

CHAPTER NINE

Climate and Vegetation Phenology

Predicting the Effects of Warming Temperatures

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WITH THE MELTING of winter snow, plant growth commences in the greater Yellowstone ecosystem, resulting in a greening of the spring landscape. Plants grow in predictable sequences of leaf, bud, flower, and seed formation, which together are referred to as the phenological stages of growth. The timing of phenological events is highly variable and depends on a suite of climatic and biotic factors. At the landscape scale, this phenological development has been characterized as a green wave that travels up the elevation gradient as snow recedes from late winter to summer (Frank and McNaughton 1992). This green wave is crucial to the area's migratory ungulates, such as elk, bison, mule deer, pronghorn, and bighorn sheep, which travel up to 550 kilometers round-trip (J. Berger 2004) as they track this highly nutritious young green forage to feed their young and accumulate fat reserves needed to survive the following winter and reproduce. In turn, a diverse suite of carnivore species preys and scavenges on these herbivores.

As around much of the globe, temperatures in and near Yellowstone National Park have been increasing over the last 50 years, leading to more

rapid snowmelt on low-elevation winter ranges (Wilmer and Getz 2005). Understanding how climate change will influence plant phenological development at both local and landscape scales, and its impacts on wildlife, requires a comprehensive understanding of the park's climate system and how it interacts with plants and animals. We review what is currently known about the park's climate system and assess how the green wave dynamics may be transitioning in a changing climate.

Yellowstone National Park experiences two distinct climatic regimes (Whitlock and Bartlein 1993; Curtis and Grimes 2004). A winter-wet/summer-dry regime is driven from the west by the jet stream bringing moist air and precipitation from the eastern Pacific in winter and is blocked by subtropical highs in the eastern Pacific as the jet stream moves poleward in summer. A separate summer-wet/winter-dry regime is brought about by the North American monsoon, which brings precipitation from the gulfs of California and Mexico as far north as Yellowstone National Park in late spring and early summer.

Winter precipitation arrives primarily as snow, leading to a seasonal snowpack that is the dominant climatic control on wildlife. Several different physical characteristics of the snowpack are important. The total depth of the snow is perhaps the most universal metric of the impact of snow on wildlife, but snow density is also important in both beneficial and adverse ways depending on the species and the time of year. Density measures the mass of snow within a given volume (kilograms per liter; usually stated as a percentage). Thus, it impacts the weight of snow that must be moved by wildlife to forage beneath the snow or travel through it. Mid-winter in Yellowstone is often cold (Newman and Watson 2009), leading to relatively low-density snow (less than 20 percent) in the surface layers after heavy snowfalls. With increasing time since substantial snowfall, and as warmer temperatures arrive, the density of the snowpack gradually increases to 30 to 40 percent because of such processes as vapor exchange between snow crystals and mechanical compaction under its own weight (Watson, Anderson, Kramer, et al. 2009; Watson, Anderson, Newman, et al. 2009). The combined effects of density and depth are reflected in the snow-water equivalent or total depth of liquid water that would be obtained if the snowpack were completely melted. This measure is widely used to quantify the net impacts of snowpack on wildlife at landscape scales since it is easily measured and its spatial distribution can be estimated over large areas

(Watson, Anderson, Newman, et al. 2009). Of particular importance to many wildlife situations is snowpack hardness, which is measured as the force that must be exerted over a certain distance to penetrate each layer of the snowpack. Hardness is difficult to measure and difficult to predict (Pielmeier and Schneebeli 2003). To some extent, it can be approximated by snow-water equivalent but not always. Strong winds and daily surface melt-thaw cycles can lead to a hard crust on an otherwise low-density snowpack, creating precarious situations for ungulates and opportunities for predators (Telfer and Kelsall 1984; Crête and Larivière 2003; Tucker et al. 2010).

For about half of each year, most of Yellowstone National Park is covered by snow. In an average year, the snowpack begins to accumulate in October through most of the central region at elevations from 2,000 to 2,300 meters (Newman and Watson 2009). Heavy snowfalls typically occur between December and February, and the snowpack continues to deepen until a maximum depth of about 1.1 to 1.4 meters is reached usually by late March on the central plateau (Watson, Anderson, Newman, et al. 2009; National Climatic Data Center cooperative weather station data). Melting is relatively rapid, with most of the snowpack melting within about one month of the date of maximum depth and complete melt-out occurring before the end of May. Thus, the total snowpack season is about seven months long. However, on Parker Peak, Wyoming (2,865 meters elevation), the season length averages over nine months, while at Gardiner, Montana (1,608 meters elevation), it averages only three months—with most of the interannual variation occurring at the end of the season (National Resources Conservation Service snow telemetry station summary data; Western Regional Climate Center and Cooperative Observer Network data).

The snowpack varies from year to year in a manner that depends on location within the park. The winter of 1996–1997 was severe throughout the central and southern parts of the park but not at lower elevations in the north. Snow depth peaked at 2.4 meters at the Snake River on the southern boundary (2,098 meters elevation)—the deepest snow there in 87 winters of useable records (National Climatic Data Center cooperative weather station data). There were near-record snow depths of 1.9 meters at Lake Yellowstone (2,368 meters elevation) and 1.7 meters at Old Faithful (2,243 meters elevation)—about 40 to 50 percent above average. In the north at Mammoth Hot Springs (1,902 meters elevation), snow depth peaked at only 0.31 meter, and this was actually 24 percent below average.

The snowpack melted completely by mid-May at Snake River, Lake Yellowstone, and Old Faithful. At Mammoth, snowpack melted by mid-March, leaving a six- to eight-week period between mid-March and mid-May with an exceptional contrast between the snowbound south and interior and the snow-free northern valleys.

In contrast, a universally mild winter occurred in 1986–1987. Snake River, Lake Yellowstone, and Old Faithful peaked at 28 to 39 percent below their average snow depths of 0.84 to 1.04 meters. Snake River experienced its third lowest peak on record, Old Faithful its fifth lowest, and Lake Yellowstone its tenth lowest in 102 years of useable records. Mammoth experienced its second lowest peak, 62 percent below its mean, at a snow depth of only 0.15 meters. The snowpack came and went several times, and snow was on the ground for a total of only about two months. These interannual variations have a substantial impact on the population dynamics of wildlife, such as elk (P. J. White et al. 2010), bison (Geremia et al. 2009), and bighorn sheep (P. J. White et al. 2008).

Snowpack characteristics vary markedly throughout Yellowstone National Park at various scales and due to a variety of influences. There is more snow on the high-elevation peaks and plateaus, an intermediate amount of snow below these on the central plateau, and less snow in the valleys, particularly the Lamar and Yellowstone valleys (Watson, Anderson, Newman, et al. 2009; Watson and Newman 2009). At a given elevation, there tends to be more snow in the west and south, since the major winter storms tend to arrive from these directions, fully laden after traveling up the Snake River Valley in Idaho and becoming depleted as they move eastward and northeastward over the park (Watson, Anderson, Newman, et al. 2009; Watson and Newman 2009). More snow tends to accumulate in the meadows than in the surrounding forests, but the same tree cover that reduces snow accumulation can slow down snowmelt, so the snowpack often persists longer into the spring in the forests (Watson, Anderson, et al. 2006; Watson, Newman, et al. 2006). In the open country, there is less snow on exposed ridges and hilltops and more snow in the sheltered hollows—particularly on the downwind side of windblown ridges (Watson, Anderson, Kramer, et al. 2009). Some meadow complexes are characterized by hummocky terrain and exhibit large areas of both reduced and increased snowpack relative to flatter meadows where the snow is more homogeneous (Watson, Anderson, Kramer, et al. 2009). During the spring melt, slopes that face the sun are more rapidly depleted of the snow and become

snow-free well before surrounding areas (Watson, Anderson, et al. 2006; Watson, Newman, et al. 2006). There is no snow on any of the intense geothermal features and a substantially reduced snowpack on the large low-intensity geothermally influenced patches that might otherwise go unnoticed (Watson, Newman, et al. 2009). The combined effect of these influences is greatest in spring, when the park becomes a receding mosaic of snowbound and snow-free areas (Watson, Anderson, Newman, et al. 2009). In an average year, the melt-out works its way up the lowest valleys in March, reaching the meadows on the central plateau in late April and the highest plateaus in June (Watson, Anderson, Newman, et al. 2009; Watson and Newman 2009). At smaller scales, melt-out on sunny, exposed, and non-wooded patches precedes the large-scale pattern by a few weeks, while shaded, sheltered, and wooded patches hold snow for a few weeks after the large-scale melt sequence has passed.

Monsoonal precipitation arrives in late spring and early summer with a somewhat different spatial pattern than winter precipitation (Whitlock and Bartlein 1993; Mock 1996). Monsoonal airflow moves northward along the Great Plains to the east of the park, bringing afternoon thunderstorms to areas along the eastern front of the Rocky Mountains (Curtis and Grimes 2004). The northern valleys and northeastern passes in the park are most exposed to these systems (Mock 1996; S. T. Gray et al. 2004), and up to 42 percent of their annual precipitation occurs during May through July (Western Regional Climate Center and Cooperative Observer Network data). Higher-elevation areas in the central and southern portions of the park also receive precipitation peaks in May and June, but the contrast with the winter months is much less than in the north. In January, precipitation increases about 6.9 millimeters with every additional 100 meters in elevation, but in June the corresponding increase is only about 2.5 millimeters (Western Regional Climate Center and Cooperative Observer Network data). By about late July, the monsoonal influence subsides and the entire park moves into a relatively dry period. In some years, the monsoon fails to reach as far north as Wyoming and drought conditions ensue (Curtis and Grimes 2004).

The climate and snowpack of Yellowstone National Park have changed in the past and are expected to change in the future. The details depend heavily on the temporal and spatial scales under consideration. During the past century in the western United States, temperatures have generally warmed by 1 to 2 °C, precipitation has increased, the fraction of



In winter, moose feed extensively on the twig tips of woody plants such as willow that generally protrude above the snowpack and allow feeding without the energetically costly need to displace snow to uncover grasses, sedges, and forbs at ground level. This moose was feeding in deep snow on willows growing along Crystal Creek. *Photo by Cindy Goeddel.*

precipitation falling as snow versus rain has decreased, annual peak snow-water equivalent has decreased, the snowpack has melted earlier, and the peak in spring runoff has occurred earlier (Mote et al. 2005; Regonda et al. 2005; I. T. Stewart et al. 2005; Knowles et al. 2006; I. T. Stewart 2009; McWethy et al. 2010; Ray et al. 2010; Littell et al. 2011). In this regional context, Yellowstone is typical with respect to a warming in temperature but not necessarily an increase in precipitation (Newman and Watson 2009). The past century of variation in Yellowstone's precipitation lies within the range observed during the past millennium (S. T. Gray et al. 2007; Whitlock, Dean, et al. 2008). Despite substantial swings at decadal and multidecadal timescales, there has been no clearly observable longer-term precipitation trend throughout Yellowstone National Park (S. T. Gray et al. 2007; Newman and Watson 2009). Complicating matters further, the changes that have been observed vary throughout the park because it straddles the boundary between several climate regimes (Whitlock and Bartlein 1993; Mote et al. 2005; L. R. Stevens and Dean 2008; McWethy et al. 2010). Predictions of future change reflect historic change, with temperatures predicted to increase substantially during the next century, but precipitation predictions are uncertain and variable (Ray et al. 2008; I. T. Stewart 2009). There is weak agreement among models that winter precipitation will increase and minimal agreement about whether summer precipitation will increase or decrease (Ray et al. 2008).

The response of snowpack to increasing temperature and precipitation depends on the absolute temperatures involved. If the temperature is near freezing, as is the case throughout much of the western United States during winter, then an increase in temperature will cause a decrease in snow-water equivalent because of a state change in precipitation from snow to rainfall and enhanced warming of remaining snowpack. At high elevations where the temperatures are well below freezing, however, a change in temperature has minimal effect, and any increase in precipitation will translate to an increase in snowpack. This dichotomy is borne out throughout the western United States in historical observations (Mote et al. 2005; Knowles et al. 2006) and future predictions (Littell et al. 2011). The elevation range of Yellowstone National Park straddles this dichotomy (Regonda et al. 2005; Newman and Watson 2009). Low-elevation areas experienced decreases in snow-water equivalent from 1948 through 2003 (Wilmers and Getz 2005), and these decreases are predicted to continue (Littell et al.

2011). However, increased snow-water equivalent was observed in some higher-elevation locations in and near the park between 1950 and 1997 (Mote et al. 2005), and continued increases in snow-water equivalent at high elevations are not inconsistent with the varied coarse-scale model predictions that are available (Ray et al. 2010; Littell et al. 2011).

There are four moderately high-elevation snow courses at Yellowstone National Park where snow conditions have been measured since the 1930s (Crevice Mountain, 2,512 meters elevation; Lake Camp, 2,371 meters; Thumb Divide, 2,432 meters; and Aster Creek, 2,362 meters). The immediate environs of the Thumb Divide and Aster Creek sites were burned in 1988 (Watson and Newman 2009), and a fire-related decrease in snow-water equivalent at these sites began in 1989 (analysis of Natural Resources Conservation Service data measured on March 1st). Crevice Mountain had no trend in snow-water equivalent from 1939 through 2010, and snow-water equivalent at Lake Camp trended upward at a rate of 34 millimeters per century from 1936 through 2010. The annual peak snow depth at the moderately high elevation of the Lake Yellowstone climate station (2,368 meters elevation) also trended upward at 16 millimeters per century from 1904 through 2010 (National Climatic Data Center cooperative weather station data), while the lower-elevation Snake River and Old Faithful sites trended downward from 1905 through 2010 at 53 and 71 millimeters per century, respectively. Mammoth is at the lowest elevation of the long-term sites, and its peak snow depth trended downward at 182 millimeters per century. Thus, snowpack depth and water equivalent appear to be decreasing at locations below about 2,000 meters elevation but stable or increasing at locations above 2,300 to 2,500 meters (about 40 percent of the park and adjacent mountains; Romme and Turner 1991). The integrated runoff response from the Yellowstone River has been toward earlier spring runoff peaks (Regonda et al. 2005; I. T. Stewart et al. 2005), which suggests that the majority of the park is experiencing shorter winters and longer summers as a result of snowpack changes.

PLANT PHENOLOGY AND CLIMATE CHANGE

Yellowstone's climate influences plant phenology at both the plant and landscape scale. At the plant scale, the phenological development of individual

plants from first growth to fruit set and senescence (aging past maturity) are influenced by a number of environmental conditions, such as snow depth, soil moisture, photoperiod, and temperature. The melting of the snowpack initiates the first growth of low-lying vegetation. The interaction between soil moisture, temperature, plant genetics, and photoperiod determines the timing of later phenological stages as well as the amount of biomass accumulated during the growing season.

Studies of plant reproductive phenology elsewhere suggest that flowering date has advanced in response to climate change (Abu-Asab et al. 2001; Fitter and Fitter 2002; Primack et al. 2004; Miller-Rushing et al. 2007), though this effect can be highly species dependent (Tooke and Battey 2010). While some species have considerably advanced their flowering date (Abu-Asab et al. 2001), others have not (N. L. Bradley 1999). Species whose life cycles are strongly synchronized with the start of snow melt may experience a significant increase in fitness if earlier onset of vegetative activity also allows them to benefit from a longer growing season (Galen and Stanton 1995; Dunne et al. 2003; Wipf 2009). For species where snowmelt has little direct impact on their life cycle, other cues such as stable summer temperatures and increased photoperiod may be advantageous (Wipf 2009). Longer day lengths and warm summer temperatures allow them to benefit from peak pollinator densities.

Plants that are adapted to flowering early in the season are most likely to show a strong response to changing environmental drivers (Fitter and Fitter 2002). Evidence from high-latitude systems suggests that flowering and pollinator activity initiate soon after snowmelt (Hoye and Forchhammer 2008; Forrest and Miller-Rushing 2010). However, it is unclear whether organisms are responding to snowmelt as an immediate cue or if the relationship can be explained by associated environmental changes. For example, earlier snowmelt allows for a greater number of days over which warming temperatures can influence both flowering time and insect pollinator development (Thorhallsdottir 1998). Thus, rapid snowmelt facilitated by lower snow accumulation in a previous winter may not advance phenology without a concomitant rise in spring temperatures (Forrest and Miller-Rushing 2010).

Increasing temperatures are not only responsible for triggering an earlier onset of spring but also have other positive impacts on plant growth. Warmer temperatures alter nitrogen mineralization rates, which allow

plants greater access to nitrogen. The resulting increase in foliar nitrogen can then trigger higher rates of photosynthetic activity over the duration of the longer growing season (Richardson et al. 2009). Further, earlier spring onset is also known to increase area of leaf exposure to sunlight, resulting in a greater degree of photosynthetic activity (Jolly et al. 2005; Luyssaert et al. 2007). If soil moisture levels are low, however, increased temperature can lead to desiccation-induced reductions in biomass and reproduction.

Unlike strong evidence documenting an earlier start of spring onset, evidence for changes in autumn phenology have been less compelling (Cleland et al. 2007; Hülber et al. 2010). The end of the growing season can be initiated by changes in photoperiod, temperature, genetic sensitivity of plants, and nutrient requirements (Shaver and Kummerov 1992; Oberbauer et al. 1998). This suggests that the majority of effects observed on plant phenology are mediated through changes arising from spring advancement rather than from a delay in autumn phenology. Studies of experimentally warmed plots in Greenland showed that elevated temperatures resulted in earlier phenologies but also compressed life histories (Post et al. 2008a). Whereas some species respond to warming by shifting the date of only one phenological stage (such as leaf emergence), others respond by accelerating their entire life history. This results in fewer days between leaf emergence and seed set under warming scenarios. From an herbivore's perspective, accelerated life histories by plants mean fewer days that they are available as high-quality forage. The Greenland study also revealed that warming synchronized plant phenology across space, resulting in a more narrow time window over which high-quality forage is available to herbivores (Post et al. 2008b). As a consequence, caribou calf survival was much lower during warm years than cool years.

At the landscape scale, snow recedes from low to high elevations with the onset of spring warming. Grasses and shrubs initiate vegetation growth and quickly progress through various phenological stages resulting in a burst of vegetative activity known as the green wave (Frank and McNaughton 1992; Merrill et al. 1993). As the growing season progresses, green biomass concentration peaks early and then decreases as dead tissue begins to accumulate. When grasses enter later phenological states, nutritional values decrease because of lower crude protein content, lower nitrogen, and a concurrent decrease in digestibility resulting from accumulation of indigestible fiber (R. G. White 1983). The peak of the green wave occurs during early

phenological states when green biomass concentration is maximized. Herbivores preferentially select plants in this state because they provide the most efficient nutritional yield (Frank and McNaughton 1992). In Yellowstone National Park, this peak occurs on average 28 days after snowmelt (Frank and McNaughton 1992).

The elevational gradient of the green wave in Yellowstone National Park is driven by the influence of topography on temperature and precipitation. At higher elevations, more snow accumulates and lower temperatures prolong the growing season by delaying melt-out. As temperatures warm with the progressing summer, the gradual melt-out is responsible for the distinct elevational gradient of the green wave (Thein et al. 2009). The total snow accumulated in a season can also impact total vegetation productivity because prolonged snow cover leads to an increase in biomass in the subsequent growing season (D. H. Knight et al. 1979). However, this effect was significant only in dry meadows and had little effect in wet meadows, suggesting that increased snowfall and subsequent melt creates a deeper water table that allows grass roots to penetrate further, acquire more nutrients, and produce a greater biomass (Thein et al. 2009).

The green wave can be measured using either field- or satellite-based methods. Frank and McNaughton (1992) measured aboveground net primary productivity by using the canopy intercept method, whereby standing biomass is related to the number of hits a pin makes when it is passed at an angle through vegetation. They measured productivity at several sites across an elevational gradient multiple times through the growing season. Fences were used to exclude ungulates so that they could test the influence of herbivory on rates of productivity among sites. Satellite methods use remotely sensed imagery to indirectly measure plant phenology and biomass. The most commonly used satellite product is the Normalized Difference Vegetation Index (NDVI). Plants absorb light in the visible spectrum to conduct photosynthesis, which results in a low visible spectrum score, and scatter light in the near-infrared spectrum to avoid overheating, which results in a high near-infrared spectrum score. NDVI measures the difference in near-infrared and visible spectrums. Thus, the more leaves a plant has, the higher the NDVI value. Once snow disappears, NDVI values increase as plants begin to grow. NDVI peaks later in the growing season when plants reach maximum biomass and then decreases as plants senesce. The period during which NDVI is increasing most rapidly corresponds with

when plants are at their peak nutritive value. This has been validated by studies comparing vegetation reference plots (Hebblewhite et al. 2008; Thein et al. 2009) and studies correlating peak fecal crude protein levels in ungulates (Christianson and Creel 2009) with satellite-derived NDVI values. Unlike field-based methods, satellite methods allow exploration of green wave dynamics over large spatial and temporal scales but cannot control for factors such as herbivory.

In mid-winter (December through February), most grassland areas have negative NDVI values due to snow cover. In early spring (April), large expanses of the northern grassland and lower- to middle-elevation portions of the central range exhibit sharp increases in NDVI values that reflect the combined effects of snowmelt and new vegetation growth. By late spring or early summer (May–June), most grassland areas in Yellowstone National Park have increasing NDVI values, including the high-elevation summer ranges for ungulates, while vegetation growth in some low- and middle-elevation grasslands has already peaked. Yellowstone National Park is at its greenest in mid-summer (July), after which NDVI in most patches slowly decreases in August. Rapid decreases in NDVI during October and November signal the beginning of winter and the end of the growing season (Thein et al. 2009). In some years, autumn rains can initiate a second smaller-scale green-up that may be important to ungulate nutrition heading into winter.

Specific patterns of snowmelt and the onset of new vegetation growth in northern Yellowstone are typically earliest in the Gardiner basin of Montana and progress upslope along the valleys to the south and east, with the high meadows on the Mirror Plateau having the latest onset dates. The patterns of new vegetation growth in central Yellowstone are more complex because the first patches to green up are generally in the mid-elevation meadows (Lower Geyser basin, Nez Perce Creek, Madison Canyon, and Norris) where geothermal features facilitate snowmelt. This is followed shortly thereafter by the lower-elevation Madison Valley region to the west, and later the higher-elevation Hayden and Pelican valleys begin to green. Meadows along the upper reaches of Pelican and Raven creeks are consistently the last areas in the central range to green up. There is considerable local variation in vegetation growth leading to significant overlap in green-up between meadow complexes. Thus, patches just starting to green up can be found in a number of meadows spanning a range

of elevations. However, in lower areas onset of the growing season typically occurs approximately 100 days earlier than in the highest areas (Thein et al. 2009). The date of peak biomass is also correlated with elevation, with lower elevations peaking approximately 30 days before higher elevations. Peak biomass dates tend to occur approximately 70 days after onset at low elevations and 40 days after onset at high elevations, which is consistent with the periods of measurable vegetation production reported by Frank and McNaughton (1992). Peak biomass is relatively low in the Gardiner basin (where a lack of precipitation limits production), near geothermal features, and in a few areas in the Madison Valley. High maximum NDVI values indicating dense vegetation biomass occur in the Pelican Valley, despite a relatively short growing season (Thein et al. 2009).

Temperature, through its interactions with snowmelt and precipitation, influences spatial and temporal patterns of the summer green wave in Yellowstone National Park. An analysis of NDVI data for growing seasons between 2000 and 2010 suggests that the peak green wave occurs at higher elevations during years with warmer temperatures. The peak green wave also spans a wider elevation gradient in warmer years. Within elevational bands, a strong interaction between snowmelt and temperature lead to an increase in distance over which green wave is synchronized, with larger patches more pronounced in lower elevations. Thus, climate change is likely to speed the progression of the green wave up the elevational gradient and decrease spatial variability within elevation bands—though there is much uncertainty in this prediction.

Interactions between moisture levels and fire regime could greatly expand or contract the geographic extent of Yellowstone's grasslands. Also, certain warming scenarios may favor the spread of invasive species, which might be less palatable to grazers. Invasive species often have short generation times, high dispersal ability, and high fecundity. Thus, they may expand more quickly than native species into newly suitable habitat as the climate changes (B. A. Bradley et al. 2010). Because of their short generation times, invasive species may also be better able to evolve and adapt to climate change. In addition, carbon dioxide fertilization favors a range of invasive plants, with elevated carbon dioxide increasing the invasion of annual grasses into perennial shrub lands, perennial shrubs into forests, and annual forbs into grasslands (B. A. Bradley et al. 2010).

CONSERVATION IMPLICATIONS

Many ungulates undertake seasonal migrations across distinct geographical ranges to maximize energy intake, and such strategies are believed to have evolved in response to spatial heterogeneity in resource availability (Fryxell and Sinclair 1988; J. Berger 2004). In fact, seasonal fluctuations in vegetation green-up as derived from NDVI data suggest that migratory routes strongly track seasonal changes in vegetation (Boone et al. 2006). As ungulates migrate across the landscape, they preferentially forage on early plant phenological stages to maximize weight gain (Mysterud and Langvatn 2001).

Both snowpack and forage green-up appear to influence the timing of spring migration (10 to 140 kilometers) by northern Yellowstone elk to higher-elevation summer ranges, with elk delaying migration after winters with high snowpack but migrating earlier in years with lower snowpack and earlier vegetation green-up (P. J. White et al. 2010). Elk spending winter at lower elevations are generally able to begin tracking the retreat of snowpack and phenology of vegetation green-up earlier than elk spending winter at higher elevations (P. J. White et al. 2010). Likewise, the 15- to 50-kilometer migrations of Yellowstone pronghorn from their winter range to various summer ranges occur as snow melts and vegetation green-up progresses. Autumn migrations occur before snow covers migrant summer ranges (P. J. White, Davis, et al. 2007). In addition, bison move from higher-elevation summer ranges to lower elevations during autumn through winter, until returning to the summer ranges in June (Meagher 1989b; Bjornlie and Garrott 2001; Bruggeman et al. 2009). As winter progresses and snow depths increase on the summer range, the available foraging areas for bison are reduced to increasingly limited areas at lower elevations and on thermally warmed ground, even though many geothermal areas contain relatively little and poor-quality forage (Meagher 1989b; Bruggeman 2006; Bruggeman et al. 2009). Also, snow melts earlier at lower elevations, so there are earlier green-up and energy-efficient foraging opportunities while summer ranges are still covered with snow (Bjornlie and Garrott 2001; Bruggeman et al. 2006). Thus, there are often mass movements of bison to lower-elevation areas along the western boundary of the park and nearby areas of Montana during mid-April through mid-May that coincide with the onset of vegetation green-up and growth (Thein et al. 2009). The return



Snow is a major factor that influences nearly all the animals in the Yellowstone area. While some species such as small mammals may benefit from a thick layer of snow that protects them from predators, snowpack also makes it difficult for Yellowstone's large ungulates to obtain forage. A bull bison rests after plowing the snow with his massive head to graze. *Photo by Cindy Goeddel.*

migration of bison from lower-elevation winter ranges aligns with temporal and spatial patterns of new vegetation growth, which progresses at the rate of approximately 10 days for every 300 meters of elevation gained (Despain 1990; Thein et al. 2009).

Ungulates that inhabit seasonal environments typically time their reproductive events around periods of peak vegetation green-up (Rutberg 1987) to enable temporal overlap with high-quality plant phases during development, thereby allowing juveniles to build up fat reserves (Gaillard et al. 2000). The impacts of climate change might positively or negatively impact newborn ungulates. Advancement of spring can lead to a longer snow-free season where forage access and movement are not encumbered by snow. An increase in growing season length without a corresponding increase in access to high-quality forage, however, might negatively impact herbivores. Juvenile survival in Alpine ibex (*Capra ibex*), bighorn sheep, and mountain goats was lower when warming increased the rate of green-up and made high-quality forage available for a shorter period of time (Pettorelli et al. 2007). Also, earlier plant phenologies as a result of warming temperatures resulted in a mismatch in the timing of caribou calving and the date of peak forage resources, resulting in high mortality of newborn calves (Post et al. 2008b).

Changes in the spatial heterogeneity of the green wave might also importantly impact ungulate weight gain and newborn survival. When green-up is highly synchronized in space, as is predicted under warming scenarios, ungulates are limited to a shorter period of time during which early phenological plant stages are available as forage. This can lead to lower neonate survival (Post and Forchhammer 2008) and lower body weights entering winter. A longer growing season, however, allows ungulates access to snow-free forage for a longer period of time, which can result in higher body masses (Pettorelli et al. 2005). Warming might also result in milder winters, leading to increased winter survival of ungulates. These opposing forces of warming on ungulate foraging dynamics make predicting the ultimate consequences of climate change on ungulate populations a difficult task (Alonzo et al. 2003).

As climate change increases the speed of the phenological development of plants, resulting in a narrower window of time during which ungulates have access to high-quality forage, this could tip the predator–prey balance, causing ungulates to adopt alternate behavioral strategies. In the Clark's

Fork elk herd northeast of the park, some elk are now resident year-round near their historic winter range, while others continue to migrate during summer into the high-elevation meadows of Yellowstone National Park in search of forage. Research suggests that a decrease in forage availability on the summer range for migrant elk due to a contraction of the growing season, combined with increased predation, is leading to a decrease in the number of migratory elk (Milius 2010). This pattern of decreasing migratory elk compared with resident elk is also occurring elsewhere, such as in Banff National Park (Hebblewhite et al. 2006), where supplemental feeding of resident elk is also a factor influencing elk behavior.

Within Yellowstone National Park, wolf prey selection of elk appears to be driven by phenological development on the summer range. In the early years after wolf reintroduction, wolves killed bull elk primarily in late winter after the cumulative effects of the autumn rut and long winter weakened them. This weakened state was reflected by poor bone marrow condition of bulls killed by wolves in late winter. However, wolves began to prey on bulls in early winter during the drought years that followed. These bulls already had poor marrow condition in early winter, possibly due to below average snowfalls in the prior winter contributing to an abbreviated and lower magnitude green wave during spring and summer. This resulted in bulls entering the rut with low fat reserves such that by early winter they were already in poor condition and susceptible to wolf predation. In recent years, above average snowfalls have led to a resumption of the winter predation pattern whereby wolves kill bull elk primarily in late winter.

The dynamics of winter snowpack and summer phenological development of plants are primary drivers in animal movement, physiology, behavior, interactions with other species, and, ultimately, population dynamics. Understanding the links between climate change and these drivers will be critical to informing the ecology and management of Yellowstone's pronghorn, bighorn sheep, mountain goats, deer, elk, bison, and their predators in the years to come. Future work needs to elaborate on mechanisms driving the summer green wave and the resulting influence on wildlife.