the poleward shift of species distribution of about 4 miles per decade, a retreat upward on mountains of about 20 feet per decade, and earlier onset of spring activities by many species of plants and animals.

As global warming progresses, varied precipitation patterns, decreases in amount and duration of snowfall, and increases in weather extremes are expected to occur. Key biotic responses to these changes include expanded distribution of woody species, reduced nutritional quality of forages, increased frequency of stand-converting wildfires, and spread of invasive plants and insects. These changes and trends have increased in the past 150 years, resulting in different biotic communities and interactions between species. As global warming progresses, the extent of these changes and altered biological interactions will increase.

Elk and mule deer reached western North America by the end of the Pleistocene Ice Age and have been an important component of the native fauna for at least 10,000 years. In many areas these species are sympatric, but tend to segregate by selection of microhabitat features. Environmental variables such as climate, weather, structure, quantity and nutritional quality of vegetative communities, fire regimes, topography, and human activities influence habitat suitability for elk and mule deer. Under current climatic conditions, many mule deer and elk populations migrate from summer to winter ranges to avoid adverse deep snow conditions. Winter ranges are thought to be of particular importance to survival of elk and mule deer populations on ranges where high levels of snowfall occur. Adverse impacts to winter ranges in the short-term would likely diminish populations.

Although abundance and distribution of elk have increased since about 1950, abundance of mule deer has declined in the recent past, and distribution has remained stable. Differences in digestion efficiency between elk and mule deer—elk are better suited to utilize lower quality forages—contribute to these trends. In contrast, mule deer have a less diverse diet and are selective concentrate feeders that require higher quality forages. As global warming progresses, it is likely that forage quality will be adversely affected throughout elk and mule deer ranges because of the lower nutritional value of faster growing plants, and the higher concentrations of defensive chemicals such as phenols and tannins.

Considerable research indicates that large-scale climate influences dynamics of ungulate populations across North America, but effects vary and may be mediated by small-scale local processes. The best available science suggests that climate changes will not be uniform across North America. As a result, there will be ecoregional differences in the impact to mule deer and elk populations at both temporal and spatial scales. We expect the abundance and distribution of mule deer and elk in hotter and drier ecoregions to be adversely affected most as climate change progresses. Conversely, in ecoregions where extreme winters presently limit these populations in some years, short-term effects on abundance and distribution may be positive, but long-term effects are uncertain. It will be a challenge for some ungulate populations to adapt to the changing environment in locales where the rate of change is unprecedented in any interglacial period. It is incumbent on the natural resource community to become aware of the expected changes caused by global warming, inform the public about the consequences of global warming and its effect on wildlife populations, and develop and implement plans to ensure that habitat components critical to mule deer and elk survival remain a viable component of the biological communities and ecoregions of western North America as they have for 10,000 years.

Introduction

Extensive glaciers covered much of Earth's surface during most of the Pleistocene epoch, which extends throughout the past 2.4 million years (Flannery 2005). In North America, glaciers advanced southward from the North Pole to about mid-continent, reaching maximum extent about 18,000 years ago. Most land to the north of mid-continent was uninhabitable ice, and land to the south was drier and consisted of extensive desert regions. Glaciation affected significant portions of Earth many times in the remote past, but the Pleistocene Ice Age was one of the most intense, and ended only about 12,000 years ago (Ward and Brownlee 2003). The transition from the ice age to the warmth of today was not a gentle global change, as melting of glaciers varied in the northern and southern hemispheres. Until some 10,000 years ago, extreme cold, low levels of CO₂, and great climatic variability persisted (Flannery 2005).

Regulation of global temperature involves complex and delicate mechanisms. Temperature has averaged about 57 °F over the last 10,000 years since the Pleistocene Ice Age. Greenhouse gases, orbital variations of Earth around the sun, sun spots, and volcanic eruptions can affect global thermal balance, but atmospheric concentrations of greenhouse gases are the primary factors affecting global temperatures since the end of the Pleistocene Ice Age, and particu-

larly over the past 200 years. Greenhouse gases are rare in the atmosphere; they trap heat from the sun near the Earth's surface, and are key factors in maintaining thermal balance of the planet. Carbon dioxide (CO₂) comprises up to 60% of the 30 greenhouse gases; atmospheric concentrations of CO₂ thus are used by scientists to index average global temperature. Importantly, concentrations of CO₂ act as a trigger for effects of water vapor, another potent greenhouse gas. Carbon dioxide heats the atmosphere, allowing it to take up and retain more moisture, which then further warms the atmosphere. This creates a feedback loop which forces the planet's temperature higher or lower with increased or decreased levels of CO₂, respectively. Thus, CO₂ and water vapor form a primary feedback loop which warms the atmosphere as CO₂ concentrations increase (Weart 2003).

Prior to the Industrial Revolution of the 1800s, concentration of CO₂ in the atmosphere was 280 parts per million (ppm); concentration today is 380 ppm. The present rate of global warming is 30 times faster than the rate that occurred between 10,000 and 20,000 years ago. Since the 1970s, average global surface temperatures have increased each decade (Hansen et al. 2006). Scientists predict that increasing atmospheric CO₂ concentrations could increase average global temperature by 3 °F to 8 °F by the end of the 21st century. Human activities, including land use practices and burning of fossil fuels and other biomass, are primary factors contributing to increasing atmospheric concentrations of greenhouse gases and the present global warming trend and climate changes. Plants absorb CO₂ during photosynthesis and have absorbed about half of all carbon emitted by humans since 1800, when life on land began adding carbon to the atmosphere. About 55% of CO₂ released from various sources is absorbed again by oceans, forest regrowth, and increased plant growth (Lomborg 2001, Ward and Brownlee 2003, Flannery 2005).

As temperatures warmed since the last ice age, different tree species in North America advanced northwards at average rates of about 330 to 1,312 feet per year (Davis 1981). Scientists have found that global warming—especially since about 1950—corresponds with some widespread trends in distributions and ecology of animals and plants. There has been a poleward shift of species distributions of about 4 miles per decade, a retreat upward on mountains of about 20 feet per decade, and earlier onset—more than 2 days per decade—of spring activities of many plant and animal species. These trends correspond strongly with the scale and distribution of warming trends resulting from increased human-related emissions of greenhouse gases (Flannery 2005).

Other changes associated with increasing atmospheric CO₂ concentrations and global warming are apparent, as well. Higher concentrations of CO₂ increase plant

growth, however, increased atmospheric levels of CO₂ benefit growth of trees more than shrubs, and benefit grasses least of all. Increased CO₂ concentrations of the gas in some locations are leading to replacement of slower-growing species by faster-growing plants, thus altering community composition. Plants consumed by herbivores are growing faster, but tend to have lower nutritional value and higher concentrations of defensive chemicals such as phenols and tannins. Scientists estimate that as many as one-third of animal and plant species may become extinct if the average global temperature increases more than 3.6 °F. In summary, atmospheric concentrations of CO₂ and global warming have increased in recent years primarily because of human-related combustion of organic fuel sources. Changes in global climate comprise disturbances that are affecting ecological communities (Jones et al. 1998, Inouye et al. 2000, Prichard et al. 2000, Sillett et al. 2000, Schulze et al. 2002, Flannery 2005, Barbraud and Weimerskirch 2006).

Fossil records indicate that elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*; includes black-tailed deer, a subspecies

of mule deer) reached western North America by the end of the Pleistocene Ice Age or earlier (Dawson 1967, Kurtén and Anderson 1980, Bryant and Maser 1982, Harris 1987, Geist 1998). Thus, the natural history of elk and mule deer in western North America essentially developed during the interglacial period (Holocene) following the



Pleistocene Ice Age. Documented changes and trends in atmospheric concentrations of greenhouse gases and global temperatures potentially influence forage resources and abundance and distribution of elk and mule deer in western North America. Our objective is to examine changes that have occurred and are projected to occur in atmospheric concentrations of CO₂, temperature, and climate in western North America. We will attempt to discern possible implications of these changes during the 21st century in relation to

future environmental conditions, and abundance and distributions of elk, mule deer, and other selected big game species.

We elected to examine mule deer and elk as species that are widespread and occupy many ecoregions, and are the two most socially and economically important big game species in western North America (deVos et al. 2003). Both of these ungulate species are sensitive to environmental conditions (Mule Deer Working Group 2003). Climate change is projected to result in changes that will likely have both adverse and beneficial effects on habitat conditions in many ecoregions where these species occur. Mule deer in desert regions would be adversely affected by diminished food resources (Mule Deer Working Group 2003) caused by increased drought periods that are projected to occur in the future (IPCC 2007). Conversely, decreases in snowfall projected by the Intergovernmental Panel on Climate Change (Lemke et al. 2007) would have a positive effect on both mule deer and elk in ecoregions where these species die during periods of extreme snowfall. Developing an understanding of the role that climate change will have on distribution and population trends for these important species will help managers to develop proactive strategies to sustain healthy elk and mule deer herds in the face of andropogenic-caused climate change.

Regulation of Global Climate

Pathways of CO₂ cycling in global ecology have been known for decades, but many discoveries of how Earth works as a system were made in the last few decades (Odum 1971, Schulze et al. 2002, Ward and Brownlee 2003, Flannery 2005). Carbon dioxide enters the atmosphere from volcanic eruptions, weathering of rocks and soils, the oceans, decomposition of animals and plants, respiration of animals, and respiration and combustion of fossil fuels by mankind. Carbon dioxide from the atmosphere and oceans enters bacteria and plants in seas and on land. Carbon dioxide from organic decomposition and respiration reenters the carbon cycle. Earth has maintained average temperatures cool enough to support life by storing high amounts of CO₂ in “reservoirs” of forests, rocks, soil, and oceans.

The CO₂ cycle thus is intimately linked among pathways, and has maintained a relatively stable average global temperature over millions of years. As an example of this stability, in the 10,000 years prior to 1750, CO₂ concentrations remained at about 280 ppm (Indermühle et al. 1999). Only in the 20th and 21st centuries has Earth’s average temperature apparently begun to increase as humans contribute increasing amounts of CO₂ from combustion of fossil fuels and agricultural practices that today are contributing to a

global warming trend. Most trees in America's forests are less than 60 years old. Young plants in the northern hemisphere helped cool the atmosphere for a few decades by absorbing excess CO₂ as forests and shrublands recovered from burning and clearing for development and agricultural purposes. As forests and shrublands mature, they extract less CO₂ than younger stands. The ocean, the only major carbon sink on our planet, may be absorbing decreasing amounts of CO₂ derived from human sources (Flannery 2005).

Variations in solar radiation and concentrations of greenhouse gases affect Earth's climate, but in fundamentally different ways. The Earth's atmosphere consists of 4 distinct layers, based on levels and gradients of temperature. The troposphere extends from Earth's surface to about 7 miles above and contains 80% of atmospheric gases. The bottom third of the atmosphere is the only part that is breathable, contains half of all atmospheric gases, and is warmest at its lowest level. The atmosphere is comprised primarily of nitrogen (78%), oxygen (20.9%), and argon (0.9%); these gases comprise 99.5% of the air we breathe (Flannery 2005). The stratosphere extends about 30 miles above the troposphere, and temperature increases toward its highest level. Solar radiation warms the upper level of the stratosphere, whereas greenhouse gases warm mainly the bottom of the troposphere, where their concentrations are greatest (Bradley et al. 2003, Flannery 2005).

Carbon dioxide emitted into the atmosphere remains there for at least a century (Flannery 2005). Atmospheric concentrations of CO₂ presently are rising only about 0.5% per year, but even if we are able to halt this rise, atmospheric concentrations of the gas probably will not decline substantially for more than 700 years (Schulze et al. 2002). Continued emissions of CO₂ thus increase concentrations of the gas, and effects of reduced atmospheric emissions in lowering levels of CO₂ have a very long lag time. About 56% of all CO₂ liberated by burning fossil fuels is still in the atmosphere, which directly and indirectly accounts for about 80% of all global warming (Kump 2002). No factor contributes more to the uncertainty of predicting future changes in climate than water vapor, which forms clouds, and reflects light energy and traps heat (Flannery 2005).

Global Climate Change

The Interglacial Period

The last interglacial period, the Holocene period in which we now live, began about 10,000 years ago. Transition from the Pleistocene Ice Age to the warmth of today was comparatively rapid and characterized by wide temperature fluctuations. Climatologists estimate

that during this interglacial period, the surface of the Earth warmed by 9 °F, the fastest rise in recent history (Flannery 2005). Ice core data from 400,000 years of Earth's history suggest the Holocene is the longest warm and stable interglacial period. However, scientists have attempted to construct a global temperature series only for the northern hemisphere and only during the last millennium. Essentially, these data suggest a weak declining temperature trend between 1000 and 1900, possibly reflecting a trend towards a new ice age, despite rapidly increasing temperatures in the 20th century.

Temperatures prior to 1900 were much colder than now; average global temperature from 1860 to 2000 increased less than 1 °F, and increased primarily after about 1910 (Lomborg 2001). Mean global temperature now appears to be increasing at a rate of up to 6 °F per 100 years, 30 times faster than at the end of the previous interglacial period. Atmospheric concentrations of CO₂ are greater than in the past 600,000 years. The rate of global warming likely is a key factor affecting responses of animals and plants to increased temperatures. If efforts to stem global warming are ineffective, temperatures might rise about 5 °F during the 21st century (Lutgens and Tarbuck 2004).

Glacial cycle patterns of CO₂ concentrations in the atmosphere are well documented by scientists. Levels generally rise rapidly as a glacial stage ends and slowly decline toward the next cold period. Atmospheric concentrations of CO₂ over the past 8,000-year interglacial period increased from about 160 ppm to 280 ppm by the start of the Industrial Revolution in about 1800. Until recently, atmospheric concentrations never exceeded 280 ppm, but are currently 380 ppm. During the decade of the 1990s, average CO₂ concentrations increased about 1.8 ppm per year; levels increased 2.5 ppm per year between 2000 and 2003. Some suggest CO₂ levels might reach 550 ppm by 2100 if emissions from human sources are not reduced (Flannery 2005).

Causes of Global Climate Change

Explanation for apparent global warming and climate change is based on the greenhouse effect, i.e., the role greenhouse gases play in affecting climate and average global temperatures. Carbon dioxide comprises 60% of greenhouse gases. The IPCC (2007) indicates that CO₂ is the most important greenhouse gas in the regulation of global climate, and may become even more important in the future. In addition, both methane and nitrous oxide have increased markedly as a result of human activities since 1750, and now far exceed pre-industrial values determined from ice cores spanning thousands of years. Humans have increased concentrations of greenhouse gases, particularly

CO₂ in the atmosphere. About 80% of the extra CO₂ in the atmosphere comes from combustion of coal, natural gas, and oil, and 20% derives from deforestation and other land changes in the tropics (Lomborg 2001).

Fossil fuels, coal, gas, and oil, are the remains of organisms that lived many millions of years ago. Burning them releases carbon previously excluded for eons from the CO₂ cycle (Flannery 2005). About 55% of released CO₂ is absorbed by oceans, regrowth of northern forests, and the growth of plants that use the gas in production of biomass. Remaining CO₂ is added to the atmosphere, where concentrations have increased about 31% from the pre-industrial era to the present time. Scientists agree that the current century is warmer than previous centuries (Lomborg 2001). Increasing concentrations of CO₂ in the atmosphere have led most scientists to conclude that global warming has occurred in recent years, particularly since about 1900 (Lomborg 2001, Ward and Brownlee 2003). There is no doubt that mankind has influenced and continues to increase atmospheric concentrations of CO₂, and that this influences global climate and temperature (Lomborg 2001, Ward and Brownlee 2003, Flannery 2005).

Evolution of Animals and Plants

Animals and plants evolved initially in the oceans. The earliest animals evolved about 700 million years ago, and the earliest plants emerged about 200 million years later. Plants and animals emerged on land about 400 to 450 million years ago, and plants preceded animals on land by several million years (Capra 1996). Without plants and their pathways of photosynthesis, life today would be much different. Development of oxygenic photosynthesis was the singular event leading to our modern environment (Margulis and Sagan 1995). Plants use CO₂ in photosynthesis, return it to the environment through decomposition of organic matter, and produce oxygen as a waste product. Oxygen produced by plants is concentrated in the lower troposphere, allowing existence of plants and animals. If not for plants and algae, animals would suffocate in CO₂ (Flannery 2005).

In the aggregate, the factors that determine a region's climate determine the biological distributions and patterns that influence seasonal patterns such as reproductive activities of many organisms (Gates 1993). Of climate factors, precipitation and temperature, and the interaction between these factors, limit biodiversity and distribution of animals and plants, and rising global temperatures potentially affect evolution and extinction (Ward and Brownlee 2003, Lovejoy and Hannah 2005). Although global warming is projected to increase average precipitation (Lomborg 2001, Flannery 2005), local and regional changes in precipitation are diffi-

cult to predict. Each degree of global warming might result in a 1% increase in average rainfall, but this increase will not be distributed evenly over Earth's surface; some areas will become wetter, but other areas will become drier. Moreover, the average amount of snowfall has declined over the past half century, as global warming progressed. Snowpacks in some areas may melt earlier and decline by half or more as global warming leads to hotter summers (Flannery 2005). Global dimming due to atmospheric pollution of particulate matter may have masked effects of global warming over the past few decades by reducing energy input from the sun by as much as 30% (Lomborg 2001, Tudge 2006).

Over the past 540 million years, mean global temperature has been as cold as 41 °F and as hot as 77 °F, neither of which imperiled existence of animals and plants (Ward and Brownlee 2003). Average surface temperature of the Earth has been about 57 °F for the last 10,000 years. Rising temperature potentially affects animals and plants. For example, about 14,000 years ago—just prior to the Holocene—deciduous forests that now grow in areas of southern Canada occurred only in northern Florida (Flannery 2005). If mean global temperature were to exceed 100 °F, the planet would begin to die at the equator, and multicellular life would have to emigrate toward the poles (Ward and Brownlee 2003). Predicted changes in global climate likely will cause large shifts in geographic ranges of many animal and plant species in the western hemisphere, but various models differ in their predictions (Lawler et al. 2006).

A rise in average temperature of about 11 °F could shift climate zones 500 miles toward either pole (Ward and Brownlee 2003). Global warming already has caused northward and upslope movements by animals and plants in some areas (Flannery 2005, Lovejoy and Hanna 2005). No pattern of change was apparent before 1950, but since then a global pattern has emerged indicating a shift in distribution of many species poleward about 4 miles per decade, a retreat up mountainsides of 20 feet per decade, and an earlier onset of spring activity in plants and animals of 2.3 days per decade. These trends correspond strongly with the scale and direction of temperature increases resulting from emissions of greenhouse gases (Parmesan and Yohe 2003). Throughout the globe, increased concentrations of atmospheric CO₂ correspond to changes in distribution (including migration) of species such as butterflies, seasonality of plant reproduction, and reproductive patterns of birds and moths (Flannery 2005, Lovejoy and Hanna 2005).

Photosynthesis does not occur below a critical CO₂ level of about 10 ppm, and reaches maximum levels between 350 and 550 ppm CO₂, depending on species (Ward and Brownlee 2003). Photosynthesis increases with rising temperatures to about 95 °F, and declines at higher temperatures (Schulze et al. 2002). Climate changes associated with

global warming trends and increased atmospheric concentrations of CO₂ threaten accelerated losses of animal and plant biodiversity that are already occurring due to other human-related stressors (Lovejoy and Hannah 2005). In remote rainforests, increased concentrations of atmospheric CO₂ have led to fast-growing species crowding out slower growing species, diminishing forest biodiversity (Flannery 2005). These patterns of change have implications for abundance and distribution of plants and animals (Lovejoy and Hannah 2005), including elk and mule deer in North America.

Global Warming and Vegetation

There is a strong association between plant communities and climate. A rapid warming of global climate could result in extensive reorganization of natural communities (Graham and Grimm 1990). Changes in vegetative communities have been observed as a result of increased greenhouse gases including CO₂, changes in precipitation and snowfall patterns, increased temperatures, and interactions between these and other factors (Davis 1981, Davis and Zabinski 1992). Although climate change has influenced the distribution and composition of plant communities, it is important to note that there are a number of other factors that make full understanding of the role of climate change on plant communities difficult. Two key factors that influence the quality of mule deer and elk habitat are long-term fire suppression and over-utilization by domestic livestock (Lutz et al. 2003). Accidental introduction of invasive weed species such as cheatgrass (*Bromus tectorum*) in the late 1800s has also changed western rangelands. Cheatgrass was first found in Washington in 1883 (Warg 1938), but has spread through much of the American West (Lutz et al. 2003). This and other weed species are expanding relatively quickly and pose a serious threat to biodiversity (Schwartz 1992). Climate-induced changes could begin to expose native plant communities to invasive weed species (Peters 1992).

In spite of varied causes for vegetative changes, it is clear that a warmer planet generates more evaporation, rain, and wind (Ward and Brownlee 2003, Flannery 2005). Climatologists have warned that no region is safe from the possibility of megadrought as global warming progresses (Lovejoy and Hannah 2005). A trend toward developing semi-persistent El Niño-like and La Niña-like conditions may, in part, explain this apparent discrepancy. Oscillations in sea surface temperatures along the equator in the Pacific Ocean give rise to El Niño and La Niña conditions. The western tropical Pacific Ocean, a great regulator of weather, has warmed as global warming progressed. This ocean

controls most tropical precipitation and position of the jet stream, whose winds bring rain and snow to North America. El Niños are a major climate force that seem to originate in the central Pacific Ocean, and can cause droughts, floods, wetter winters, and other extreme weather events. El Niño influences rainfall and temperatures over land, and increases incidence of wildfires, which result in more emissions of CO₂. In contrast, below-average precipitation is experienced during La Niña winters. Global warming may be contributing to development of semi-permanent El Niño-like conditions and trends (Flannery 2005, Lovejoy and Hannah 2005, Crimmins 2006).

Since 1976, persistent El Niño-like conditions have brought less winter rainfall to northwestern North America; winter in southern Alaska now is 4 °F to 5 °F warmer than 30 years ago. Present climate conditions in the American



A stand of cheatgrass that resulted from a 2001 wildfire, showing the skeletons of dead sagebrush plants that will not resprout due to the lack of moisture at this elevation. By Mike Cox.

West also suggest a relationship between warmer temperatures, rainfall and snowfall, and drought. Near record rainfall in the Southwest in 2005 was insufficient to make up for preceding dry years, and northwestern states are experiencing unprecedented drought. Much water in the Southwest comes from winter snowfall that accumulates in high mountain ranges, and average snowfall in that region has declined over the last 50 years. During this time, the Southwest has warmed by 1.4 °F, reducing snowpacks (Flannery 2005).

Arid ecosystems are believed to be among the most responsive to elevated concentrations of atmospheric CO₂ (Jason et al. 2005). Climate change associated with increased atmospheric CO₂ concentrations, increased temperatures, and variability in precipitation contribute to changes in distribution of desert regions and increased woody plant invasion in the Southwest (Brown et al. 1997, Weiss and Overpeck 2005). Warming throughout the western United States

has contributed to more winter precipitation falling as rain rather than snow, and earlier seasonal snowmelt (Knowles et al. 2006).

Growth of plants depends on their capacity to incorporate atmospheric carbon (CO_2 is a primary substrate; nitrogen and phosphorus also are involved in photosynthesis) through absorption of light energy during photosynthesis. Photosynthesis increases with increasing atmospheric concentrations of CO_2 and with temperature, resulting in increased growth of plants. Most plants in desert and temperate woodlands function at about half of maximum rates of photosynthesis. Plants reach maximum photosynthesis between about 350 and 550 ppm atmospheric CO_2 , depending on differences in mechanisms of photosynthesis. Photosynthesis levels off at higher concentrations of CO_2 . Regardless of CO_2 concentrations, maximum photosynthesis tends to occur between about 85 °F and 115 °F, and declines rapidly at higher temperatures (Mooney 1986, Schulze et al. 2002).

Plants evolved different pathways of photosynthesis— C_3 plants use 3 carbon atoms and C_4 species use 4 carbon atoms. This pathway of photosynthesis developed as an adaptation to low concentrations of CO_2 in the atmosphere. Plants that use C_4 photosynthesis tend to dominate under conditions of high temperatures and low CO_2 concentrations. C_3 plants are competitively superior to C_4 plants under conditions of increasing CO_2 atmospheric concentrations and increasing temperatures. The vast majority (> 95%) of vascular plants on Earth are C_3 plants. Higher concentrations of atmospheric CO_2 favor development of woody C_3 species such as pine (*Pinus* spp.), fir (*Pseudotsuga* and *Abies* spp.), hardwoods, and shrubs, and increase their dominance over C_4 species.

In the American West, woody shrubs and trees use the C_3 photosynthetic pathway, whereas many dominant grasses possess the C_4 pathway, and their photosynthetic processes are stimulated little by increased CO_2 . Although elevated CO_2 levels reduce nutritional quality of C_3 grasses more than that of C_4 grasses, nutritional quality of C_3 grasses remains higher under conditions of increased atmospheric CO_2 (Barbehenn et al. 2004). Increased temperature and atmospheric levels of CO_2 in the American West are projected to correspond with increased precipitation during winter/spring and decreased precipitation during summer. This will contribute to a competitive advantage of C_3 shrubs and trees over C_4 grasses and accelerate invasion of grasslands and shrublands by woody plants. However, establishment and growth of grass and shrub seedlings on semi-arid rangelands may be affected little by projected climate changes (Schulze et al. 2002, Perkins and Owens 2003, Howery 2006, Koch 2006). Despite this report, studies have projected that rare plant species may be at great risk

to declines or extinctions due to climate change (Davis and Shaw 2001, Parmesan and Yohe 2003). Climate change can alter the distribution and abundance of widespread species such as pinyon pine (*P. edulis*). A 7-year drought in northern Arizona has caused up to 70% mortality in some pinyon pine populations (Ogle et al. 2000). Furthermore, a study conducted in central Arizona evaluated the extinction risk to an endemic species, Arizona cliffrose (*Purshia subintegra*). Maschinski et al. (2006) documented increased mortality to Arizona cliffrose seedlings with increased aridity and temperatures and projected that these conditions, if unabated, likely would result in extinction of this species.

Herbaceous plants that use C_4 photosynthesis tend to predominate in subtropical and tropical grasslands; C_4 shrubs are common in desert and saline regions. Photosynthesis incorporating C_4 metabolism is a relatively recent evolutionary variation, and occurs most often in herbaceous species, occasionally in woody shrubs, and almost never in trees. Worldwide, about half of all grass species use the C_4 pathway (Hattersly 1992), and grasses occupy nearly every environment including alpine, Arctic, tropical, wet marshes, and dry deserts (McClaran 1995). Within desert grasslands, C_4 plants have greater photosynthetic capacity at higher temperatures and use water more efficiently than plants that use the C_3 pathway. The proportion of C_4 grass species is higher in desert grasslands than in all other North American grasslands, and more than 95% of grass production in desert grasslands is from species using the C_4 pathway (McClaran and Devender 1995).

In North American grasslands, C_3 grasses are active during spring, whereas C_4 grasses predominate during the hotter summer months (Mooney 1986). Production of C_4 grasses is reduced during drought, but the grasses are drought resistant (Fernández and Reynolds 2000). More than 95% of grass production in desert grassland habitats involves species that use C_4 photosynthesis; the proportion of C_4 species is higher than in all other North American grasslands (Sims et al. 1978, French 1979). Maximum photosynthesis is reached at about 550 ppm and 350 ppm CO_2 for C_3 and C_4 species, respectively, and photosynthesis levels off at higher concentrations (Schulze et al. 2002). Photosynthetic systems incorporating C_3 and C_4 mechanisms continue to function from 95 °F to 104 °F and from 113 °F to 140 °F, respectively (Crawley 1986). Photosynthesis is affected by leaf concentrations of nitrogen and phosphorus, and available nitrogen might limit response of plants to elevated concentrations of CO_2 (Schulze et al. 2002, Johnson et al. 2006).

A final category of photosynthesis involves crassulacean acid metabolism (CAM), which occurs in some desert plants. These species, such as agave (*Agave* spp.) and cacti, grow slowly and are adapted to hot, dry regions. Many

of the species can switch from CAM to C_3 photosynthesis (Mooney 1986, Schulze et al. 2002). Elevated atmospheric concentrations of CO_2 increase efficiency of water use (more photosynthesis per unit of water used), but water balance is strongly affected by climate (Tjoelker et al. 1998, Anonymous 2006, Koch 2006). Water-use efficiency is highest in CAM species, but growth and photosynthesis of these plants is slower than for C_3 and C_4 species; water-use efficiency is higher for C_4 than for C_3 plants (Schulze et al. 2002). Plants that are resistant to desiccation may be among beneficiaries of increased atmospheric concentrations of CO_2 (Tuba et al. 1998). Increased frequency, severity, and variability of drought conditions in the western United States may occur due to climate changes, and spatially heterogeneous climate changes likely will have dramatic impacts (Diffenbaugh et al. 2005). Trees increase water-use efficiency in response to elevated CO_2 , and scientists project that elevated atmospheric concentrations of CO_2 will lead to expansion in distribution of woody plant species throughout the American West (U. S. Forest Service 2004, Anonymous 2006, Koch 2006). Trees and shrubs may increase and grasses decrease in transition zones between forests and grasslands as global warming progresses (Polley 1997).

Plants that use C_3 pathways are usually competitively superior to C_4 plants under conditions of higher atmospheric CO_2 concentrations and higher temperatures, and conifers are competitively superior to deciduous species (Schulze et al. 2002, Howery 2006, Koch 2006). Despite potentially positive effects of increased CO_2 concentrations on abundance and biomass production of C_3 species, abundance and distribution of coniferous and other forests in the American West likely will shrink and move poleward and upslope due to higher mean temperatures and drought (Parmesan and Yohe 2003). Computer models predict an increase in mean global temperature as high as 1 °F per decade, an increase that could shift climate zones 35 to 50 miles northward. Forests likely can move northward only about 5 miles per decade, but will leave behind dead and dying trees. Shrubby woodlands may replace forests as they advance poleward. In comparison, distribution of most tree species in North America shifted poleward at a rate of only 5 to 25 miles per

century as climate warmed more slowly at the end of the Pleistocene Ice Age (Wilson 2002).

Forests and woodlands occupy about 444 million acres in western North America (Lutz et al. 2003). Coniferous and mixed conifer forests composed of species such as ponderosa pine (*Pinus ponderosa*), fir, spruce (*Picea* spp.) and other species in western North America occur generally between 5,600 and 10,000 feet elevation, and precipitation ranges from 18 to 20 inches per year (Brown 1994). Ponderosa pines and spruce may live more than 300 and 500 years, respectively, and age and structures of these forests tend to stabilize as trees reach about 120 and 220 years of age, respectively (Knowles and Grant 1983). Densities of younger



Removal of juniper and reestablishment of sage-steppe habitat on slope in southern Oregon. By George Buckner.

trees have increased in ponderosa pine forests since about 1900, corresponding with fire suppression regimes (Crockner-Bedford et al. 2003, Cunningham et al. 2003, deVos and McKinney 2003).

In comparison to the projected northward advance of forests with warming trends, juniper (*Juniperus* spp.) and pinyon pine woodlands have expanded distribution and increased in density since the late 1800s, and these woodlands presently are distributed extensively in western North America (Tausch et al. 1981; Miller and Wigand 1994; Miller and Rose 1995, 1999; West 1999; Lutz et al. 2003). Many pinyon pine and junipers live 600 and 1,000 years, respectively, and pinyon and juniper trees in 60% to 90% of some areas are less than 130 years old (Lutz et al. 2003).

Pinyon-juniper woodlands presently occur between about 3,500 to 8,800 feet elevation, and are one of the most

extensive vegetative types in the North American Southwest. These woodlands extend southward through Colorado, Utah, Nevada, California, Arizona, New Mexico and into Mexico. Precipitation in pinyon-juniper woodlands ranges from about 10 to 20 inches per year (Brown 1994). Expansion of these woodlands probably has been facilitated by multiple factors, including climate change, fire suppression, livestock grazing, and human modifications (Jameson 1987, Lutz et al. 2003). During the late Pleistocene Ice Age, pinyon-juniper woodlands occurred on sites that currently are occupied by desert scrub vegetation (Betancourt 1987).

Sagebrush (*Artemisia* spp.) occurs on about 91 million acres in the western United States, and distribution has not changed much during the last century, although human intervention has been a primary factor affecting sagebrush and associated mountain shrub communities (Lutz et al. 2003). These communities generally occur at elevations of about 4,000 to 9,000 feet, and annual precipitation ranges from 15 to 22 inches, but in some regions is less than 10 inches (Brown 1994). Livestock grazing and suppression of fires have been key factors contributing to broad changes in communities of sagebrush and shrubs. These communities continue to become less productive, and plants continue to become less vigorous resulting in reduced suitability of many winter ranges used by mule deer and elk (Lutz et al. 2003).

Stand-converting wildfire (fires that are hotter and more extensive) activity in the western United States increased suddenly and dramatically in the mid-1980s, with higher frequency and longer duration of fires and longer fire seasons, particularly in mid-elevation forests in the western United States (Brown et al. 2004; Westerling et al. 2003, 2006). These findings and others (Simard et al. 1985, Swetnam and Betancourt 1990, Jones et al. 1999, Amiro et al. 2003, Peterson nd) suggest global climate change will increase frequency and severity of wildfires.

Non-native annual plants, such as cheatgrass, are invading throughout the Intermountain West, causing a widespread transition from perennial sagebrush communities to fire-prone annual herbaceous communities and grasslands (Prater et al. 2006). Regardless, some research suggested that climate changes in the western United States will result in increased growth and range expansion of sagebrush near northern or high-elevation range boundaries (Perfors et al. 2003). Dry stalks of cheatgrass increase the frequency of fire, and *Artemisia* is not fire-tolerant (Schulze et al. 2002). Higher atmospheric concentrations of CO₂ may have contributed significantly to cheatgrass productivity and fuel load, potentially affecting frequency and intensity of fire (Ziska et al. 2006). Recent studies suggest sagebrush communities burn less often than forests and may require 35 to more than 100 years to recover after fire (Baker 2006). In some burned

pinyon-juniper sites invaded by cheatgrass, tree cover remained minimal 60 years after fire (Lutz et al. 2003). Cheatgrass has invaded throughout the American West in desert shrub communities, sagebrush zones, pinyon-juniper woodlands, and some ponderosa pine and Douglas fir (*Pseudotsuga menziesii*) zones, increasing frequency and intensity of wildfires, and destroying native shrublands important to elk and mule deer for food and cover. However, prescribed burning in Montana transformed sagebrush-dominated communities into native herbaceous communities that persisted for 15 years without sagebrush re-invasion. Compared to unburned habitat, forage production and protein content and use of burned areas by elk increased and remained higher during the 15-year period (Dyke and Darragh 2006).

In contrast to negative effects of fire, quaking aspen (*Populus tremuloides*) typically is a successional species in the American West, dependent primarily on fire for regeneration (DeByle and Winokur 1985). Quaking aspen has the widest distribution of any North American tree (Tudge 2006), but aspen communities today occur in old-age stands (the trees rarely survive more than 100 to 125 years) that are fewer in number due largely to fire suppression. Elevated levels of atmospheric CO₂ likely will enhance photosynthetic rates, growth, and water-use efficiencies of quaking aspen seedlings (Tjoelker et al. 1998). Thus, warming trends and increased wildfires in western North America potentially benefit aspen production and distribution if fires do not burn in a fashion that would alter the woodland to a shrubland. However, effects of elevated atmospheric CO₂ concentrations in enhancing growth of aspen in forest ecosystems may decline over years if occurrence of cloudy summers and cool autumns increases. Moreover, concentrations of ozone under some conditions may offset or prevent positive effects of higher levels of atmospheric CO₂ on aspen growth (Kubiske et al. 2006).

Aspens presently occupy up to 6.9 million acres in western North America, and are commonly found from 6,000 to 10,000 feet elevation. Quaking aspen occur in many forest types, and provide nutritious forage, thermoregulatory hiding cover, and critical parturition habitat for mule deer and elk (Armentrout et al. 1997, Beck et al. 1997, Lutz et al. 2003). Overbrowsing by ungulates might be a factor contributing to decline of aspen in some areas (Kay 1997). Compared to coniferous forests, understory of shrubs and herbaceous species is much more abundant in aspen stands (Gruell and Loope 1974).

Major shrub and desert regions occur in the American West below the sagebrush zone, and include chaparral, Mohave Desert, Chihuahuan Desert, and Sonoran Desert scrub vegetation types. Chaparral vegetation occurs at elevations of about 160 to 9,000 feet in California, and 3,600 to 6,500 feet in Arizona. These regions have 12 to 30 inches of

annual precipitation. The desert scrub regions occur below 3,600 feet elevation, and annual precipitation ranges from less than 2 inches to 10 inches in Mojave and Sonoran deserts, and from about 8 to 12 inches in the Chihuahuan Desert (Brown 1994). Distribution of mule deer, but not elk, includes chaparral and desert regions.

Projected Climate and Vegetation Changes

Scientists have documented the link between atmospheric concentrations of greenhouse gases and global temperature trends (IPCC 2007), and are confident in the utility of modeling to characterize future climate at a continental level. They predict global surface temperatures could increase an average of 1.6 °F to 6.3 °F by 2100. However, regional climate changes and responses of vegetation could vary significantly, and warming in the United States is projected to be greater than the global average (Breshears et al. 2005, Diffenbaugh et al. 2005). Calculations of global climate change are more reliable than projections of regional climate changes. However, Christensen et al. (2007) predict several changes will occur in North America, including varied precipitation, decreased amount and duration of snow presence, and increases in temperature. These authors predict that the American South and Southwest and northern Mexico will become drier as the remainder of the continent experiences increased precipitation.

Responses of plant communities to environmental differences and change are exceedingly complex and difficult to predict (Schulze et al. 2002). Effects of increasing CO₂ concentrations and associated plant mechanisms are well documented and understood (Tjoelker et al. 1998, Tuba et al. 1998, Lloyd 1999, Norby et al. 2005, Johnson et al. 2006, Sherwood and Idso 2006*a*), but regional variability of other factors influence growth of plants. It is well known that precipitation affects vegetation. Drought conditions negatively affect soil moisture and availability of water to plants, increase evaporation, and reduce primary production. Soil texture, topography, type of vegetative cover, and elevation influence soil moisture, and plant species vary in response to changing conditions (Noy-Meir 1973, Halvorson and Patten 1974, Salve and Allen-Diaz 2001). Both C₃ and C₄ plant species may be affected by drought (Kemp 1983), but herbaceous and woody species can differ in responses to variability in climate and weather (Post and Stenseth 1999). Distribution of conifer forests and other forests in western North America presently varies with elevation, slope aspect, and precipitation (Brown 1994).

Although projected climate changes indicate increased global precipitation, regional patterns of precipitation and occurrence of extreme hot and cold events likely will be altered as global warming progresses (Perkins and

Owens 2003, Brown et al. 2004, Diffenbaugh et al. 2006). Projections of regional changes in precipitation thus vary. Some models suggest western North America likely will experience wetter winters and drier, warmer summers throughout the 21st century (Perkins and Owens 2003, U. S. Forest Service 2004). Boreal forests extend over more than one-third of Canada (Tudge 2006). The forests in much of western Canada are experiencing less precipitation and warmer temperatures (Flannigan et al. 1998, Stocks et al. 1998, Flannigan et al. 2001). The area burned by wildfires in western North America's boreal forests has doubled during the past 20 years (Chapin et al. 2000, Amiro et al. 2003).

In Idaho and Wyoming, precipitation might tend to increase during this century in spring and autumn (10%) and winter (20–30%), and decrease during summer (0–10%), and temperatures might increase 4 °F to 6 °F during all seasons (Environmental Protection Agency 1998*a,b*). Global warming in western North America potentially contributes to increased frequencies of both wet and dry conditions in various areas (Diffenbaugh et al. 2006). Some projections show increased frequency and severity of drought as warming progresses (Breshears et al. 2005, Westerling et al. 2006), and others project patterns of relative humidity that indicate general drying of some areas of the American West during the 21st century (Brown et al. 2004).

Predicted climate changes are likely to exert a strong influence on biodiversity of forests and other vegetation communities in western North America. However, potential changes in habitats of plant species and communities in western North America can vary locally and regionally. Results of modeling indicate ponderosa pine and arid hardwood communities will expand in distribution. Habitats for dominant rain forest conifers will decrease west of the Cascade Range, but may expand into mountain ranges throughout the interior American West. Habitats for some subalpine conifers may contract substantially. Potential habitat for big sagebrush (*A. tridentata*) is expected to shift largely from the United States into Canada, and may be replaced in the American West by potential habitat for shrubs such as creosote bush (*Larrea tridentata*), which now occurs only in the Southwest. Ranges of many plant taxa in western North America will shift northward and upslope, but topographic complexity will result in shifting of some conifer species associated with wetter conditions south and east in the Rocky Mountains (Hansen and Dale 2001). Aspen communities may increase as conifers decline in the southern limits of Canada's boreal forest (Hogg and Hurdle 1995).

Predicting changes in climate is difficult because complex feedback loops influence global warming and concentrations of atmospheric CO₂, and affect local and regional weather, and distribution, structure, and composition of communities of animals and plants. For example, every

portion of the Earth's surface has characteristic albedo, the degree to which it reflects solar radiation. Ice and snowpacks reflect more radiation and heat than bare ground or rock surfaces, and melting of ice and snowpacks will result in increased warming of Earth's surfaces. Cloud cover, in contrast, may increase as temperatures and evaporation increase, and tend to cool surface temperatures.

Plants grow faster in a CO₂-enriched atmosphere (Norby et al. 2005). Fast-growing plant species in rain forests are growing faster in response to increased levels of CO₂ and are crowding out slower growing species. Although plants used by herbivores are growing faster, their leaves are less nutritious due to inadequate available nutrients. In plants grown experimentally with enrichment of CO₂, nutritional value is reduced, leaves are tougher, and concentrations of phenolics and tannins that potentially interfere with digestion may be higher, making them a much poorer food source (Mansfield et al. 1999, Flannery 2005, Zvereva and Kozlov 2006). High concentrations of CO₂ might lower forage quality by reducing tissue nitrogen concentrations up to 30% (Koch 2006, Zvereva and Kozlov 2006). Elevated concentrations of atmospheric CO₂ under natural conditions reduce nutritional value of most herbaceous species more than for most woody species (Nowak et al. 2004).

Other Sources of Human Disturbance

Human land use practices, including fire suppression and grazing by domestic livestock, historically have contributed to expansion of shrubs in habitats used by elk and mule deer, a pattern that is likely to continue (McClaran and Devender 1995, Lindzey et al. 1997, Carpenter 1998, Lutz et al. 2003). Cattle range over about 70% of federal lands in western United States (McKibben 1989), and land use practices interact with regional effects of increasing ambient temperatures and levels of atmospheric CO₂ on shrub encroachment. Development of croplands, forests, and other open spaces has reduced habitats for elk and mule deer by millions of acres in western states during recent years (Lutz et al. 2003).

Ozone is an atmospheric gas that occurs at very low concentrations (about 0.001% of atmospheric gases), but absorbs ultraviolet radiation and in the process emits heat; concentrations are 6-fold higher in the stratosphere than at sea level (Flannery 2005). Concentrations in the troposphere increase with high levels of solar radiation and high air temperatures. Ozone near the Earth's surface today is considered to be a toxic trace gas responsible for declines in forest growth. At high concentrations, ozone reduces uptake of CO₂ by plants, and may predispose them to greater exposure to ultraviolet radiation, nutrient deficiency, water shortage, and attack by pathogens (Schulze et al. 2002). The

primary source of ozone near the Earth's surface is gasoline engines in the vehicles humans drive.

Methane (CH₄) is a trace atmospheric gas (1.5 to 1.7 ppm) that absorbs radiation and traps heat as much as 30 times as effectively as CO₂, and thus influences climate. Atmospheric methane concentrations have increased at about 1% per year, have doubled over the past few hundred years, and have paralleled but likely are rising faster than concentrations of CO₂. Methane in the atmosphere is produced primarily by anthropogenic factors such as burning of biomass, animal husbandry (mainly cattle, but all animals produce the gas), garbage dumps, and rice production. Globally, domestic livestock and rice production might release nearly 200 million tons of methane each year into the atmosphere. Methane might cause about 15% to 17% of global warming in this century (McKibben 1989, Asimov and Pohl 1991, Schulze et al. 2002, Flannery 2005).

Nitrous oxide (NO₂) is rarer than methane in the atmosphere, but is 270 times more effective than CO₂ at trapping heat, and lasts 150 years in the atmosphere. Anthropogenically-produced oxidized nitrogen in the atmosphere also potentially influences global warming, and comes from sources such as burning processes, production of reduced nitrogen (NH₃) from domestic animals, sewage systems, and industrial production of ammonia (Schulze et al. 2002, Flannery 2005). Although the world's forests assimilate atmospheric CO₂ and potentially lower concentrations of the greenhouse gas, this effect is reduced by extensive deforestation practices. During the late 1980s, for example, about 25 million acres per year of forests in the Pacific Northwest and more than 2,500 acres per day in Brazilian rain forests were being logged (Asimov and Pohl 1991). Annual global reforestation during this period added about 1 to 2.5 billion tons of carbon to the atmosphere, or about 20% of the amount produced by burning fossil fuels (McKibben 1989). Atmospheric concentrations of CO₂, methane, and NO₂ today are at the highest levels recorded for the past 400,000 years (Wilson 2002), and various greenhouse gases combined, exclusive of CO₂, might account for half of projected global warming (McKibben 1989). Recent studies suggested that emissions of non-CO₂ greenhouse gases have declined during the past decade, possibly reducing the danger of dramatic climate change (Hansen et al. 2000).

Effects of Global Warming in Western North America

Vegetation

Recent computer simulation models project that dramatic changes in vegetation communities will likely occur throughout western North America dur-

ing the 21st century (Hansen and Dale 2001, Rapp 2004). Climate changes may manifest themselves in forests as increased growth and changes in disturbance regimes—long-term patterns of fire, drought, insects, and diseases that influence forest development. Compared to current climate, the western United States, excepting the Southwest, likely will experience wetter winters and warmer summers (Christensen et al. 2007), corresponding with expanded growth of woody plant species. Precipitation is expected to increase, primarily during the traditional October to April wet season, and summers will be hotter and longer than the current climate. Slow migration of forests will occur northward and upslope. Drier forests such as juniper and ponderosa pine likely will expand, junipers will spread into grasslands and ponderosa pine forests, and abundance of understory plants will increase in ponderosa pine forests. Low elevation forests in the interior American West that now are limited by aridity could expand into grasslands as precipitation increases. Sagebrush ecosystems may shift largely from the United States into Canada. Sagebrush areas of the intermountain West likely will be replaced by many types of forests or woodlands. In the Pacific Northwest, broadleaf components likely will increase in coniferous forests. Many deserts in Arizona and New Mexico will likely expand.

Production of forests increases with higher concentrations of atmospheric CO₂ (Norby et al. 2005, Sherwood and Idso 2006*a,b*). Increases in CO₂ will likely benefit trees more than production of shrubs and grasses (Lloyd 1999, Shaw et al. 2002, Flannery 2005, Norby et al. 2005). However, forests may have limited response of growth to increased CO₂ levels where soils are poor or prolonged water limitation occurs (Norby et al. 2005). Although increased atmospheric CO₂ levels stimulate above- and below-ground plant biomass, availability of soil nutrients may influence growth responses (De Graaff et al. 2006). Climate models indicate wetter winters and warmer summers will occur throughout western North America in future decades, but drought conditions are likely to increase in the region. Fine-scale variability of factors such as natural land cover, human land use, and topography will influence changes in extreme precipitation and temperature events (Rapp 2004, Diffenbaugh et al. 2005, Flannery 2005).

Drought conditions in some areas likely will tend to offset expansion of woody plants, and contribute to die-offs or reduced production of overstory woody species such as juniper (*J. monosperma*), pinyon pine, and ponderosa pine in western North America (Ogle et al. 2000, Law et al. 2001, Breshears et al. 2005). Conditions of drought and high temperatures may result in 2% to 26% mortality of relatively drought tolerant junipers, and more than 50% reduction of some grasses. Mortalities of more than 90% of conifers such as pinyon pine across tree age and size classes were

associated with drought, high temperatures, infestations by bark beetles (*Ips confusus*), and plant water stress (Breshears et al. 2005). Warmer temperatures will increase development, distribution, survival, and abundance of insect herbivores (Volney and Fleming 2000, Bale et al. 2002), which could be an important factor as plant species become stressed by increased aridity and decreased precipitation.

Warming trends are widespread in the Sonoran Desert, leading to warmer winters and springs, higher minimum temperatures, decreasing frequency of freezing temperatures, and lengthening of the freeze-free season. These trends may result in constriction of the Sonoran Desert's southeastern boundary, and expansion of the desert eastward, northward, and upward in elevation, coincident with changes in distribution of plant species. Potential trajectories of vegetation change are difficult due to uncertain variability of warm season precipitation and fire (Weiss and Overpeck 2005). Increased interannual rainfall variability in dryland regions likely reduces grass cover and potentially leads to increased vulnerability of drylands to more frequent, longer lasting degradation (Williams and Albertson 2006).

Impacts of Climate Change on Mule Deer and Elk

Both mule deer and elk occur throughout most of western North America. Mule deer occupy most regions from Alaska, in Canada west of Alberta, and south into northern Mexico (Mule Deer Working Group 2003, Heffelfinger 2006). Elk are distributed in many of the same regions as mule deer, but occur in a more patchy distribution. Vegetation communities characteristic of mule deer ranges in western North America have been categorized into 7 broad zones, or ecoregions (Heffelfinger et al. 2003).

Climate, weather, and projected patterns of global warming affect vegetation communities and ungulate populations. Characteristics of each of the ecoregions summarized below influence abundance and distributions of elk and mule deer (Lindzey et al. 1997).

1) *California Woodland Chaparral* predominates on the Coastal Range of southern California and at lower elevations on the western slope of the Sierra Nevada. Interior chaparral is a modification of this vegetation type that extends eastward from California into much of the area from northwestern to southeastern Arizona (Swank 1958). Climate is Mediterranean, characterized by hot, dry summers and wetter winters with periodic droughts. Vegetation is largely oak (*Quercus* spp.) woodlands and various aridland shrubs and trees interspersed with forb/grass understory. Average rainfall varies from 8 to 30 inches, with most falling between November and April. Mule deer have been declining in this ecoregion during recent decades.

ECOREGIONS

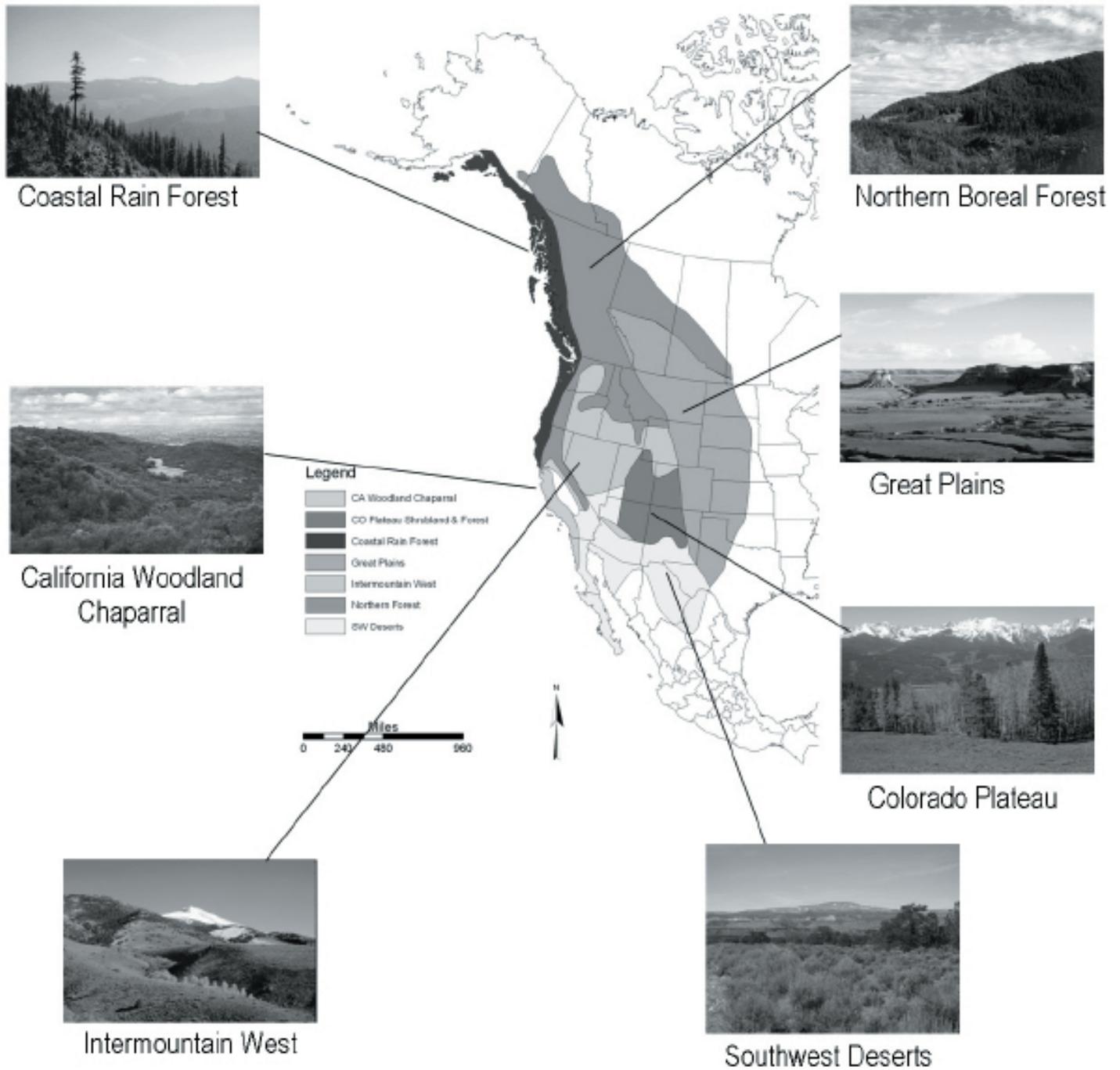


Figure 1. Biologists have identified seven mule deer ecoregions in western North America.

2) *Coastal Rain Forest* occurs along the west coast from northern California through southwestern Alaska. The marine climate is characterized by short, dry summers, with higher precipitation during autumn to spring. Dominant overstory vegetation is tall, dense-canopy coniferous forest that includes western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*) in wetter areas, and Douglas fir in drier areas. Productivity and recruitment of mule deer populations, which are non-migratory, has declined in this ecoregion during recent years.

3) *Colorado Plateau Shrubland and Forest* occurs mainly at elevations near or above 5,000 feet encompassing western Colorado, eastern Utah, southern Wyoming, and northern parts of Arizona and New Mexico. The ecoregion has great diversity of local climates and weather due to high variation in topographic relief, but typically experiences long, cold winters and short summers. Precipitation occurs relatively evenly throughout the year. Vegetation types vary considerably, including sagebrush, pinyon-juniper woodlands, mountain shrubs, montane forest, and subalpine forest. Common species in forested areas are ponderosa pine, Douglas fir, blue and Englemann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and quaking aspen.

4) *Great Plains* ecosystem consists of mixed and shortgrass prairies, and extends from central Manitoba, Saskatchewan, and Alberta, Canada south to the Texas panhandle and west to the Rocky Mountains. The ecoregion is semi-arid, with occasional volatile fluctuations in temperature during all seasons. Rough, steeply sloping areas and shrub/hardwood draws are common. Forage availability and quality can become critical for mule deer in the ecoregion during drought and heavy snowfall.

5) *Intermountain West* consists of various mountain ranges and valleys west of the Rocky Mountains, east of the Sierra Nevada, and south of the Canadian border. Most of the annual precipitation occurs as snow in northernmost portions of the ecoregion and at higher elevations. Pinyon-juniper woodlands, conifer forests, and aspen woodlands are common on summer ranges at higher elevations and on plateaus. Total amount and quality of summer ranges are key factors affecting abundance and productivity of mule deer populations. Deep snows in winter can present a problem for mule deer, which are migratory in the ecoregion, moving in winter to areas where saltbush (*Atriplex* spp.), greasewood (*Sarcobatus vermiculatus*), and sagebrush predominate on lower elevation ranges.

6) *Northern Boreal Forest* ecoregion includes northern Idaho and Washington, western portions of Montana

and Wyoming, high elevations of the Cascade and Sierra Nevada ranges in Washington, Oregon, and California, and extends northward through the Canadian provinces. Vegetation in this mountainous region varies with terrain aspect and elevation; at higher elevations pine, fir, spruce, Douglas fir, and larch (*Larix* spp.) are interspersed with aspen, riparian areas, and meadows. Productivity of mule deer populations is low in this ecoregion, particularly during droughts or severe winters. Average temperatures vary widely with elevation and topography, and precipitation ranges from 10 inches in valleys to 120 inches in alpine zones. Winters typically are long and cold, with snow accumulations up to more than 100 inches at higher elevations. Most mule deer populations are migratory, follow the retreating snow line in spring, and experience high productivity and potential for rapid growth.

7) *Southwest Deserts* extend through southern portions of Arizona, California, New Mexico, and western Texas. Annual precipitation is highly variable and ranges from 5 to 20 inches; summer storms produce most of the annual moisture in southeastern areas of the region, but rainfall in more northern and western areas is more balanced between seasons. Snow is uncommon, and the non-migratory mule deer populations depend on production of forbs in spring associated with rainfall between October and March.

Of these ecoregions, the Colorado Plateau, Northern Boreal Forest, and the Intermountain West have migratory mule deer and elk herds that are reliant, in part, on suitable winter range conditions. The remaining ecoregions may also have local conditions where migratory mule deer and elk herds occur, but this is generally less prevalent than in the colder, northern ecoregions. The Mule Deer Working Group (2003) and Heffelfinger et al. (2003) indicate that habitat quality in winter range was a concern within the ecoregions with migratory herds and that improvements to winter range would enable higher mule deer populations in these ecoregions. Conversely, if winter range continues to decline in quality as a result of climate change and other factors and the consequential change in species composition and forage quality, both mule deer and elk, but primarily mule deer, will remain at levels below that which resource managers prefer. Winter range throughout western North America is comprised primarily of relatively small, fragmented patches (Mule Deer Working Group 2005). As vegetative communities move northward and upslope, this key resource will become even more fragmented, resulting in negative impacts on mule deer and elk populations where winter range is a crucial habitat component.

Being able to meet their metabolic demands for life processes such as reproduction, survival, and migration is essential to both mule deer and elk. It is important that

these demands are met during all seasons of the year, particularly in winter when both mule deer and elk concentrate to avoid adverse environmental conditions that occur on summer range (Mule Deer Working Group 2003). Several of the ecoregions occupied by mule deer and elk are at some stage of dysfunction—improvements to winter range is a key management action. Mule deer are considered to be selective, concentrate feeders (Hofmann 1985), and although their diet varies greatly throughout their distribution, their productivity is linked with the ability to find and consume high quality foods that contain highly digestible nutrients. Typically, these types of foods are found in early successional or disturbed areas where new growth plant parts from browse species or newly-emergent forb species are readily available to support metabolic demands for mule deer (Wakeling and Bender 2003). In contrast, elk are considered

to be an intermediate feeder, able to utilize a wider array of forages to meet their metabolic demands. Elk consume food sources with concentrated nutritional quality, as well as food sources that are higher in cellulose such as grasses and older-growth form plant parts (Wakeling and Bender 2003).

Over the past century, mule deer populations have fluctuated widely, however, recent trends indicate there are less mule deer in many regions of the American West. Although the causes for this decline are varied, much of the decline can be attributed to direct habitat loss—particularly on the winter range—deteriorating forage base, and weather extremes including large-scale droughts and severe winters (Heffelfinger and Messmer 2003).

The Mule Deer Working Group (2005) has mapped all of North America where mule deer occur and has clas-



Figure 2. Mule deer winter range (shaded) in the western United States.



A group of mule deer bedded in deep snow in Colorado. Critical loss of mule deer winter range is negatively affecting mule deer populations. By Len Carpenter.

sified two types of winter range. Winter range is defined as the part of the overall range where 90% of the individuals are located during the average 5 winters out of 10 from the first heavy snowfall to spring green-up, or during a site-specific period of winter. A subset of this definition includes “severe winter range”—areas within the winter range where 90% of the individuals are located when annual snow pack is at its maximum and/or temperatures are at a minimum in the 2 worst winters out of 10. This habitat includes that part of the winter range where densities are at least 200% greater than the surrounding winter range density during the same period used to define winter range in the average 5 winters out of 10. In addition to identifying and mapping habitat classifications where mule deer are found, factors that limited habitat quality for mule deer were recorded.

Elk and mule deer are sympatric within many ecoregions, and distribution of mule deer presently overlaps that of elk. Elk do not inhabit California Woodland Chaparral and Southwest Desert ecoregions. Recent studies suggest that abundance and distribution of elk have increased since about 1950. In comparison, abundance of mule deer has varied widely in the last century and has declined in most regions of the American West since the mid-1990s, however there has been little change in distribution (Mule Deer Working Group 2003). Within areas where they are sympatric, habitats occupied by elk and mule deer often overlap, but the species tend to select different habitat features. Elk tend to use more gentle slopes and forest openings away from roads, whereas mule deer use more rugged, steeper terrain, and areas nearer to roads. Mule deer may tend to avoid microhabitats occupied by elk. Elk seem to select habitats for foraging based on forage biomass, whereas mule deer likely select habitats more randomly for feeding. Use of microhabitats is diverse for both species, but elk often oc-

cupy and use more diverse areas and resources than mule deer during both summer and winter. Biologists often have suspected that elk and mule deer compete for resources, but there is little evidence to support this conclusion (Lindzey et al. 1997, Keegan and Wakeling 2003).

If competition occurs between the species, it likely is most severe on winter ranges, where browse is a major diet component for both species and where the amount or quality of the winter range is limited, a common condition in much of the shared winter range (Mule Deer Working Group 2003). Environmental variables such as climate, weather, structure, quantity and nutritional quality of vegetation

communities, fire, topography, and human activities potentially influence suitability of habitats for elk and mule deer. Climate and weather are key variables influencing habitat conditions and dynamics of elk and mule deer populations; these variables and vegetation communities differ widely throughout regional ranges occupied by the species (Adams 1982, Nelson and Leege 1982, Skovlin 1982, Heffelfinger et al. 2003).

Mule deer abundance and home range size, population trajectory, and abundance of forages in the Southwest Desert ecoregion are linked positively to patterns and levels of rainfall (Smith and LeCount 1979; Relyea et al. 2000; Marshal et al. 2002, 2005). Elk populations also are affected by weather patterns and habitat conditions, but they are less sensitive than mule deer to these variables (Lindzey et al. 1997, Keegan and Wakeling 2003).

Previous studies of wildlife responses to climate change in North America have focused on species other than elk and mule deer (Schneider and Root 2001). Elk in western North America occur throughout most of the area inhabited by mule deer. Where they are sympatric, elk and mule deer occupy many of the same habitats, but the species tend to segregate by habitat features within areas of distribution overlap. Recent studies in Oregon suggested mule deer avoided areas used by elk. Elk selected more gentle slopes, westerly aspects, and areas farther from roads, whereas mule deer selected steeper slopes, easterly aspects, and areas closer to roads (Johnson et al. 2000). Elk populations have increased in western North America during the past few decades, whereas populations of mule deer generally have declined concurrent with increased abundance of elk (Lindzey et al. 1997, Keegan and Wakeling 2003).

Selection of diets and digestive morphology indi-

cate that elk and mule deer utilize foods differently. Mule deer are adapted to exploit shrub habitats with low forage biomass in which plant parts provide readily digestible, high quality nutrition. Elk are better adapted to less digestible forage in herbaceous or mixed vegetation communities with high forage biomass. Elk digest grasses better than mule deer, and thus do well on predominantly grass diets. Mule deer do poorly on grasses and require higher quality forages. Elk diets usually are dominated by grasses and lesser quantities of browse and forbs, whereas mule deer consume predominantly browse and forbs (Lindzey et al. 1997). Diets of elk contained predominantly shrubs and trees in pinyon-juniper habitat in a southern area of the Colorado Plateau Shrubland and Forest ecoregion (Howard and Mangold 1998). Elk usually eat a greater variety of plant species than do mule deer, but composition and nutritional quality of their diets can overlap considerably. Consumption of the same forages does not necessarily denote competition for resources, but failure to document competition between species does not verify its absence (Nelson 1982, Leslie et al. 1984, Lindzey et al. 1997, Heffelfinger et al. 2003, Keegan and Wakeling 2003).

Elk tend to eat a greater variety of plant species and are better adapted to high-volume roughage diets compared to mule deer. Mule deer consume plant parts more selectively than do elk and are restricted to more highly nutritious diets. If elevated levels of atmospheric CO₂ increase concentrations of secondary plant compounds that potentially inhibit digestion, forage digestion by mule deer likely



Deep snows on winter range increase competition between mule deer and elk .

would be inhibited more than elk (Baker and Hansen 1985, Lindzey et al. 1997, Keegan and Wakeling 2003). Elevated concentrations of atmospheric ozone also might increase concentrations of secondary plant compounds from 8% and 16% (Valkama et al. 2007). Reductions in herbaceous and shrub productivity and senescence of browse are asso-

ciated with declining abundance of mule deer in the American West during recent decades (Germaine et al. 2004), whereas abundance of elk increased as these changes occurred. We suggest differential trends in abundance of elk and mule deer reflect, at least in part, greater capability of elk than mule deer to utilize more diverse and poorer forage resources.

In colder regions, sympatric elk and mule deer populations usually migrate seasonally between higher elevation summer ranges and lower elevation winter ranges, often occupying mid-elevation transitional ranges. Winter ranges are thought to be of particular importance to elk and mule deer populations where high levels of snowfall during winter restrict movements, foraging, and forage availability and quality. Lower snowfall is projected to occur in much of western North America. These regional climate changes reduce the importance of traditional winter ranges for both elk and mule deer. Global warming patterns are projected to lead to loss of sagebrush winter ranges over much of the American West. Coupled with increasing pinyon-juniper communities, the quality of these habitats that are broadly used as winter range by elk and mule deer will lessen (Lutz et al. 2003). Poor understory growth of herbaceous species characteristic of pinyon-juniper habitats potentially favors elk over mule deer. Elk and mule deer populations in more southern regions of the American West often inhabit mountains and mesas year-round on rugged terrain with mixed pinyon-juniper forests and intermittent but extensive grasslands and shrubs.

In Rocky Mountain National Park, winter ranges of elk and deer are delineated by distribution of shallow snow accumulation that allows foraging in winter. Simulations suggest snow reduction accumulations of 25% to 40%. Computer simulations indicated warmer temperatures and elevated atmospheric concentrations of CO₂ will result in less snowfall and increased vegetation biomass in the region. Projections indicated that higher average minimum winter temperatures increased recruitment of juvenile elk, whereas increased precipitation during summer enhanced survival of calves. Warmer winters and wetter summers could double equilibrium sizes of elk populations, but if warmer winters are coincident with drier summers, populations might increase by 50%. Projected climate changes in Rocky Mountain National Park should result in elk that reproduce faster, experience less mortality, and are in better body condition (Wang et al. 2001, Hobbs et al. 2006).

Considerable research indicates that large-scale climate influences dynamics of ungulate populations across North America, but effects vary and likely are mediated by small-scale local processes. Studies in Banff National Park, Canada found that large-scale climatic variations associated

with colder winter temperatures, increased snowfall, and higher frequency of winter storms reduced elk populations. In areas with wolf (*Canis lupus*) populations, predation by wolves increased with winter severity and exacerbated effects of climate conditions, suggesting increased predation under conditions of deeper snow (Hebblewhite 2005).

Based on a simulated doubling of atmospheric CO₂, biologists suggested there is little possibility elk will spread to new regions, and distribution of elk in the continental United States might shrink in response to changes in climate. Distribution of elk is likely to be affected more by changes in vegetation than by changes in temperature (Johnston and Schmitz 1997). We offer the caveat that local and specific regional climate changes are difficult to predict and exhibit spatial and temporal variability across western North America. We expect that local and specific regional changes in climate and the resultant change in vegetative communities will be key variables potentially influencing abundance and distribution of elk and mule deer. Although predicting the impact of climate change at a local or regional scale is difficult, some research has documented recent local changes that have resulted due to climate change. Walther et al. (2002) documented changes in plant phenology, species composition, and abundance of many species as a result of recent warming trends. Hanski (1999) suggested that climate change can decrease habitat quality and lead to extirpation of populations when small, interconnected populations exist, which has occurred in several wintering areas occupied by mule deer and elk. Further, temperature and precipitation changes have affected both the plants and animals in the Southwest (Turner et al. 2003).

Increased concentrations of atmospheric CO₂ and warming trends characterized the period since 1950, coincident in some locations with poleward and upslope shifts in distributions of some animal and plant species, and advance of spring by about 2.3 days per decade (Parmesan and Yohe 2003, Flannery 2005). Northward movements of forests are slow, but encroachment of woody shrubs is more rapid. It may be that trends of CO₂ and temperature and likely shifts in plant communities since 1950 influenced observed changes in abundance and distribution of elk and abundance of mule deer since that time, but this is speculative. Declines in abundance of mule deer in western North America seem to have been independent of elk encroachment into mule deer ranges (Lindzey et al. 1997, Keegan and Wakeling 2003).

Prediction of future abundance and distribution of elk and mule deer is confounded by limited ability to forecast specific local and regional changes in climate and the resultant vegetation community responses. Based on the evaluation of the IPCC (2007), it is very likely that several climatological changes will occur in the American West and that these changes will influence population trajectory for

both mule deer and elk. This panel projects that warming will continue at a rate that is higher than in any previous interglacial period, snowfall will decrease in both timing and amount, several key greenhouse gases will continue to increase, precipitation patterns will vary, and these factors and others will influence the biotic community of the world.

Precipitation is a key to the quality of mule deer and elk habitat (Mule Deer Working Group 2003). Changes to precipitation will undoubtedly result in changes in the capacity of the land to support populations of these species. The timing and amount of precipitation affects plant growth, which in turn influences forage availability and quality. Further, long drought periods or the occurrence of megadroughts can directly lead to mule deer and elk mortality, although the effects of these phenomena are more likely to influence mule deer than elk populations. Given the likelihood that precipitation patterns will vary in the American West, with most ecoregions likely receiving additional precipitation, but some experiencing increased aridity, it is very likely that mule deer populations in some ecoregions will benefit, but others will be adversely impacted.

At this time, there has been no reported research that investigated the role of climate change on mule deer or elk, but rapid changes in climate have been documented as having an adverse impact on bighorn sheep (*Ovis canadensis*). Findings may aid in understanding the role that rapid climate change may have on mule deer or elk in more xeric ecoregions. Epps et al. (2004) investigated the role of climate change on bighorn sheep in southern California and concluded that increased temperature and decreased precipitation in the late 1900s was an important factor in bighorn sheep population extirpations in California. Although bighorn sheep occur in hot, dry regions, the increase in aridity (Turner et al. 2003) and temperatures (Lane et al. 1994, Turner et al. 2003) have been particularly severe and have adversely impacted desert bighorn sheep populations (Epps et al. 2004).

Several studies have documented poleward and upslope movements of vegetative communities, which leaves a different vegetative community behind. Encroachment of woody plant species is expected to increase due to climate changes in western North America. If grasslands and traditional winter ranges for elk and mule deer diminish as a result of changing precipitation, higher temperatures, increased atmospheric levels of CO₂, increases in invasive species, interruption of normal fire regimes (or the introduction of catastrophic fires due to changes in vegetative density or composition), continued urbanization, and other detrimental factors, it is likely that mule deer and elk will be adversely impacted, at least in some ecoregions. In contrast, declining snow amounts and duration will benefit both elk and mule deer if the vegetative community on winter ranges

meets the nutritional demands of these species.

Based on the predictions of the IPCC (2007), it is very likely that there will be many changes in global biotic communities, and that many of these changes will occur on the North American continent. Specifically, how mule deer and elk will respond to these changes is speculative. We believe that impacts to these species will vary by ecoregions in which they occur; more mesic ecoregions will be influenced least, and more xeric ecoregions have the highest potential for adverse impacts as a result of vegetative and climate changes. We believe it is also likely that timeframe will play a role in the level of impact that ecoregions experience due to climate changes. It is likely that mule deer, which have a more restricted ability to exist in marginal habitats than do elk, will fare more poorly than will elk. We suggest abundance of elk may increase in many areas of western North America during the 21st century. We expect abundance of mule deer in local or regional areas will remain relatively low and might decline if frequency and intensity of drought conditions prevail. However, in the short-term, mule deer populations could remain essentially stable or even increase moderately if encroachment of woody and herbaceous plants and precipitation patterns benefit forage abundance, and nutritional quality of available forages does not become deficient. It is likely that long-term (>100 years) impacts to mule deer will not be beneficial.

Diseases and Parasites

As global climate warms and environmental limitations from cold extremes are no longer a factor—at least in some years—health risks increase for many wildlife species. One species of tick (*Dermacentor albipictus*) contributes to moose (*Alces alces*) mortality in regions south of about 60 degrees north latitude. This parasite can cause moose mortality or reduced vigor when tick populations are high (Lankester and Samuel 1997). Tick infestations in years when April temperatures are warmer than normal result in increased moose mortality the following year. Adult female ticks that drop from moose are able to survive and produce eggs; in colder winters, cold temperatures would kill the ticks. As rapid global warming continues, this condition will likely occur more frequently and have adverse impacts on moose and other ungulate species.

Other parasites that can influence elk and mule deer are also limited by cold temperatures and may be able to expand both in range and impact as winter temperatures warm. Cold weather influences the life cycle and abundance of giant liver fluke (*Fascioloides magna*). The intermediate host for this parasite is inhibited by prolonged spring snowcover, and freezing temperatures can kill its eggs (Pybus 2001). Although this parasite is not a major source of mortality in elk

and mule deer, severe infections can cause fatalities, which are more likely to occur if global warming allows this parasite to expand into more northern regions.

Another parasite of concern as global warming continues is the mule deer musclemo (*Parelaphostrongylus odocoilei*), a common parasite of black-tailed deer and mule deer in western North America. The musclemo has the potential to for population-level impacts to mule deer and other native cervids and bovids (Lankester 2001). Northern distribution of this parasite is likely limited by cold temperatures suitable for larval development, but climate warming may soon eliminate such constraints. Northward range expansion of mule deer musclemo into native populations of Dall's sheep in the Arctic may be an artifact of global warming. Further, in subarctic regions the length of the parasite 'growing season' (i.e., when temperatures were above the threshold for larval development) and amount of warming available for parasite development has increased during the last 50 years. Further climate warming and extension of the seasonal window for transmission may lead to amplification of parasite populations and disease outbreaks in host populations (Jenkins et al. 2005).

Climate Change and Selected Other Species

Given the paucity of research on the relationship between mule deer and elk and climate change, some insight may be gained from examining other wildlife species in which more definitive data exist. Arctic regions are currently experiencing some of the most rapid and severe climate changes on Earth, and climate change is expected to accelerate during this century, contributing to major ecological changes (IPCC 2007). The temperature in the Arctic during the past few decades has increased at nearly twice the rate as in the rest of the world. Melting of glaciers and sea ice and rising permafrost temperatures are widespread, coincident with shortening of the snow season, increased chemical contaminants entering the regions, and land use changes that are destroying and fragmenting habitats. Average annual temperatures in Alaska and the Canadian Yukon have increased about 3.6 °F to 5.4 °F over the past half-century, and in the Arctic are projected to warm about 7.2 °F to 12.6 °F during this century. Vegetation zones in the Arctic include polar deserts, tundra, and northern parts of the boreal forest. Coincident with warming trends, treeline is projected to move northward and to higher elevations, and forests and polar deserts will replace much of existing tundra (Stirling 2002, Arctic Council and International Arctic Sciences Committee 2004, Stirling and Smith 2004, Flannery 2005, Gagnon and Gough 2005, Stirling and Parkinson 2006).

Climate warming in the Arctic is expected to increase abundance and extent of shrubs in tundra areas, and shrub cover has increased over the past half-century in some tundra regions of Alaska and Canada (Tape et al. 2006). Recent research indicates that cover of shrubs, live vegetation, plant litter, and canopy height likely have increased on Arctic tundra, whereas cover and diversity of lichens have declined (Hollister et al. 2005, Wahren et al. 2005). Repeat photography in tundra areas indicated an increase in shrub cover on tundra in northern Alaska in the past 50 years (Tape et al. 2006). As temperatures warm, vegetation becomes drier and more combustible, increasing the risk of fire (Derocher et al. 2004). Moreover, melting of permafrost on tundras as climate warms likely would increase release of methane due to bacterial action, contributing to further warming (Asimov and Pohl 1991).

Polar bears—Changes in distribution, characteristics, and timing of formation and breakup of sea ice potentially have profound effects on polar bears (*Ursus maritimus*) and their prey. Average annual extent of sea ice has decreased from 8% to 10%; thickness of sea ice has decreased about 15%. Extent of sea ice has declined particularly during summer, with a loss of 15% to 20%. Thickness of sea ice in some areas has declined up to 40% since the 1960s, and additional declines of up to 50% in sea ice extent are expected by 2100. Perennial sea ice cover in the Arctic is declining at a rate of about 9% per decade (Derocher et al. 2004, Flannery 2005).

In addition to effects of climate change on extent and thickness, sea ice is breaking up earlier and forming later. Breakup of sea ice in areas of Hudson Bay is now occurring about 2.5 weeks earlier than it did 30 years ago, shortening the amount of time that polar bears are able to feed on seals during the crucial period of spring and early summer. Condition and reproductive rates of adult polar bears, and survival of subadults may be reduced by progressively earlier periods of sea ice breakup. Season of sea ice presence has shortened by 0.5 days per year in many coastal regions (Derocher et al. 2004, Gagnon and Gough 2005, Sterling and Parkinson 2006).

Snow cover over Arctic land areas has declined about 10% since the mid-1970s. Some models project an additional decline of 10% to 20% during this century. Increased frequency of freeze–thaw events in winter also are expected, coincident with more rainfall, leading to formation of ice and snow crust that restricts access of land animals to food and nesting sites. Increased snowfall, freezing rains in autumn, and freeze–thaw events that limited access to forages likely resulted in a 95% decline in abundance of Peary caribou (*Rangifer tarandus pearyi*) between 1961 and 1997 (Flannery 2005). Climate warming in the Arctic also likely will lead to more rainfall during early spring, poten-

tially exposing young ringed seals (*Phoca hispida*) to increased predation and negatively affecting populations of both polar bears and seals (Sterling and Smith 2004).

Polar bears inhabit the circumpolar Arctic, depend on sea ice for survival, and use sea ice to hunt ice-dependent prey and travel among different areas. Pregnant females build winter dens under deep snow on sea ice and land. Thus, climate trends and changes in snow and rain patterns, and extent, thickness, and seasonal breakup and formations of sea ice potentially influence populations of polar bears and their prey. Effects of climate warming on populations of polar bears and their prey are uncertain, but it is likely that polar bears will become extinct if sea ice disappears completely (Stirling 2002, Derocher et al. 2004).

Ice-dependent seals, particularly the ringed seal, give birth to and nurse pups on sea ice. Earlier seasonal sea ice breakup, along with increasing frequency of spring rainfall, could lead to greater mortality of ringed seal pups. Ringed seal pups are the primary prey of polar bears, and productivity of ringed seal and polar bear populations are believed to be closely linked; less availability of seal pups likely corresponds with fewer polar bears. Warmer spring temperatures cause earlier seasonal breakup of sea ice, polar bears come ashore in poorer condition, and populations have lower birth rates. Moreover, earlier breakup of sea ice results in increased mortality of ringed seal pups (Stirling 2002, Derocher et al. 2004). Although quantitative associations between climate change and populations of polar bears and their prey presently are uncertain, Arctic warming poses potentially serious threats to these species. Some models project an almost complete loss of summer sea ice by the end of this century, a change that scientists have concluded threatens extinction of polar bears.

Mountain sheep—Mountain sheep in North America can be categorized as thinhorn (Dall's, Stone's; *Ovis dalli*) and bighorn (Rocky Mountain, California, desert; *Ovis canadensis*). Mountain sheep, much like mule deer and to a lesser extent elk, inhabit the highest and coldest alpine regions of Alaskan and Canadian mountains (Dall's, Stone's), the American and Canadian Rocky Mountains (Rocky Mountain bighorn), and the desert mountains in California (California bighorn) and the western United States into northwestern Mexico and Baja California (desert bighorn). Melting glaciers 10,000 years ago created extensive habitats for mountain sheep, but favorable habitats later diminished as forests eventually encroached up mountain slopes. Mountain sheep are adapted to arid habitats characterized by rugged, precipitous terrain and sparse vegetation, and they tend to avoid areas of taller vegetation that obstruct their vision (Valdez and Krausman 1999).

Thinhorn sheep largely inhabit alpine areas, but Stone's sheep are not as limited as Dall's sheep to alpine

habitats and can occupy glaciers, sub-alpine brushlands, and forests. Thinhorn sheep are primarily grazers that forage on grasses and sedges, but their diets correspond with the diversity of available forages among specific microhabitats (Nichols and Bunnell 1999).

Rocky Mountain and California bighorn sheep inhabit mountain ranges that tend to be relatively warm and arid, but experience cold, dry winters. Habitats include alpine and sub-alpine, open grasslands, shrub-steppes, and open deciduous and conifer forests. Seasonal migrations occur in most populations, and open grasslands and shrublands typically provide winter ranges. Annual precipitation on habitats ranges from about 8 to nearly 16 inches. Diets are diverse—depending on the population diets can be dominated by grasses and sedges, browse, or forbs; forbs often contribute the greatest number of plant species eaten (Smith 1954, Wikeem and Pitt 1979, Shackleton et al. 1999).

Desert bighorns presently inhabit mountain ranges in 7 deserts where climates range from alpine conditions to arid deserts below sea level. Annual precipitation ranges from 1 to more than 20 inches. Daily and seasonal temperatures fluctuate widely, and seasonal temperatures can range from -20°F to 120°F . Composition of diets varies widely, but browse and forbs usually predominate, and proportions of grasses usually are low. Desert bighorns can subsist on decadent and desiccated forages. Desert bighorn habitats have been fragmented by highways (McKinney and Smith 2006), fences, residential developments, and water impoundments, forcing populations into the most isolated remnants of their historic range, threatening their persistence (Krausman et al. 1999). Mountain sheep populations of southwestern Canada, western United States, and northern Mexico have declined due to human impacts, but thinhorn sheep populations have remained relatively unaffected by humans (Valdez and Krausman 1999). Mountain sheep face a precarious future. They are an ecologically fragile species that are adapted to limited, increasingly fragmented habitats. Future conservation efforts likely will succeed only if land managers and conservation efforts succeed in minimizing fragmentation (Valdez and Krausman 1999), and maintaining or enhancing habitat quality in areas where wild sheep exist.

Mountain sheep inhabit precipitous, rocky terrain. We believe their habitats will be affected little by poleward and upslope movements of forests in the short-term, with long-term changes difficult to assess. Thinhorn sheep are migratory, and summer weather influences availability of forages on both summer and winter ranges. Winter conditions and plane of nutrition during the summer growing period for forages are thought to influence lamb survival. Snow deeper than about 12 inches can inhibit movements and foraging. Most thinhorn sheep populations fluctuate

considerably in abundance, likely influenced by differences in nutrition. Although thinhorn sheep primarily are grazers that consume mostly grasses and sedges, they can eat from 50 to more than 100 plant species. Browse and forbs can comprise about half of their diets. Diets during summer reportedly range from 11% to 14% crude protein, whereas winter diets can decline to about 7% crude protein (Nichols and Bunnell 1999). Concentrations of dietary crude protein less than about 7% during winter might indicate deficiencies of protein and energy (Irwin et al. 1993), but this is uncertain. Thus, lower snowfall associated with warming trends might benefit availability of forage. Thinhorn sheep likely would be able to shift diets from primarily grasses to more browse and forbs if these plant species encroach on their habitats.

California and Rocky Mountain bighorn sheep inhabit alpine, subalpine, open grassland, and shrub-steppe areas that are relatively warm and arid, but experience cold, dry winters. Most populations are migratory, and winter ranges are snow-free due to aspect, light snowfall, or high winds. These bighorns generally avoid snow depths more than about 12 inches, and snow crusts due to freeze-thaw events can impede movements and forage availability. Low annual precipitation is thought to be a key factor potentially affecting survival of lambs. Higher precipitation corresponds with higher indices of dietary protein. Grasses, sedges, and rushes tend to dominate diets, but diets can be dominated by grasses, forbs, or shrubs in various populations, and feeding is thought to be opportunistic. During periods of snow cover, bighorns may increase forage availability by shifting feeding from more open sites to areas of higher shrub cover. Populations tend to be relatively stable, and there is no direct evidence that food shortages limit populations, but it has been speculated that populations are regulated by available nutrition (Goodson et al. 1991, Shackleton et al. 1999, Blanchard et al. 2003).

Vegetation is sparse in areas inhabited by desert bighorn sheep, and they tend to avoid areas with taller vegetation that obstructs their vision (Valdez and Krausman 1999). Precipitation is highly variable spatially and temporally in desert regions, and influences availability and nutritional quality of forages, and desert bighorn productivity (McKinney et al. 2006). Concentrations of protein are higher in forbs and shrubs than in grasses, although concentrations vary between forbs and shrubs depending on location.

Diets of desert bighorns vary spatially and temporally and are affected by rainfall levels and seasonal plant growth, but bighorns in most populations eat primarily browse and forbs and consume little grass. Recent studies suggested lower rainfall affected dietary protein and energy by shortening seasonal highs in these variables during winter to spring, rather than reducing peak seasonal concen-

trations. Abundance of populations and lamb survival are positively influenced by increased precipitation, reduced by drought conditions, and vary widely spatially and temporally. However, drought likely seldom leads to extinction of local populations (McKinney et al. 2006). Extirpations have occurred in southern California, where climate change was the cause (Epps et al. 2004).

Climate change has caused reductions in bighorn sheep populations in southern California (Epps et al. 2004). Populations increase when climatic conditions are favorable, and numbers decline during drought events. As the frequency of droughts increases, repeated bottlenecks in these herds increases the potential for genetic consequences to occur. This is especially true where loss of connectivity between adjacent herd units has occurred. After measuring the genetic diversity of 25 desert bighorn sheep populations in southern California, Epps et al. (2006) found that the populations in low-elevation habitats, which presumably were most affected by increased temperatures and decreased precipitation, had lower genetic diversity than populations at higher elevations. This trend of reduced genetic diversity in drought-affected fluctuating populations is also likely to occur in mule deer populations in areas fragmented due to habitat isolation, particularly in the warmer, drier ecoregions where mule deer are found.

Abundance of Rocky Mountain and desert bighorn sheep populations also is closely linked with abundance of escape terrain. Fragmentation of desert bighorn sheep habitats by fences, highways, residential communities, water impoundments, and fire suppression has led to declines in abundance and extinction of populations throughout their range. Desert bighorn sheep presently are restricted essentially to isolated, remnant populations of questionable viability in many areas (Wakelyn 1987; Bleich et al. 1990; Krausman et al. 1999; Rubin et al. 2002; Bender and Weisenberger 2005; Cain et al. 2005; McKinney et al. 2003, 2006). If global warming and increased atmospheric concentrations of CO₂ lead to higher growth and encroachment of woody species, these trends could lead to further habitat fragmentations, and decline in abundance and distribution of local populations.

Much the same as mule deer and elk, the effect of global warming will likely affect wild sheep differently in the different ecoregions where they occur. We suggest that global warming during the 21st century will have comparatively little influence on distribution of mountain sheep in northwestern North America, but that populations in the American Southwest and Mexico—areas projected to experience expanded droughts (IPCC 2007)—will likely be adversely affected. In more northern ecoregions, warming trends may lead to more benign conditions due to less snowfall in winter, particularly for thimhorn, Rocky Mountain,

and California bighorn sheep, although climate changes may necessitate shifts in their diets. We assume historically high diversity of diets represent adaptability to changes that may occur in composition of available forages. Global warming trends potentially may contribute to higher availability of forage for all races of mountain sheep, and movements of forests poleward and upslope likely will have an effect on their abundance and distribution. Climate change may reduce abundance of mountain sheep if it results in decline in nutritional quality of food resources, via expected declines in concentrations of nitrogen by as much as 30% in key forages, or if encroachment of woody species fragments habitats. Potential effects on abundance and distribution of mountain sheep are unknown in relation to effects of climate change on local and regional occurrence of drought, insect infestation of vegetation, and wildfires.

Conclusions and Recommendations

Conclusions

Climate changes caused by increasing atmospheric concentrations of greenhouse gases are expected to result in marked changes in climate throughout the world (IPCC 2007), including the areas inhabited by mule deer and elk. Habitats in North America have been undergoing changes in flora and fauna as the region has become warmer and drier in the last 12,000 years. The greatest rate of change has occurred in the last 150 years (Fredrickson et al. 1998). It will be a challenge for some species to adapt to the changing environment where the rate of change is unprecedented in any interglacial period, particularly a rate of change that will be different than the rate in which mule deer and elk have evolved. Changes that will likely occur due to the expected warming include increased frequency and severity of wildfires, increased frequency of extreme weather events, regional variation in precipitation, period of snowfall, northward and upward shifts in vegetative communities, and replacements of biotic communities. These changes are expected to affect abundance, distribution, and structure of animal and vegetation communities. We caution that although it is difficult to predict effects of global warming at local and specific regional scales, there are empirical data on which to base reasonable predictions for responses of some wildlife species to these climate changes.

We expect that local and specific regional changes in climate and vegetation will be key variables influencing abundance and distribution of elk, mule deer, and many other wildlife species. Winter range is a crucial and limited resource for mule deer and elk in the colder, more northern ecoregions and locally in other ecoregions. As the Mule

Deer Working Group (2005) documented, winter range has declined in both extent and quality in the recent past and likely will continue to decline into the future, regardless of the role that global warming will play. It is likely that global warming will act in synergy with other detrimental factors to hasten the decline of winter range quality in many ecoregions.

We expect that the distribution of elk and mule deer in western North America may extend somewhat northward, in response to warmer temperatures and reduced snowfall. However, this northern expansion during the 21st century will likely be minimal in response to large-scale predictions of climate changes. We suggest abundance of elk may increase at least locally in many areas of western North America due to their ability to utilize a wide array of low to moderate quality forage to meet their metabolic demands. In the short-term, abundance of mule deer in some regional areas also could increase if encroachment of woody and herbaceous plants and precipitation patterns benefit forage abundance and quality. But in the long-term, global climate change, acting in synergy with other factors, will adversely affect mule deer populations in at least the Southwest Deserts and the California Woodland Chaparral ecoregions, where drought-like conditions are most likely (IPCC 2007). Further, the IPCC indicated that although average precipitation will increase in many regions of North America and drought episodes are more likely to occur, we expect these droughts will depress local mule deer and elk populations.

Forecasting and model accuracy

Scientists have reached consensus that concentrations of greenhouse gases in the atmosphere will increase over the next century unless emissions from human sources decrease. Continued increase in concentrations likely will raise the average temperature of Earth, influence precipitation and some storm patterns, and raise sea levels, but the magnitude of these trends is uncertain. Estimates of how climate could change are based on using computers to develop general circulation models that provide the only available experimental laboratory for climate. However, these models are imperfect. Simulations are limited by uncertainties in their formulation, limited size of calculations, and complexities of interpretation (National Research Council 2001). Uncertainties of models increases at regional scales, in which models sometimes yield differing results. Thus, results and interpretation of models do not provide definitive forecasts. Rather, they usually provide hypothetical examples of how climate might change within a range of possibilities. Although these caveats are understood, the concordance between modeling conducted by the IPCC and monitoring of observed values since the first IPCC report

strengthen the utility of the IPCC modeling effort. In the 1990 report, the IPCC suggested global average temperature increases from about 0.15 °C to 0.3 °C per decade from 1990 to 2005. This can now be compared with observed values of about 0.2 °C per decade, strengthening confidence in near-term projections.

Climate presently is changing largely because of human activities, and likely will continue to change regardless of any mitigation actions (Trenberth et al. 2006). Even if CO₂ emissions were stopped immediately, it would take an estimated 750 years to reduce present atmospheric concentrations of the greenhouse gas by half. This is because concentrations of the greenhouse gas are determined by re-assimilation and respiration during litter decomposition (Schulze et al. 2002). Nonetheless, greater efficiency of energy use, and development and use of energy sources other than fossil fuels (e.g., geothermal, nuclear, and solar energy, wind power, hybrid cars) might tend to ameliorate increasing concentrations of atmospheric CO₂ (Hoffert et al. 2002, Brown 2004, Flannery 2005). Wind power development, for example, is occurring throughout North America (Walter et al. 2006).

The composition and structure of ecological communities likely will continue to change and evolve at unprecedented rates into the future if global warming progresses as expected. Despite present understanding of factors that potentially affect global warming and climate change, our projections remain uncertain regarding changes in abundance and distribution of elk, mule deer, and other species, and the composition and structure of ecosystems at local and regional scales in the heterogeneous landscapes of western North America.

Recommendations

Recommendations relative to the effects of global climate change on mule deer and elk fall into two general areas; public information and education tools and habitat management programs aimed at reducing the impacts of global climate change on local habitats.

Information and Education

- Use a proactive strategies approach to develop information for the general public relative to effects of global climate change on wildlife in specific regions, and communicate key messages and concepts through agency-specific, and more importantly, regional/national organizations such as the Western Association of Fish and Wildlife Agencies and the Association of Fish and Wildlife Agencies.
- Develop outreach tools that would be used by conservation organizations to apprise interested stakeholders and the general public of the issues and the fact that agencies, and

collectively the western states, are actively involved in addressing effects of global climate change on wildlife species and the habitats in which they depend.

- Evaluate the potential to develop classroom materials that would be provided to schools with the intent of incorporating these materials into science curriculums in an age-appropriate fashion.
- Add a node to existing websites where current climate change information can be posted.
- Agencies should actively participate in programs that provide new information on global climate change as it becomes available, so that information and education materials are current.

Habitat Management Programs

- Ensure that the issue of global climate change is incorporated into all land use planning documents and that these planning efforts incorporate steps to minimize effects of changing climate on biotic communities.
- Develop planning and implementation programs to maintain or enhance vegetative conditions in early successional stages and to ensure connectivity between summer and winter ranges.
- Initiate monitoring programs designed to collect and evaluate data on biotic community responses related to climate change.
- In areas where winter or summer range is a crucial component of mule deer and elk habitat, implement the following:
 - Limit disturbances on winter ranges.
 - Retain as much existing mule deer winter range as possible and acquire and secure additional winter range that provides food resources and thermal protection and maintains connectivity between summer and winter ranges.
 - Aggressively pursue land use planning in areas of rapid urbanization to minimize the loss of key winter and summer habitats.
 - Develop management actions that minimize encroachment of invasive weeds or tree species on important seasonal mule deer and elk ranges.
 - Ensure that key browse species are maintained as a component of the vegetative community on winter ranges.

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