Yellowstone Science

volume 16 • number 1 • 2008

Moose Population History on the Northern Yellowstone Winter Range

Plants Exposed to High Levels of Carbon Dioxide

Economics of Wolf Recovery in Yellowstone

NPS/JIM PEACO

Three moose in the snow at Round Prairie, May 1997.

Counting Moose

I am especially fond of the moose article in this issue by Dan Tyers, as years ago I helped count moose for this project while commuting from Cooke City to Mammoth. Those early spring mornings I would occasionally count more than 20 moose between Cooke City and Round Prairie. We are pleased to be able to reprint his article on moose population history on the northern Yellowstone winter range that reports on the results of that study. This is the first article on moose that has been printed in *Yellowstone Science,* and we hope to see more.

Mike Tercek et. al's article reports on the first concerted effort to study and characterize plant communities exposed to high levels of CO_2 in Yellowstone. Their findings support the idea that Yellowstone is a valuable resource for studying the long-term effects of impending global climate change on plants and plant communities.

The article by John Duffield et. al reports on two primary results from a 2005 visitor survey: preferences for wildlife viewing among Yellowstone visitors and the regional economic impacts attributable to wolf presence in the park.

I want to take this opportunity to point out the announcement and Call for Papers for the 9th Biennial Scientific Conference on the Greater Yellowstone Ecosystem on page 2. *The '88 Fires: Yellowstone and Beyond* will be held September 22–27, 2008 (please note this change in dates if you have received previous information), in Jackson Hole, Wyoming. Detailed conference information is available on the International Association of Wildland Fire's website at http://www.iawfonline.org/yellowstone/.

Please also visit the redesigned Greater Yellowstone Science Learning Center website at www.greateryellowstonescience.org. It has been restructured and is now resource-centric, and we are interested in feedback. You can send comments to Tami_Blackford@nps.gov or call me at 307-344-2204.

Alert readers may have noted that *Yellowstone Science*, usually a quarterly magazine, skipped an issue in 2007. Unexpected delays put us well behind our normal production schedule and we decided to omit Vol. 15(4).

We hope you enjoy the issue.

Yellowstone Science

a quarterly devoted to
natural and cultural resources

volume 16 • number 1 • 2008

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Bozeman, Montana
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Yellowstone Science is published quarterly. Support for *Yellowstone Science* is provided by the Yellowstone Association, a non-profit educational organization dedicated to serving the park and its visitors. For more information about the association, including membership, or to donate to the production of *Yellowstone Science*, visit www.yellowstoneassociation.org or write: Yellowstone Association, P.O. Box 117, Yellowstone National Park, WY 82190.

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Submissions are welcome from all investigators conducting formal research in the Yellowstone area. To submit proposals for articles, to subscribe, or to send a letter to the editor, please write to the following address:
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Yellowstone Science is printed on recycled paper with a soy-based ink.

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Silhouette of moose in pond.
Photo by Dan Tyers.

BOB WESELMANN

Winter visitors watch a wolf in Hayden Valley.

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Call for Papers, Posters, and Special Sessions

http://www.iawfonline.org/yellowstone/call_papers.php

Fourth Announcement

International Association of Wildland Fire

The '88 Fires: Yellowstone and Beyond

And, 9th Biennial Scientific Conference on the Greater Yellowstone Ecosystem

Jackson Hole, Wyoming
Sept. 22-27, 2008

For more information, visit:
www.iawfonline.org/yellowstone

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The International Association of Wildland Fire and the Association for Fire Ecology in association with the 9th Biennial Scientific Conference on the Greater Yellowstone Ecosystem is sponsoring a conference to remember the events of the Yellowstone area fires of 1988. These history-making fires will provide springboards for discussions and presentations about lessons learned, fire effects, large fire management, wildland fire policy, research related to the fires, the use of fire as a management tool, and many other issues. Post-conference field trips will be scheduled as well as companion and family-friendly activities. The Co-Incident Commanders are Paul Woodard and Don Despain. Visit our web site for more details at www.iawfonline.org/yellowstone

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Moose Population History on the Northern Yellowstone Winter Range

Daniel B. Tyers

This article has been adapted with permission from Alces*, a journal devoted to the biology and management of moose* (Alces alces). *It was originally published in* Alces *42:133–149 (2006).*

OBTAINING RELIABLE demographic information on any free-ranging ungulate population is difficult, but moose are among the most difficult ungulates to monitor because they are the least social North American deer and frequently occupy habitats with poor observability (Houston 1974). In 1985, I initiated a study (Tyers 2003) to identify moose habitat needs and population status on the northern Yellowstone winter range (NYWR). I also searched agency files and archives for statements on moose populations specific to the study area. Documents not considered by other authors that provided a historical context for population monitoring were of special interest.

NPS photo by John Brandow

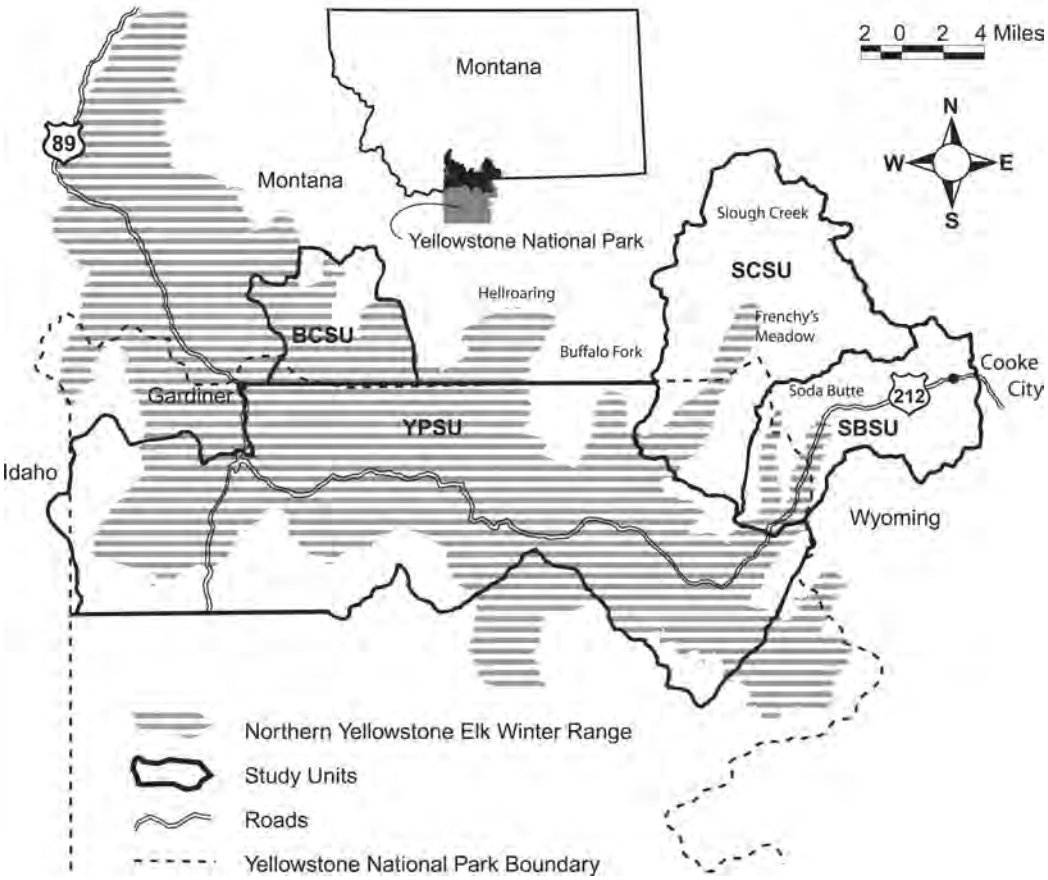

Figure 1. Map of the Northern Yellowstone Winter Range study area showing prominent features and sampling areas. BCSU =Bear Creek Study Unit; YPSU=Yellowstone Park Study Unit; SCSU=Slough Creek Study Unit; SBSU=Soda Butte Study Unit.

Moose population size is typically assessed in three ways: total area counts, sample estimates, and indices (Timmermann and Buss 1998). I used multiple population monitoring methods, including aerial surveys, horseback surveys, road surveys, and spatially restricted counts, to determine if vegetation changes associated with the massive 1988 wildfires in the Yellowstone ecosystem precipitated changes in moose population size. My monitoring efforts during 1985–2001 allowed me to evaluate the efficacy of several techniques for developing moose population indices and to identify reasonable techniques for monitoring future trends.

Study Area

The boundary of the NYWR is based on winter distribution of elk (Houston 1982); it includes parts of Yellowstone National Park, Gallatin National Forest, and mixed private and state lands (Fig. 1). During this study, elk were the dominant ungulate species (10,000–25,000), but mule deer (2,000–3,000), bighorn sheep (100–200), bison (500–1,000), and pronghorn antelope (100–300) also occupied the NYWR. Moose numbers were unknown, but they wintered throughout the study area in scattered areas of suitable habitat, usually at higher elevations than elk.

Vegetation on the NYWR varies from low elevation (<2,000 m) sage (*Artemisia* spp.) steppe to high elevation (3,000 m) coniferous forests. Willow (*Salix* spp.) stands occur along streams and in wet areas within forests. Lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), Douglas-fir (*Pseudostuga menziesii*), and whitebark pine (*P. albicaulus*) are the most common conifers in the NYWR. The 1988 fires burned approximately 43,000 ha of mature conifer forest in the NYWR, converting about 30% of the NYWR's mature forest to early seral stages (Tyers 2003).

Population Monitoring Techniques

Horseback transect index. In 1947, 1948, and 1949, Montana Fish and Game Biologist Joe Gaab looked for moose each September on about 177 km of trail in what is now the Absaroka-Beartooth Wilderness. Other observers repeated his route through the Hellroaring, Buffalo Fork, and Slough Creek drainages 34 times between July and late October from 1985 to 2001 while carrying out other tasks (trail maintenance, hunter compliance checks, and outfitter camp inspections). Like Gaab, they recorded the age (calf or >1 year of age) and gender (for moose >1 year of age) of all moose sighted during

daylight hours; sightings were reported as number of moose seen per day per observer group. Observer group size varied from one to six.

Road transect index. Moose sightings along the 89-km stretch of road from Gardiner to Cooke City (elevation 1,585–2,134 m), one of only two roads in the park maintained for wheeled vehicles year-round (the other is a section of U.S. Highway 191 that runs from Bozeman to West Yellowstone, Montana, through the park), were used as an index of moose distribution and abundance. Each trip was considered one sample regardless of the direction of travel. The estimated likelihood of sighting a moose each year was calculated by dividing trips with moose sightings by the total trips in a calendar year. Seasonal likelihoods of seeing a moose were determined from analysis of two-month periods (November/December, January/February, etc.). No attempt was made to standardize time of day, but at least four trips were completed every month. Data collected January 1987–December 1992 and January 1995–December 1997 were used to determine if there were differences in the number of moose seen seasonally and before and after the 1988 fires. To determine if changes between pre- and post-fire counts were consistent across the NYWR, the road was divided into five sections, each of which traversed similar vegetation and topography: (1) Gardiner to Mammoth (8.0 km), broken topography with arid grasslands and dry sagebrush unaffected by the 1988 fires; (2) Mammoth to Tower Junction (29.1 km), diverse topography where a mosaic burn pattern left open grasslands and Douglas-fir, but also mature spruce-fir forests, isolated stretches of stunted willow and aspen, and one small area of insect-killed Douglas-fir; (3) Tower Junction to Round Prairie (30.9 km), mostly a broad open valley with expanses of grasslands and sagebrush along the Lamar River where the 1988 fires did not cause much change in vegetative structure; (4) Round Prairie to Warm Creek (13.2 km) through mature lodgepole pine that was reached by the fires; (5) Warm Creek to Cooke City (8.0 km), which follows Soda Butte Creek through the largest willow stands in the transect, mature lodgepole pine and spruce-fir; only the area north of the road burned in 1988.

NPS/JIM PEACO

Bull moose near upper Soda Butte Creek.

Willow stand overflight index. Barmore (1980) identified several willow stands where moose were frequently observed during 1968–1970 aerial elk counts on the NYWR. Two of the largest, Frenchy's Meadow in the Slough Creek drainage and the willow stands along Soda Butte Creek outside the park's east boundary (Fig. 1), were sampled using fixed-wing aircraft between first light and 9 AM twice a month year-round from June 1987 to December 1990. All moose visible in and adjacent to the willow stands were counted, and seven radio-collared animals were located to determine what proportion of radio-marked animals in the drainage were in the willow stand.

Two indices of abundance were calculated for each flight: (1) the number of moose observed; and (2) the percent of available radio-collared moose seen. There were too few radio-collared animals to make valid estimates of total moose numbers in willow stands using mark-recapture methodology, but they did provide an estimate of the proportion of animals in the vicinity of the willow stands that were visible. The moose counts in willow stands were used to determine if moose numbers in favored willow stands varied among months or among years.

Daily willow stand observations. Because over-flights of willow stands were limited in number and were restricted to morning hours, ground observations were used to better delineate the time of year and time of day that moose were most easily observed in willow stands. From April 1996 through June 1997, moose were counted every half-hour daily, from first light until dark, in the willow stand between Silver Gate and Cooke City. Observations were limited to a standardized segment of the stand. These data allowed me to determine if counts from fixed-wing aircraft were optimally timed (diurnally and seasonally) and provided another potential population index. To account for the changes in number of daylight hours during the year and occasional gaps in data collection, data were standardized as number of moose seen per number of observation attempts.

Census flights. Data collected from road transects and willow stand flights suggested that moose were most observable around December 1 and May 1. Two fixed-wing aircraft were scheduled for eight survey nights in December and May 1988–1992. For the first two flights, pilots were instructed to follow transects (0.4-km parallel spacing on flat terrain and contour flying on slopes) as suggested by Gasaway et al. (1986), but this method was subsequently abandoned because of difficulties following transects due to wind and topography, limited visibility created by dense forest canopy, and observer frustration along unproductive sections. In the last six flights, searches were limited to areas where moose were most likely to be seen: the major willow stands along the park's north boundary. These

stands were covered carefully on all eight flights, with one plane covering the north half and the other plane the south. Aircraft were flown about 97–113 kph at 61–152 m above the ground, depending on obstacles.

Results

Historical Documents. The earliest reports on moose located in agency files did not have consistent assessments of population status in areas immediately north of and within the park during the early 1900s (Tyers 1981). McDowell and Moy (1942) reported that "old timers" regarded moose as a rarity in drainages along the park's north boundary between 1907 and 1915, while Rush (1942) reported that moose were considered "fairly common" by 1913 in the same area. In 1920, Stevenson (1920) noted that 13 moose were wintering in two drainages currently designated as prime moose winter habitat in the NYWR (12 in Hellroaring and 1 in Buffalo Fork) and that the habitat could support more wintering moose.

In 1921, the U.S. Forest Service began more extensive patrols (non-systematic snowshoe surveys conducted December to April) to deter poaching and monitor wildlife near the park's north boundary. Crane (1922) counted 16 moose during the winter of 1921–1922. Uhlhorn (1923) estimated 25 moose the winter of 1922–1923. Johnson's (1925) report for 1924–1925 accounted for 65 moose. He noted that calf survival was high and he believed the population was increasing. By 1936, U.S. Forest Service reports (USDA 1936, McDowell and Moy 1942) expressed concern over the long-term status of willow stands in the area and with the moose population that used them. These reports noted that willow condition was positively related to elevation and negatively related to access by elk and moose. The moose population wintering along the park's north boundary in 1935–1936 was estimated at 193 (54 in the Hellroaring, 80 in the Buffalo Fork, and 60 in the Slough Creek drainage). Over-winter utilization of willow in stands used by moose was estimated at 90%, and 75% of the willows in moose winter range were described as recently dead.

Montana Fish and Game Department personnel surveyed drainages north of the park from June to October 1942 (McDowell and Moy 1942). They covered 341 miles (549 km) on foot and 1,341 miles (2,158 km) on horseback. They reported 194 unduplicated moose and suggested that moose had expanded their range into the area from the park and that the population was increasing. They noted that more than 50% of willow plants were severely damaged in some areas where ungulates wintered while little or no degradation in willow stands was observed at elevations above ungulate winter range. They called for a controlled harvest of moose to prevent further willow damage. Cooney et al. (1943) reported an increase in moose numbers in 1943 over that reported for an area covered by McDowell and Moy (1942) during their 1942 survey.

In 1942 and 1944, Montana Fish and Game Department employees conducted winter moose surveys north of the park (Parsell and McDowell 1942, McDowell and Page 1944). They found 10–15 moose utilizing major willow stands in and around Frenchy's Meadow, but were surprised at the large number of moose occupying forested slopes adjacent to the willow stands. Parsell and McDowell (1942) estimated that elk and moose had utilized 90% of current willow growth by December 1942 and reported moose foraging on alder (*Alnus incana*), Engelmann spruce, lodgepole pine, and subalpine fir.

The 1945 Montana State Legislature authorized the Montana Fish and Game Commission to "remove and dispose of moose increasing in numbers and damaging property by the limited license method" (Montana Fish and Game Department 1945). McDowell (1946) reported that 40 permits were issued to hunters who killed 35 moose in autumn 1945 across an area that included the Hellroaring, Buffalo Fork, and Slough Creek drainages north of the park and the Cooke City area (McDowell 1946). Reports of the impacts on moose varied. A Forest Service employee reported 18 moose on a survey the following winter (McDowell 1946), where Cooney et al. (1943) had counted 31 in winter 1943. McDowell believed this decrease was likely due to moose moving to the Slough Creek drainage because willow production had declined in the Hellroaring drainage. In a 1945 winter survey, McDowell and Smart (1945) noted that 90% of the current year's willow production in some stands had been utilized despite the harvest. Only 20 of 30 permits were filled in 1946 and, at the request of hunters and guides concerned about declining moose numbers, permits were further reduced in 1947 (Couey 1947).

Montana Fish and Game biologist Joe Gaab traveled about 110 miles (177 km) of trail by horseback in September of 1947, 1948, and 1949 to count moose, using the same trails each year, and recorded 106, 71, and 30 independent moose sightings, respectively (Gaab 1948, 1949, 1950). In his opinion, the moose population was in a decline that he attributed, in part, to a continued deterioration of willow stands.

NPS, YELLOWSTONE NATIONAL PARK, YELL 28637

A man holding a moose calf at Silvertip Ranch, 1929.

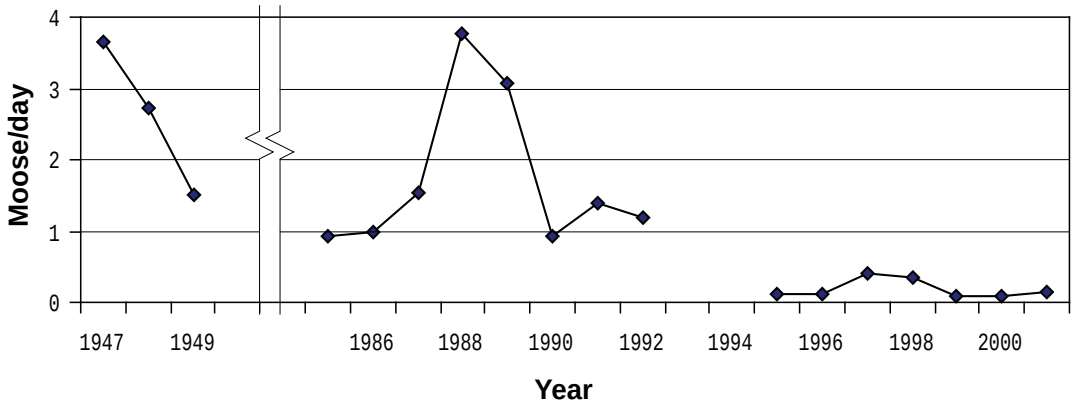

Figure 2. Average number of moose seen per party per day in horseback surveys in the Yellowstone ecosystem 1947–1949, 1985–1992, and 1995–2001. In years with more than 1 survey (1992, 1995–2001), values are the mean of multiple surveys.

Gaab stated in a 2000 interview that during the first years of quota hunting, hunters shot "many more" moose than permits allowed; he could recall anecdotes but not actual numbers (J. Gaab, Montana Fish and Game Department, personal communication).

Agency reports on moose population surveys and hunting seasons were scarce during most of the 1950s and 1960s. In 1963, Montana Fish and Game regulations listed a moose harvest quota of 45 in districts along the park's north boundary with no restrictions on age or gender. A 1964 wildlife management plan for the Gardiner Ranger District in the Gallatin National Forest noted that addressing the "moose problem" in the Hellroaring-Slough Creek area (declining moose populations and deteriorating willow stands) was a management priority (Kehrberg 1964).

A different perspective on moose population/habitat trends from the 1920s to the 1960s was provided by Tony Bliss, co-owner of a small parcel in Slough Creek near the large willow stand in Frenchy's Meadow. He summarized his observations of moose population trends (Kehrberg 1964): "1926 to 1935—lots of tall willow and few moose, elk and moose fed hay by Yellowstone Park in lower Slough Creek; 1935 to 1945—more moose, still lots of willow, feeding ended about 1936; 1941 to 1945—away at war; 1955 to 1962—fewer and fewer moose and extensive loss of tall willow."

Indices of hunter effort (such as hunting days per moose harvested) suggest that the moose population remained relatively stable through the 1970s and early 1980s (T. Lemke, Montana Fish, Wildlife and Parks, personal communication). When this project began in 1985, the moose quota for hunting districts north of the park was 55 with no restriction on age or gender. Quotas were reduced and restrictions implemented following extensive fires in the Yellowstone area in 1988. In 1990, the Montana Department of Fish, Wildlife and Parks issued 42 harvest permits (23 antlered and 19 antlerless) (T. Lemke, Montana Fish, Wildlife and Parks, personal communication). The quota was reduced to 21 (13 antlered, 8 antlerless) in 1991 in response to population declines observed during this study and to 13 in 1996 (all antlered).

Population Indices

Horseback transect index. The number of moose observed per day on the 177-km transect in the Absaroka-Beartooth Wilderness declined between 1947 and 2001 (Fig. 2). Only in 1988 and 1989 did sighting rates approach those reported by Gaab (1948, 1949, 1950). The total number of moose seen on surveys also declined. Gaab's counts averaged 69.0 (SD = 38.0, n = 3). Total counts in the 1980s prior to 1988 averaged 15.0 (SD = 4.4, n = 3). Post-fire counts in the late 1980s averaged 44.5 (SD = 6.4, n = 2). Counts in the 1990s averaged 6.0 (SD = 5.8, n = 20), and counts in 2000–2001 averaged 2.0 (SD = 2.8, n = 9).

Road transect index. The overall likelihood of seeing at least one moose while traveling the Gardiner to Cooke City road (n = 1,020) was 0.26 during the nine years data were collected (1987–1992 and 1995–1997). The likelihood of seeing at least one moose per trip was highest during May/June, when moose were observed on 50.4% of trips, and lowest during September/October, when moose were observed on only 7% of trips. Because numbers of trips were relatively consistent across seasons and years, analysis by section and of pre- and post-fire effects were based on pooled data for individual years.

The likelihood of sighting a moose during a drive between Gardiner and Cooke City was highest in 1989 (49%) and lowest in 1995 (2%). There was a statistically significant decline in moose sightings after the 1988 fires when a lag effect of a year was included in the test. No moose were seen in the Gardiner to Mammoth section either before or after the 1988 fires (Fig. 3). In the Mammoth to Roosevelt Junction section, moose were observed on 15% of trips before the fires but only 4% after the fires. In the Roosevelt Junction to Round Prairie section, the sighting incidence was 8% pre-fire compared to 1% post-fire. In the Round Prairie to Warm Creek section, incidences of sighting were similar before and after the 1988 fires (5% and 6%, respectively). The percentage of trips in which moose were observed in the Warm Creek to Cooke City section declined from 19% pre-fire to 14% post-fire, but this difference was not significant.

Figure 3. Likelihood (%) of seeing at least 1 moose while traveling the five sections of road between Gardiner and Cooke City, Montana, prior to and after the 1988 Yellowstone fires. Section 1 = Gardiner to Mammoth (8.0 km); Section 2 = Mammoth to Tower Junction (29.1 km); Section 3 = Tower Junction to Round Prairie (30.9 km); Section 4 = Round Prairie to Warm Creek (13.2 km); Section 5 = Warm Creek to Cooke City (8.0 km).

Willow stand over-flight index. The average number of moose seen per flight did not vary significantly among the four survey years (1987–1990). The highest average number seen per flight was in 1988 (4.9), followed by 1989 (3.1). Results were the same for 1987 and 1990 (1.9 moose per flight). The month with the highest average number seen per flight was November (9.3), followed by December (8.6), and May (7.6). The percent of radio-collared moose available for observation (i.e., alive in the drainage with operational radio-collars) seen per flight was not significantly different among years. Means for years varied from 0 (1987) to 12% (1988). Although no significant differences in the percent of collared moose observed by month were detected, the highest percent seen was in May (18.0%), followed by December (13.8%), and November (13.1%). This implies that in the late spring and early winter periods when moose were most visible, less than 20% of moose in a drainage were likely to be seen in fixed-wing surveys.

Daily willow stand observations. Daily counts of moose in a willow stand near Cooke City were made at half-hour intervals for 15 months. The mean number of moose seen per half-hour of daylight varied significantly among months. The highest average number seen per half-hour was in June 1997 (0.9), followed by December 1996 (0.6), and May 1996 (0.6). Average counts were highest between 0600–0930 hours and 2030–2130 hours. When times were adjusted for seasonal changes in daylight, moose were most visible in the hours near sunrise and sunset. In late spring and early winter when most moose per half-hour were recorded, the optimum times for observation were: May, 0600–0700; June, 0600 and 2130; November, 0730; and December, 0830.

Census flights. The north and south halves of the study area could not be covered on all flights, but moose sightings decreased sharply between November 1989 and May 1990 (Fig. 4). The highest number seen on a single survey was 59 in November 1989. The lowest count (13) occurred in May 1992.

Discussion

Population History

Long-term studies in North America support the idea that moose populations erupt, crash, and then stabilize at various densities depending on prevailing ecological conditions. Geist (1974) attributed this pattern to a response by moose populations to changes in habitat quality. In his opinion, over the species' evolutionary history, moose have typically occupied limited areas of permanent habitat in low densities. When fire has created transient habitat, they have rapidly colonized these areas and reached comparatively high densities. Population eruptions can also be triggered by plant succession following logging or by reduction of hunting or predation pressure if these were holding a population at low densities (Mech 1966, Peek et al. 1976, Messier 1991).

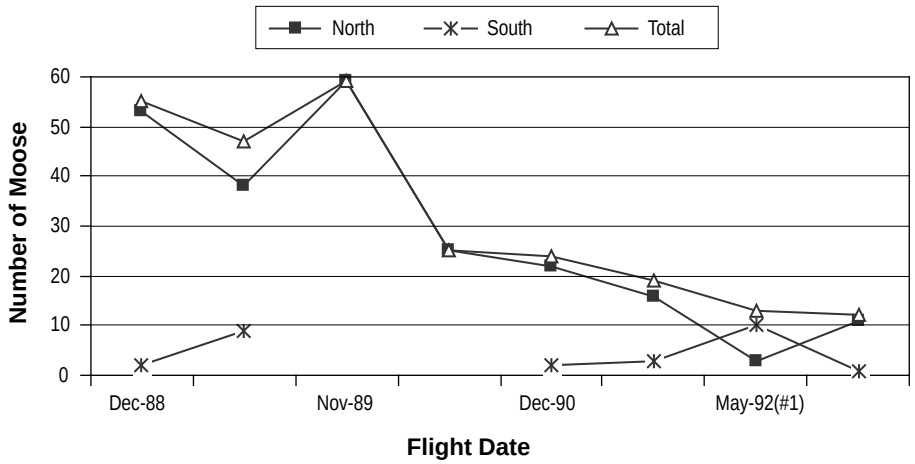

Figure 4. Number of moose seen during aerial surveys of the complete Northern Yellowstone Winter Range (NYWR) and in two segments of the NYWR (north and south of the Yellowstone River) from December 1988 to May 1992.

NPS/BRAIN HARRY

Moose evidently colonized the NYWR in the 1800s and initially increased in numbers in a manner similar to that occurring in other areas in North America, but the population did not respond positively to the 1988 forest fires as might have been expected based on Geist's (1974) theory and moose population responses to fire in Alaska (Schwartz and Franzmann 1989).

When moose arrived on the NYWR, they encountered an environment in transition due to European settlement. Human predation was initially important and then curtailed. Forest succession was altered with attempts to suppress fires. Agency reports suggest that moose had expanded into all suitable habitats on the NYWR by the middle of the twentieth century. Reports of negative impacts on willow stands (USDA 1936, McDowell and Moy 1942) indicate that at least in some drainages moose numbers may have stabilized or over-populated the area by the late 1930s. Regulated hunting, introduced in the 1940s to alleviate damage to willow stands on the NYWR, may have ended a population eruption triggered by a ban on hunting that dated from the early 1900s and by concerted efforts to eliminate predators from the Yellowstone ecosystem during the 1910s–1930s. Because no systematic monitoring of moose populations was done from 1950 to 1985, the population trends during that period will never be known, but the horseback surveys conducted from 1985 to 1987 produced similar moose sighting rates as Gaab's 1949 survey, perhaps indicating that the population remained relatively stable from 1949 to 1987.

The 1988 Yellowstone fires negatively affected moose habitat and population levels at a landscape scale. In the winter of 1988–1989 and the summer of 1990, some indices produced exceptionally high values for moose numbers. By the winter of 1990–1991, however, all indices indicated substantial declines in moose. In areas where fire effects were severe, the reduction in numbers was greater than in areas where fire impacts were minimal. No sign of population recovery was evident through 2001, the last year in which data for one or more indices was collected.

Population Monitoring

The horseback surveys, road transects, and aerial surveys identified a decline in moose numbers following the 1988 fires. The willow over-flight index did not reveal any significant decline from 1987 to 1990, but indicated a similar pattern of change (relatively low in 1987, high in 1988 and 1989, low in 1990) to that provided by the horseback survey and the road transect.

The horseback transect index had high sighting numbers per day in 1988 and 1989 and consistent, very low sighting rates from 1995 to 2001. The high numbers of moose seen in 1988 and 1989 were probably due to increased sightability resulting from the burning of climax forests and to the movement of moose into unburned willow stands along the route. Data on moose movement and survival (Tyers 2003) collected from 1996 to 2001 reflect a real decrease in moose numbers. The horseback transect index probably under-represented actual moose numbers before 1988.

The road-transect index generally mirrored results from the horseback survey; an increase in sighting likelihood in 1988–1989 and a decline thereafter. The decrease was most pronounced on the section where forests were most affected by fire (Mammoth to Round Prairie) and least pronounced where areas bisected by the road were not burned. The post-fire decline on the road transect was apparent as early as 1990 while values from the horseback survey for 1990–1992 were similar to values for 1985–1987. This may indicate that the road survey was more sensitive to population changes than was the horseback survey or it may be only an artifact of sampling greater areas of burned terrain or more marginal habitat on the road transect than on the horseback survey.

Systematic aerial surveys were not initiated until the winter after the 1988 fires and were discontinued in 1992, when moose sightings were extremely low and limited to a few large willow stands. Variability of moose counts on flights within the same stand, season, and year was so high that no significant decline was detected until 1990.

The efficiency of indices employed in this study could potentially be improved by timing sampling to optimize moose sightability. February and March are considered the most difficult months to find moose because they are more likely to be in dense cover. Sightability in November and December may be higher because moose form larger groups and have stronger preferences for vegetation with low, open canopies. This has been found in Alaska (Peek et al. 1974, Gasaway et al. 1986), Minnesota (Peek et al. 1974, Mytton and Keith 1981), Michigan (Peterson and Page 1993), Alberta (Lynch 1975), and Ontario (Bisset and Rempel 1991). However, 34 consecutive years of aerial surveys in Saskatchewan were successfully conducted in January and February (Stewart and Gauthier 1988).

In Yellowstone, Barmore (1980) found seasonal variation in moose sightability during attempts to count moose

incidental to elk distribution flights from 1968 to 1970. He concluded that moose were difficult to observe in this environment. Most of the moose Barmore saw were associated with willow, and he was most successful at finding them there in May, early June, and December. In my study, moose were more likely to be observed from fixed-wing aircraft in early winter (November and December) and May than at other times of year. A similar seasonal pattern was observed during intense ground sampling in willow stands near Cooke City.

Time of day also may influence visibility of moose (LeResche and Rausch 1974). Timmermann (1974) suggested from 1000 to 1400 hours as the optimal time for moose aerial surveys in Ontario. Peterson and Page (1993) preferred to survey moose in Minnesota just after sunrise. Data from half-hour counts in a willow stand near Cooke City for this study indicated that moose sightings in the Yellowstone area were most likely in early morning (0600–0930 hours) and late evening (2030–2130 hours).

Would aerial surveys in early winter or late spring, concentrated in early morning hours, provide an efficient means of monitoring moose associated with the NYWR at current population levels? Aerial surveys of moose have produced mixed results (LeResche and Rausch 1974, Stevens 1974, Novak 1981), but counting moose on winter ranges from aircraft is still considered the most practical method for estimating moose numbers over large areas in North America (Timmermann and Buss 1998). In some areas, aerial surveys are very efficient. Edwards (1954) reported that 78% of moose located during intense ground surveys were seen from the air. Evans et al. (1966) reported that observers in fixed-wing aircraft saw 94% of moose observed by crews in helicopters. Gasaway et al. (1978) noted that 91% of radio-collared moose available to be seen were found during intensive searches from the air.

It is unlikely that fixed-wing aircraft used in a systematic survey of the NYWR would locate a high proportion of the moose population. Even in the months with highest sightability (November, December, and May), less than 20% of radio-collared moose known to be in drainages containing preferred willow stands were observed from fixed-wing aircraft. High variability in both percent of radio-collared animals observed and in total animals observed indicates that using a large number of radio-collared moose to develop a sightability model, an expensive option that has had utility in estimating elk numbers (Samuel et al. 1987), is not likely to yield good results given the low density and low visibility of moose associated with the NYWR. Low density and low sightability would also limit the utility of helicopter surveys.

Developing an index of moose abundance using fixed-wing counts in early winter or late spring and limited to early morning hours, or perhaps even ground counts of moose in specific willow stands, does have potential for tracking changes in the moose population associated with the NYWR. Boundaries of key willow stands are easily identified from the air or ground and cover relatively small areas (most are <40 ha). Counts of moose along the highway between Gardiner and Cooke City during early winter and late spring may also provide a relatively cheap means of monitoring population trends. Summer–autumn horseback surveys, especially when costs can be mitigated by combining counts with required tasks such as trail maintenance and hunter management, may also be useful in tracking trends in moose populations. Although indices are less intellectually satisfying as a base for management of moose than are statistically valid population estimates, they may provide a reasonably reliable mechanism for determining population trends in situations where logistical constraints preclude accurate estimates of moose numbers.

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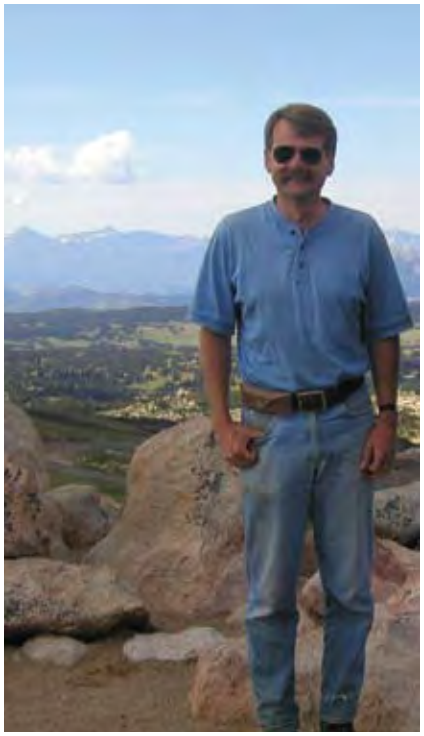
Acknowledgements

This project was conducted at the request of the Northern Yellowstone Cooperative Wildlife Working Group, which includes Montana Fish, Wildlife and Parks, Yellowstone National Park, Gallatin National Forest, and the U.S. Geological Survey Northern Rocky Mountain Research Center. Funding was provided by Gerry Bennett, Dick Ohman, Jim Wood, John and Kathryn Harris, Safari Club International Montana Chapter, Gallatin National Forest, Montana Fish, Wildlife and Parks, and Yellowstone National Park. I also wish to thank those who helped make this study possible by providing essential help in the field, office, or in analysis: Phyllis Wolfe, Tami Blackford, John Varley, Frank Singer, Tom Lemke, Sam Reid, Patrick Hoppe, Steve Yonge, Jeremy Zimmer, Par Hermansson, Sarah Coburn, Reyer Rens, Kim Olson, Maria Newcomb, Tom Nelson, Rob St. John, Tris Hoffman, Ellen Snoeyenbos, Anna Carin Andersson, Bill Chapman, Tom Drummer, Bill Gasaway, Emma Cayer, Vanna Boccadori, Mark Petroni, Tom Puchlerz, Lynn Irby, Jack Taylor, Tom McMahon, Harold Picton, Peter Gogan, Kurt Alt, Harry Whitney, Mike Ross, Kelsey Gabrian, and Randy Wuertz.



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Plants Exposed to High Levels of Carbon Dioxide in Yellowstone National Park

A Glimpse into the Future?

Michael T. Tercek, Thamir S. Al-Niemi, and Richard G. Stout

MICHAEL TERCEK

Ross' bentgrass (*Agrostis rossiae*), which is endemic to Yellowstone, often grows in areas with very high carbon dioxide concentrations.

HUMANS ARE CURRENTLY conducting a biology experiment on a planetary scale. Earth's ecosystems are being altered to such a degree by our collective activities that scientists have recently coined the term "anthropocene" to describe the current geologic age (Crutzen and Stoermer 2000) because human impacts such as land use and industrial pollution have grown to become significant geological forces, frequently overwhelming natural processes.

The burning of fossil fuels is often cited as a prime example of how we are exerting major effects on the environment. This, along with deforestation, has resulted in a 50% increase in atmospheric carbon dioxide (CO_2) since 1800. The latest estimates are that the level of this atmospheric "greenhouse gas" will more than double within the next 100 years (Solomon et al. 2007). Although the link between increasing atmospheric CO_2 and global warming has long been controversial, the vast majority of scientific evidence now strongly supports this connection (see the most recent reports from the Intergovernmental Panel on Climate Change at http://www.ipcc.ch). The general conclusions from these reports are that significant increases in both Earth's atmospheric CO_2 concentration and average air temperature will occur within this century, at historically unprecedented rates.

Such environmental changes will be extremely rapid from the perspective of biological evolution. For example, it is unclear how individual plant species and plant communities will adapt to an abruptly warmer, high-CO_2 world. These are critical questions since we depend on plants for food, fiber, and fuel, and since plants usually provide the foundation for biotic communities. Recent studies show that natural ecosystems are already responding to human-caused environmental changes (see Cleland et al. 2007 for example). But how will natural ecosystems respond to the predicted higher CO_2 levels and warmer temperatures compared to today? Plant communities that already exist under such conditions may help provide answers.

Areas with surface geothermal activity, such as Yellowstone, offer environments that often contain high CO_2 because of volcanic gas vents, and they have high temperatures due to geothermal heat. Until recently, virtually nothing was known about the magnitude of Yellowstone's CO_2 emissions, how widespread they were, or which plant species grew near them. Here we report on the first concerted effort to study and characterize plant communities exposed to high levels of CO_2 in Yellowstone National Park (YNP). Our results show that Yellowstone offers rare, natural environments for scientists to investigate the long-term effects of increased CO_2 and high temperatures (both separately and in tandem) on plants.

Background: Responses of Plant Communities to CO_2 Enrichment

In the past 20 years, scientists have been conducting both greenhouse and field experiments in order to predict how plants will respond to elevated CO_2 levels of 500 to 800 parts per million (ppm) compared to the current "background" CO_2 concentration (about 380 ppm). Most of these investigations have used either small-scale growth chambers or free air CO_2 enrichment (FACE) facilities that pump CO_2 into several acres of crops, natural grassland, or forest (Long et al. 2005; Long et al. 2006). To a much lesser extent, studies have been conducted using natural CO_2 springs (see below). It is important to realize that the physiological responses observed in plants during these experiments help us predict how productive our food crops will be and how nutritious forage species will be for grazing animals in a high-CO_2 future. These physiological changes might also determine whether some plant species survive in their current natural habitats or are marginalized or eliminated by invading plant species.

The growth chamber and FACE studies have produced somewhat complex results, but they agree in many generalities (Korner 2000). In summary, the growth chamber studies tend to indicate that higher levels of CO_2 increase crop production. However, outdoor experiments using FACE facilities tend to show that the benefits of high CO_2 on plant productivity have been overestimated and may be only short term (Long et al. 2006). At the physiological level, elevated CO_2 usually produces an increase in leaf biomass, a decrease in nitrogen content per unit of biomass, and higher water use efficiency, which is the amount of water used per unit of biomass production. We discuss these findings in more detail below.

The influence of elevated CO_2 on plant productivity is not consistent, and it partly depends on whether there are enough resources available to support a higher photosynthetic rate. Carbon dioxide is the fuel for photosynthesis, and it is in relatively short supply in our atmosphere (less than 0.04%). Therefore, it is easy to understand why increasing CO_2 availability to plants might increase photosynthesis and boost biomass production. However, plants need a variety of nutrients in order to maintain their metabolism, and carbon is only one of them. If increased carbon availability (increased atmospheric CO_2) is not accompanied by an adequate supply of other resources, particularly nitrogen, then there will be little change in plant growth rate.

Even though adequate nitrogen supply is crucial to maintaining productivity gains in the long term, an enriched CO_2 environment may allow plants to use nitrogen more efficiently. FACE studies have shown that plants often respond to extended CO_2 enrichment by reducing the concentration of their main photosynthetic enzyme, ribulose bisphosphate carboxylase (RuBisCo) (Ellsworth et al. 2004). RuBisCo captures CO_2 and begins the process of photosynthetic conversion of this gas into sugars. Usually RuBisCo is by far the most abundant protein in leaves. Plants make less RuBisCo under high-CO_2 conditions, presumably because they do not need as much of this enzyme for photosynthesis and because it allows them to conserve nitrogen. Consequently, the plant material

may have less protein content per amount of biomass and, thus, less nutritional value as forage. For this reason, some think that increased atmospheric CO_2 would likely have a negative impact on grazing animals, such as the bison and elk in YNP (Wilsey, Coleman, and McNaughton 1997).

Finally, increased CO_2 supply usually increases water use efficiency in plants. This is chiefly because stomates (the cellular pores in leaves that allow for gas exchange) tend to close when CO_2 levels increase. When opened, the stomates allow CO_2 to enter the leaf and water to escape. Land plants try to conserve water by closing their stomates if CO_2 concentration increases. This could affect the species composition of many plant communities as plants invade drier areas in which they could not grow previously and other species are eliminated.

These are only a few of the ways in which plants respond to increased CO_2. We have not addressed the issue of increased temperatures due to global warming. It's easy to see why reliably predicting the botanical effects of increased atmospheric CO_2 is highly problematic at the whole-plant level and even more so at the plant community level.

So far, we've mainly discussed how plants can acclimate to sudden increases in atmospheric CO_2. But in the long term (decades, centuries) will these conditions exert pressures through natural selection that result in genetic adaptations to elevated CO_2? And if so, what will likely be the nature of these adaptations?

Studies Using Environments Naturally High in CO_2

In attempts to answer these questions, scientists have examined plants growing near natural CO_2 springs and, to a much more limited extent, plants around seams of burning coal deposits (Raschi et al. 1997; Badiani et al. 2000; Pfanz et al. 2004). High-CO_2 environments often occur in areas of volcanic activity and are manifested as "mofettes" (carbon dioxide springs), CO_2 vents, or elevated CO_2 gas flux from the soil. Though not as controllable as greenhouse or FACE experiments, these natural high-CO_2 environments provide opportunities to examine relatively long-term adaptations of plants to high CO_2. Most studies of this kind have been from sites in Europe, primarily Italy (Raschi et al. 1997); few have been from North America. As with the above greenhouse and FACE experiments, some consistent patterns emerge, including increased biomass production and higher water use efficiency.

Even though they have contributed useful information, previous studies conducted near natural sources of CO_2 have significant drawbacks. Typically, they are limited in geographic scope, are often located in regions disturbed by human populations, and are usually not directly comparable with similar, background-CO_2 sites. Because YNP encompasses one of the largest surface geothermal areas on Earth, and since it has been relatively undisturbed by humans, most of these drawbacks may be avoided.

Like other large volcanic and hydrothermal areas on Earth, Yellowstone emits a large volume of gases, predominantly CO_2 (95–99%) (Kharaka, Sorey, and Thordsen 2000; Werner and Brantley 2003). Despite this, there have been only a few reports of the effects of CO_2 on photosynthetic algae found in Yellowstone hot springs (e.g., Rothschild 1994) and none, to our knowledge, involving plants. Therefore, we set out to explore the possibility that plants and plant communities are chronically exposed to high levels of CO_2 in YNP.

Methodology

CO_2 Measurements. To measure carbon dioxide in the field, we used several different portable CO_2 gas analyzers (see glossary). Since our initial work was largely exploratory in nature, these instruments were used to make relatively short-term (15 to 30 minutes) CO_2 measurements at multiple locations within selected study areas. At each location we measured soil temperature and pH, and noted the predominant plant species. Once high-CO_2 locations were identified, more measurements were periodically made at some locations to better establish average long-term CO_2 levels. Leaf tissue specimens were collected from hot springs panic grass (*Dichanthelium lanuginosum*) and other species at some of these high-CO_2 locations and at background-CO_2 locations nearby for subsequent laboratory analyses to test the presumption that plants in these areas were indeed chronically exposed to elevated CO_2. Two indicators of plant exposure to elevated levels of CO_2 are (1) a decrease in the key photosynthetic enzyme RuBisCo and (2) an increase in the soluble sugar sucrose. Sucrose (along with starch) is a major metabolic end-product of photosynthesis.

RuBisCo Measurements. As previously mentioned, plants typically make less RuBisCo when exposed to high levels of CO_2, presumably to conserve nitrogen. We used two independent methods to determine the relative amounts of RuBisCo in leaf specimens collected in YNP. In the first technique, we used commercially available antibodies that specifically bind to RuBisCo. Such antibodies can be used in immunoassays (see glossary) in order to identify and quantify proteins, even in complex mixtures. In the second technique, we specifically tagged all the RuBisCo proteins in our leaf extracts with a radioactively labeled substance (Evans and Seeman 1984) and then determined the radioactivity of each sample. The higher the radioactivity in the sample, the more RuBisCo was present. Though a bit more involved, this method is much more accurate than the antibody method.

Soluble Sugar Analysis. At elevated levels of CO_2, leaves typically contain more sugars, mainly sucrose, presumably because of higher photosynthetic rates. We extracted soluble sugars from our leaf tissue specimens and used a technique called high performance liquid chromatography (HPLC; see glossary) to identify and measure each sugar.

Results

Surveys of Suspected High-CO_2 Areas in Yellowstone. We found 15 sites in YNP that had consistently elevated CO_2 concentrations (Fig. 1). Fourteen of these sites contained several high-CO_2 plant communities, ranging in surface area from 1 m^2 to greater than 10 m^2. The fifteenth site, Death Gulch, also had very high CO_2 emissions, but its famously lethal crevices (Haines 1996) did not contain vegetation in the areas nearest to the CO_2 vents.

Most of the sites contained vegetation that is typical of thermal areas, such as hot springs panic grass, Ross' bentgrass (*Agrostis rossiae*), and the moss *Racomitrium canescens.* However, several plant communities near Mammoth, Mud Volcano (Ochre Springs), Geyser Creek, and Sylvan Springs that were distant from obvious thermal activity included lodgepole pine (*Pinus contorta*), juniper (*Juniperus communis*), or a variety of non-thermal forbs, grasses, and sedges. Without an infrared gas analyzer, we would not have suspected that these areas contained volcanic vents. Soil temperatures a few inches below the soil surface in our survey ranged from non-thermal (about the same as air temperature) to 45°C (113°F).

In this article we offer representative data for two of the areas that we have identified with above-normal CO_2: Mammoth Upper Terraces and Mud Volcano (Figs. 2 and 3). An interactive version of our entire survey is available online at http://www.YellowstoneEcology.com/research/co2/index.html. It includes photographs, graphs of our CO_2 measurements, and lists of the plant species present at each site.

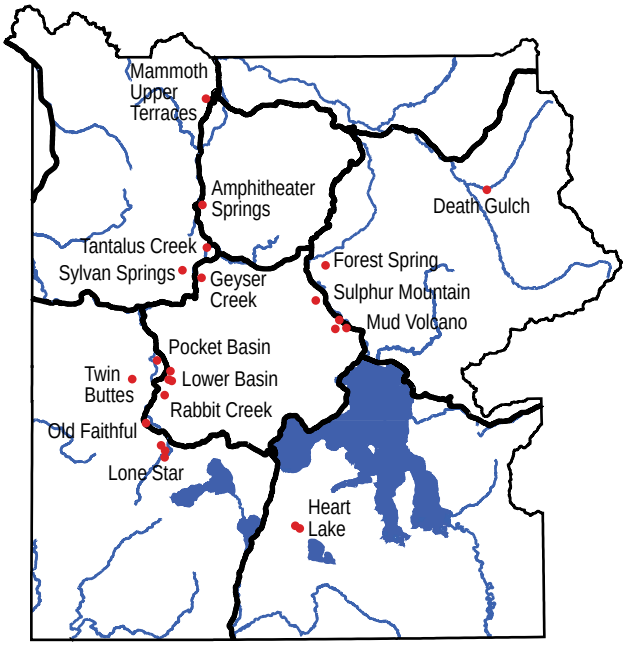


Figure 1. Each location marked on the map contains from 2 to 30 plant communities growing in above-normal CO_2 concentrations.

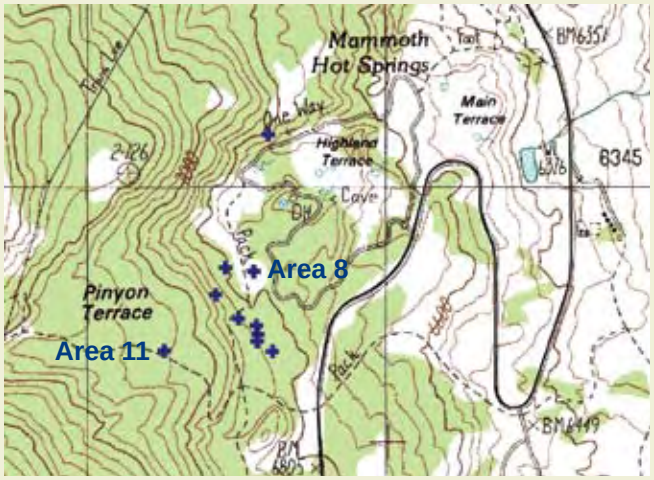
GLOSSARY

CO_2 Gas Analyzers. Because the IR (infrared) light spectrum absorbed by a particular chemical compound is unique, it can serve as a signature or fingerprint to identify that molecule. An infrared CO_2 gas analyzer consists of a light bulb that generates an IR light beam that is passed through the sample and an IR light detector set to the precise IR spectrum of CO_2. The more CO_2 present in the sample, the more IR light in this spectrum is absorbed, and the lower the amount of IR light detected.

HPLC. High-performance liquid chromatography (HPLC) is used frequently in biochemistry and analytical chemistry. Chromatography is a general term for laboratory techniques used to separate mixtures of substances. Typically, it involves passing a mixture (the "mobile phase") through a so-called "stationary phase," often packed into a small tube or column. The stationary phase may consist, for example, of cellulosic beads or of synthetic resins that separate substances on the basis of size, charge, etc. In our case, a mixture of sugars in an aqueous solution is slowly pumped through a chromatography column, and the sugars are separated on the basis of size, with the larger molecules emerging from the column faster than the smaller ones. (The column is calibrated by first running through known sugars, each of a known quantity.)

Immunoassay. An immunoassay is a biochemical test that measures the level of a substance using the reaction of an antibody to its antigen. In this case the antigen is RuBisCo. To make antibodies against this protein, it is first purified from plant tissue. A solution containing the purified RuBisCo is then injected into a mouse or a rabbit, for example. Mammals make antibodies (proteins called immunoglobulins) to this foreign protein as part of their normal immune response. After a few days, blood is drawn from the animals and the antibodies are collected from the serum. The immunoassay takes advantage of the extremely specific binding of an antibody to its antigen. The presence of the antibodies can be detected and measured using a number of biochemical techniques.

Mammoth Area



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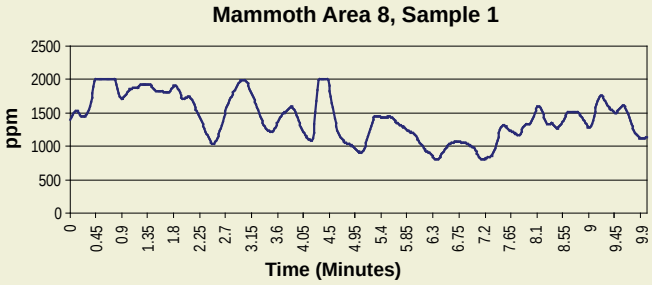
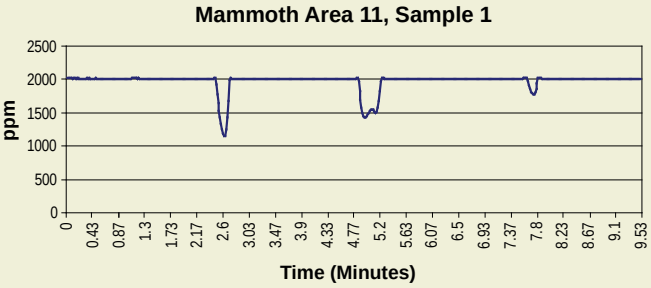


Soil Temperature = 35°C
pH = 7.0
Plant Species: sedges, asters, dalmatian toadflax



Soil Temperature = 14°C
pH = 7.0
Plant Species: lodgepole pine, juniper, strawberry, barberry, grasses

Figure 2. Crosses on the map indicate locations of high-CO_2 plant communities in the Mammoth Upper Terraces area. The location of the two representative communities are shown in the photographs and summarized in the graphs showing CO_2 parts per million sampled every 16 seconds.

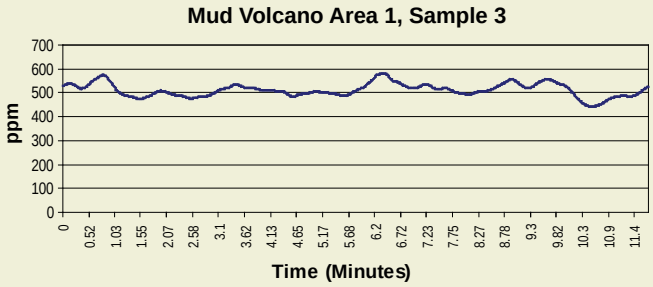
RuBisCo in Leaf Extracts. As shown in Figure 4A, immunoassays aimed at quantifying RuBisCo in our leaf specimens detected relatively lower amounts of this protein in *D. lanuginosum* from high-CO_2 study sites compared to those in control plants collected from background-CO_2 sites. These results were supported by similar, but more quantitative, outcomes using the radiolabeled marker for RuBisCo (see Figure 4B). Also, plants growing at the highest levels (>600 ppm) of field-measured CO_2 generally displayed the lowest levels of RuBisCo.

Leaf Soluble Sugars. Figure 5 shows typical results of HPLC analysis of the soluble sugars in hot-water extracts from leaf specimens of *D. lanuginosum* collected at sites with background or with high levels (450 to 2,000 ppm) of CO_2 as determined by our field measurements. In most cases, significantly higher amounts of sucrose were found in leaf extracts from plants collected at sites with measured CO_2 levels at ≥600 ppm than from plants at background CO_2 sites.

Conclusions

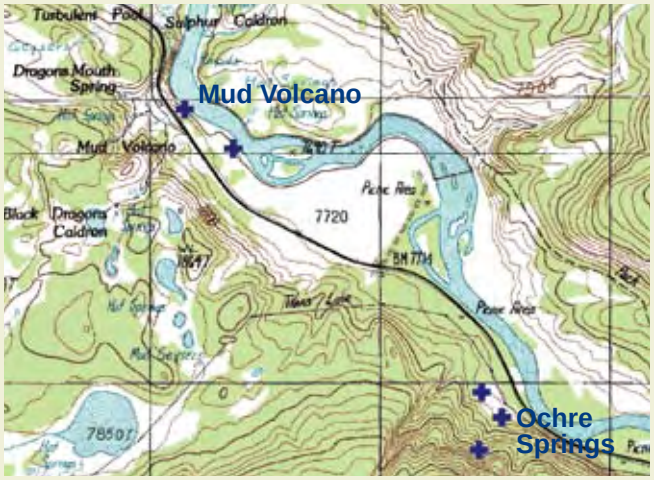
Using portable CO_2 infrared gas analyzers, we have measured the soil-surface CO_2 concentrations at dozens of vegetated geothermal areas within Yellowstone. Many of these sites displayed high-CO_2 values, ranging from 450 to more than

MICHAEL TERCEK



Soil Temperature = 14°C
pH = 4.5
Plant Species: sedges, grasses, including *Agrostis scabra*

Mud Volcano Area



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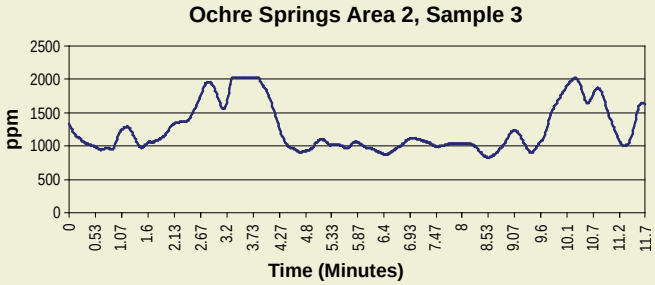

Soil Temperature = 6°C
pH = 4.0
Plant Species: lodgepole pine, spruce seedlings, sedges

Figure 3. Crosses on the map indicate locations of high-CO_2 plant communities in the Mud Volcano area. The location of the two representative communities are shown in the photographs and summarized in the graphs of CO_2 parts per million sampled every 16 seconds.

2,000 ppm. A few of the sites are greater than 10 m^2 and almost all are far removed from human disturbance. Also in contrast to most previous studies of high-CO_2 environments, our surveys of Yellowstone have identified numerous high-CO_2 sites that can be paired with control sites that have background levels of CO_2 and comparable vegetation, soil type, and environmental characteristics.

At both our background- and high-CO_2 sites, leaves were collected primarily from hot springs panic grass (*D. lanuginosum*), which is often the dominant plant species in YNP geothermal soils. We found that leaves from the high-CO_2 sites consistently had less RuBisCo, the primary photosynthetic enzyme, than similar leaves collected from plants growing at background CO_2 sites. Using HPLC analysis of leaf extracts, we also found that leaves collected at high-CO_2 sites typically had higher levels of sucrose, a photosynthetic end-product. These findings support the hypothesis that plants growing in high-CO_2 areas of YNP make physiological adjustments similar to those observed in experimental Free Air CO_2 Enrichment (FACE) studies. However, unlike plants in FACE experiments, YNP plants have likely been exposed to elevated CO_2 concentrations for many generations and, in some cases, may have also had to cope with high temperatures.

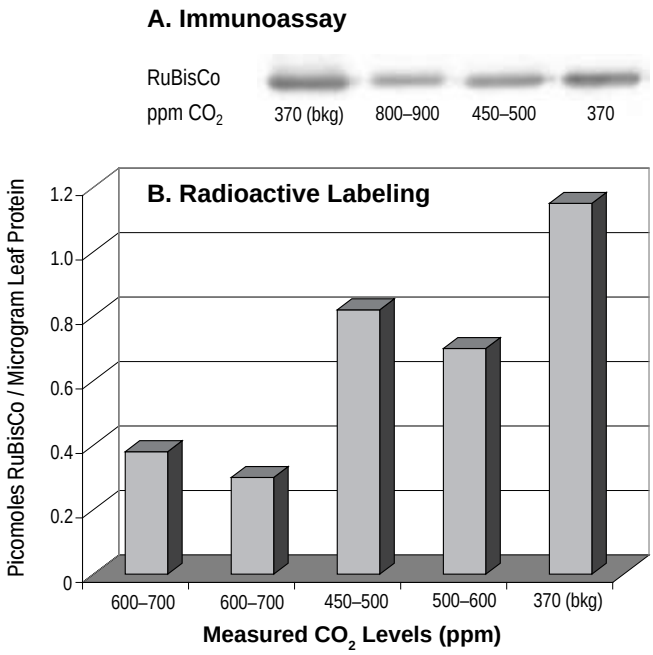

Figure 4. A) RuBisCo levels in *D. lanuginosum* from background-CO_2 (bkg) and high-CO_2 sites in YNP determined using immunoassay technique. Leaf specimens were collected from plants exposed to the field-measured CO_2 levels indicated below, wrapped in aluminum foil, and immediately frozen in liquid nitrogen. They were stored at –80°C at Montana State University until proteins were extracted from the leaf tissue in the lab. Equal amounts of the extracted proteins were fractionated, and the RuBisCo proteins (large subunit) were labeled with specific antibodies and visualized using a chemiluminescent technique (Stout and Al-Niemi 2002).
B) RuBisCo levels in *D. lanuginosum* from background-CO_2 (bkg) and high-CO_2 sites in YNP determined using a specific radiolabeling technique. Leaf specimens were collected and stored as described above. In the lab, leaf protein extracts were obtained and equal amounts of each sample were mixed with a radiolabeled analog of ribulose bisphosphate (RuBisCo substrate) [2-^{14}C]-carboxyarabinatol bisphosphate (Evans and Seemann 1984). The proteins were then precipitated and collected using microfiltraton. These filter disks were thoroughly washed to remove unbound radiolabel, and then the amounts of radioactivity on the filter disks were determined.

Figure 5 (*right*). The chief soluble sugars in hot-water extracts from *D. lanuginosum* collected from both background- and high-CO_2 sites in YNP. Each column represents the average (with standard error bar) of four replicate leaf samples from the same plant. Plants were collected from four sites, each with different amounts of measured CO_2 (as indicated in the legend).

Our findings support the idea that Yellowstone National Park is a valuable resource for studying the long-term effects of the impending global climate change on plants and plant communities. We plan to more thoroughly study some of these geothermal sites through long-term CO_2 and temperature measurements, more detailed plant laboratory analyses, and more attention to plant community structure. Such relatively undisturbed environments, which may have existed for tens of thousands of years, may contain plants that display biochemical, cellular, or developmental adaptations to chronic high temperatures and high CO_2. These plants may offer us a botanical glimpse of things to come. For example, they may provide plant ecologists and rangeland and forest managers information with which to make more accurate projections of future changes to plant communities. Such plants may also represent potential genetic resources for crop breeders and plant genetic engineers preparing for what will likely be a warmer, high-CO_2 world.

Since we initiated our studies in 2004, at least three other researchers have begun to investigate high-CO_2 environments in Yellowstone. Dr. Cathy Zabinski at Montana State University has been investigating how a ubiquitous root/fungus symbiosis, arbuscular mycorrhiza, functions in varying temperature and CO_2 environments. Drs. Shikha Sharma and David Williams at the University of Wyoming are using both radioactive and stable isotopes of carbon and oxygen in leaves to assess how the photosynthetic properties of vegetation are changing in response to elevated CO_2.

It is now generally accepted that human activity is making rapid, dramatic changes to the global environment. How will these environmental changes affect life on Earth? The experiment is already underway, but it's very difficult to predict the outcomes. Some clues may be provided by plants growing in Yellowstone National Park.

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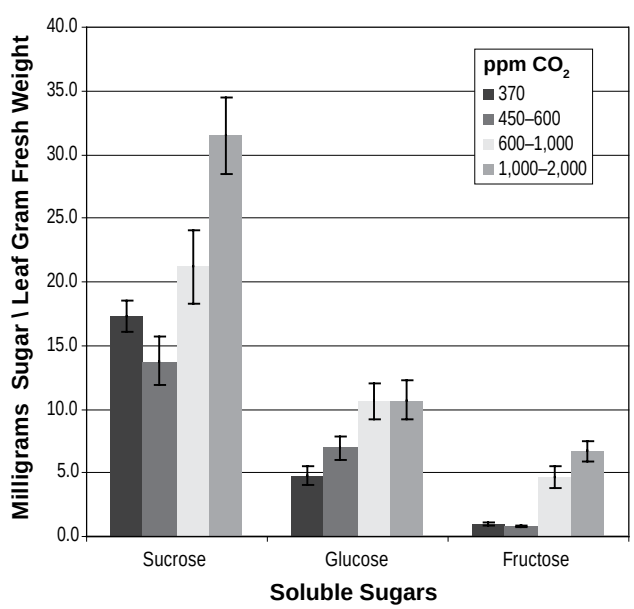

Acknowledgements

We thank the Yellowstone Center for Resources, especially Christie Hendrix and Christine Smith, for facilitating this research. Funds for this work were provided to Richard Stout by NASA Grant NAG 5-8807 through the Montana State University Thermal Biology Institute and by the Montana Agricultural Experiment Station, Project No. MONB00242.

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Dr. Richard G. Stout is an Associate Professor in the Department of Plant Sciences and Plant Pathology, Montana State University–Bozeman. He has been studying plants growing in geothermal environments in North America, including both Yellowstone and Lassen Volcanic National Park, for more than 10 years. His research on the cellular mechanisms of heat tolerance in hot springs panic grass (*D. lanuginosum*) has been published in several scientific journals (see http://www.plant-stuff.net/hotplants). He has also collaborated with scientists studying fungi that form symbiotic relationships with this plant (see *Yellowstone Science* 13(4), Fall 2005, p. 25).

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The U.S. Fish and Wildlife Service (USFWS) began reintroducing the endangered gray wolf to the Greater Yellowstone Area (GYA) and central Idaho in 1995. The restoration of wolves to the GYA has become one of the most successful wildlife conservation programs in the history of endangered species conservation. Yellowstone is now considered one of the best places in the world to watch wild wolves. The visibility of wolves within the park and public interest in wolves and wolf-based education programs have far exceeded initial expectations. But questions have persisted about the economic impact of wolf restoration that we have sought to answer.

During preparation of the Environmental Impact Statement (EIS) that was completed by the National Park Service prior to wolf restoration (USFWS 1994), one of the main concerns of wolf-reintroduction opponents was the expenditure of public federal funds for the restoration effort and the potential for negative effects on the regional economy. These assumed negative effects included the costs of wolf depredation on livestock and reduced big game populations resulting in lower economic returns to agencies and businesses that derive revenue from big game hunting. Proponents, on the other hand, predicted increased regional visitation and positive regional economic impacts as a result of wolf restoration.

Based on a 1991 park visitor survey, wolf recovery in Yellowstone was predicted to have a positive impact of $19 million annually in the regional economy due to increased wolf-related visitation to the park. If true, that would more than offset the negative economic impacts on the livestock industry and big game hunting that were expected to result from wolf restoration.

To test the economic projections that were made as part of the EIS analysis, in 2005 we surveyed park visitors about their expenditures and reasons for visiting the park. This paper focuses on two primary results from the 2005 survey: preferences for wildlife viewing among Yellowstone visitors and the regional economic impacts attributable to wolf presence in the park.

Data Collection

The Yellowstone National Park 2005 Visitor Survey was designed to collect a broad spectrum of information and opinions from park visitors. For purposes of the regional economic analysis, information was collected on visitor attitudes toward wolf recovery and wildlife and on visitor expenditures. From spring through fall, visitors at all five park entrance stations were asked to participate in the survey. Winter visitors traveling by car were contacted at the North Entrance. A separate sample of visitors was contacted at parking areas in the Lamar Valley where people specifically interested in seeing wolves tend to congregate. Because the Lamar Valley sample is not representative of park visitors as a whole, their survey responses are not included in the data represented here unless otherwise stated.

A total of 2,992 surveys were distributed from December 2004 to February 2006; 1,943 were completed and returned for an overall response rate of 66.4%: 1,431 from the park entrance sample (64.4% response rate) and 521 from the Lamar sample (74.2%). The resulting responses were weighted appropriately to reflect the actual distribution of 2005 park visitation by entrance and season. The survey procedure followed a standard Dillman (2000) mail survey methodology using initial contact and repeat follow-ups.

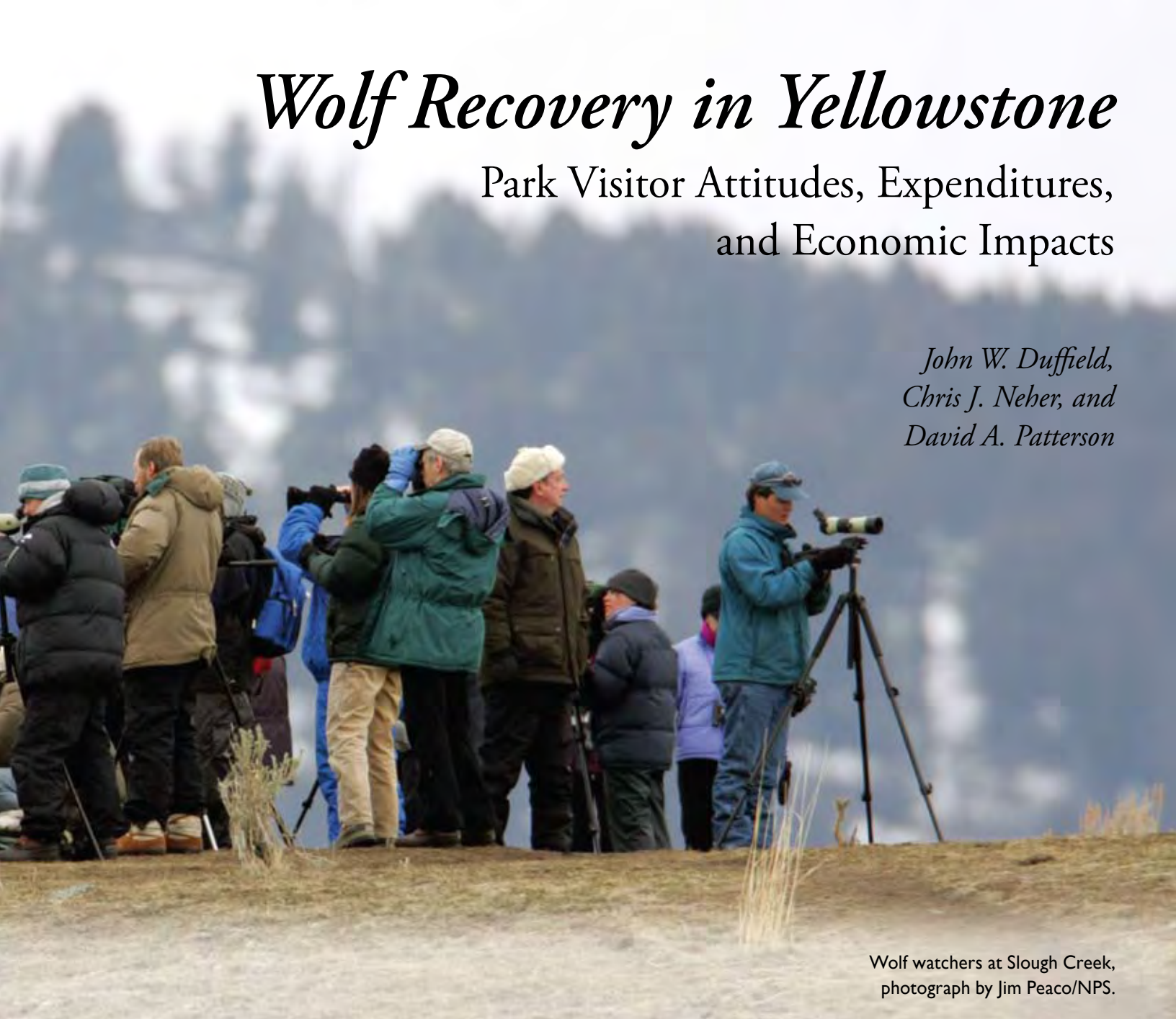
Visitor Wildlife Viewing Preferences

Visitors were asked to list the three animals from a list of 16 that they would most like to see while in the park (Table 1 compares the 2005 study results from summer visitors to

Wolf Recovery in Yellowstone

Park Visitor Attitudes, Expenditures, and Economic Impacts

John W. Duffield, Chris J. Neher, and David A. Patterson



Wolf watchers at Slough Creek, photograph by Jim Peaco/NPS.

similar surveys conducted in 1991 and 1999). The "charismatic megafauna," including large carnivores and ungulates, rank highest on the lists. The large carnivores are consistently among the top five ranked species. In the 1991 study, wolves ranked ninth in popularity; 15% of park visitors listed them as one of the three species they would most like to see even though wolves were not present in the park. In the 1999 study, following wolf reintroduction, wolves were ranked second after grizzly bears and the percentage of visitors who chose wolves had increased to 36%. In the 2005 study, 44% of visitors listed wolves as a species they would most like to see, again ranking it second after grizzlies.

When asked to indicate which species they saw on their trip to the park, nearly all respondents reported seeing bison (93% to 98%), and a large share reported seeing elk (85% to 92%). As expected, very few visitors (1.8% or less) reported seeing the rarely viewed mountain lion and wolverine. Table 2 shows the percentage of entrance sample respondents who reported seeing wolves, coyotes, and both wolves and coyotes. For purposes of analyzing the impact of wolf presence in Yellowstone, we reduced the chance of counting visitors who misidentified coyotes as wolves by using the percentage of visitors who reported seeing both coyotes and wolves.

Table 2 shows that, depending on the season (spring, summer, or fall) from 9% to 19% of visitors reported seeing both wolves and coyotes. In winter, about 37% of North Entrance visitors reported seeing wolves and coyotes. Applying these percentages to the actual 2005 recreational visitation levels yields an estimate of 326,000 visitors who saw wolves in 2005. Although this is a conservative estimate because it excludes

winter visitors who came through the West, East, and South entrances on over-snow vehicles, it is substantially higher than previous estimates. For example, according to field counts of wolf-watching visitors by Yellowstone National Park personnel (Smith 2005), about 20,000 visitors per year were viewing wolves. Given the size of the park, the widespread distribution of wolves (Smith 2005), and the limited presence of park personnel in the field, this method may have under-estimated the number of wolf observers by more than an order of magnitude.

Yellowstone Visitor Trip Expenditures

A key measure of the economic significance of a resource such as Yellowstone to the local economy is the amount of money visitors from outside the three-state area of Montana, Idaho, and Wyoming spend during their trips. To obtain an estimate of this, the survey questionnaire asked visitors to indicate the total amount they spent on their trip, as well as the amount they spent in these three states. Table 3 compares the reported average trip spending by season for residents of the three states to the spending of nonresidents.

Net Recreation Impacts of Wolf Recovery on the Regional Economy

Survey respondents were also asked if the possibility of seeing or hearing wolves had been a reason for their visiting the park and, if so, whether they would have come if wolves had not been present. Based on the responses to this question by both residents and nonresidents we estimated that the percentage of annual Yellowstone visitation attributable to wolves is 3.7%, ranging from 1.5% in the spring to nearly 5% in the fall. The percent for nonresidents only is similar, ranging from around 2% of spring visitors to almost 5% of summer visitors (Table 4). Table 4 shows the derivation of our estimate of the economic impact to the three-state region.

We estimate that approximately 94,000 visitors from outside the three-state region came to the park specifically to see or hear wolves in 2005, and that they spent an average of $375 per person, or a total of $35.5 million in the three states (Table 4). Prior to reintroduction, Duffield (1992) estimated that a recovered wolf population would lead to increased visitation from outside the three-state region resulting in an additional $19.35 million in direct visitor spending in the three states. Adjusted for inflation this would be $27.74 million per year in 2005—less than the $35.5 million estimate based on the data from our 2005 study, but well within the 95% confidence interval ($22.4 to $48.6 million).

Wolf Impacts on Livestock and Big Game Hunting

The EIS economic analysis provided estimates of the impacts of a recovered wolf population on livestock predation and big game populations in the three-state area. The estimated

Rank	1991 Study		1999 Summer Study		2005 Summer Study	
	Species	**%**	**Species**	**%**	**Species**	**%**
1	Grizzly	0.550	Grizzly	0.58	Grizzly	0.55
2	Black Bear	0.332	Wolf	0.36	Wolf	0.44
3	Moose	0.332	Moose	0.35	Moose	0.41
4	Elk	0.239	Lion	0.31	Black Bear	0.26
5	Lion	0.229	Black Bear	0.29	Lion	0.25
6	Sheep	0.219	Sheep	0.23	Sheep	0.21
7	Eagle	0.187	Eagle	0.21	Eagle	0.21
8	Bison	0.160	Bison	0.19	Bison	0.21
9	Wolf	0.154	Elk	0.14	Elk	0.14
10	Wolverine	0.047	Wolverine	0.06	Wolverine	0.06

The 2005 study also included six other species that were selected as preferred by some respondents: trumpeter swan (3%), deer (2%), fox (1.8%), coyote (0.6%), antelope (0.3%), and goose (0.1%).

Table 1. Comparison of Yellowstone National Park visitor ratings of the animals they most would like to see on their trips to Yellowstone.

livestock losses of $1,900 to $30,500 per year (mostly for cattle and sheep) were based on assumptions of a recovered population of 100 wolves. During the period when wolf numbers were near 100 (1997–2000), annual losses averaged $11,300 (based on actual payments at market prices for wolf kills verified by Defenders of Wildlife, www.defenders.org). When wolves numbered more than 300 in 2004 and 2005, losses averaged $63,818 per year, twice the high-end estimate predicted in the EIS. Even if payments by Defenders of Wildlife understated livestock losses by a factor of two due to the difficulty of verifying all actual kills, recent direct losses would still be less than $130,000 per year. Other livestock industry costs resulting from wolf reintroduction have not been quantified, but could include increased fencing and management costs associated with reducing wolf predation on a given ranch.

Based on biologists' projections of the impact of wolf predation on big game populations, the EIS projected a decline of 2,439 to 6,157 hunter days for elk, deer, and moose on the northern range and for Jackson and North Fork Shoshone elk. The associated foregone annual hunter expenditure was projected to be $207,000 to $538,000, based on approximately $85 hunter expenditure per day for those species. In 2005 dollars, this would be a loss of $342,000 to $890,000. Three of the species examined in the EIS (deer, moose, and bison) either have seen no reduction in population levels (as was predicted in the EIS) or, in the case of moose, have inadequate data to evaluate current population levels (White et al 2005). There have been no reductions for permits, animals harvested, or hunter success for mule deer or moose on the northern range as a result of wolf restoration (White et al. 2005).

The other key game species, elk , has provoked substantial concern in recent years because some herd sizes have dropped dramatically as wolf numbers have risen. While a substantial body of recent literature on wolf-prey modeling in the Yellowstone ecosystem exists, most of it focuses on the northern range elk. A review of the wildlife biology literature on the northern range elk population shows a divergence of views on the extent to which wolf predation has been responsible for its decline. However, two peer-reviewed papers (Varley and Boyce 2006, Vucetich et al. 2005) show that the impact of wolves on elk numbers has been consistent with or below the EIS prediction, which was for a long-range reduction of 5% to 30% in the hunter elk harvest. If one accepts the Varley and Boyce (2006) estimates, which also include impacts on the Jackson and North Fork Shoshone elk herds, actual declines in big game populations as a result of wolf predation and associated hunter impact are in the range predicted by the EIS ($342,000 to $890,000 in 2005 dollars). A caveat to these estimates is that they do not account for substitution behavior in response to changes in elk hunting opportunities in the GYA. This may result in an overstatement of hunter impacts. It was assumed in

Left, sample page from the 1991 survey; *below*, Female wolf pup #17 of the Rose Creek pack in Rose Creek pen, Barry O'Neill, 1995.

Statistic	Spring N=495	Summer N=477	Fall N=322	Winter N=221
% Report seeing wolves	25.4%	15.2%	18.5%	42.4%
% Report seeing coyotes	45.3%	38.9%	40.4%	71.2%
% Report seeing both	19.2%	9.1%	12.8%	36.7%
Recreational visitation (2005)	382,598	1,819,798	547,777	43,933
Number of visitors seeing wolves and coyotes	73,382	166,330	70,335	16,123
Total estimated visitors sighting wolves and coyotes (spring-fall)	310,046 (95% C.I. 257,210 to 362,882)			
Total estimated visitors sighting wolves and coyotes (year-round)	326,170 (95% C.I. 273,277 to 379,097)			
Note: winter estimate includes only North Entrance visitation.				

Table 2. Estimated number of Yellowstone visitors seeing wolves and coyotes in the park in 2005.

Season/residency	Average amount spent in ID, MT, WY	Average total trip spending	Sample Size
Spring–nonresident	$361.89	$795.14	260
Spring–3-state resident	$86.19	$112.37	101
Summer–nonresident	$369.12	$757.31	291
Summer–3-state resident	$142.06	$142.06	45
Fall–nonresident	$425.50	$855.00	149
Fall–3-state resident	$152.67	$198.64	72

Note: winter results are only representative of wheeled access and are not presented.

Table 3. Comparison of park visitor spending in Idaho, Montana, and Wyoming by season and residency based on visitors responding to 2005 entrance station surveys.

the EIS that hunters who did not receive an elk hunting permit in the GYA would not hunt elsewhere in the three-state area for elk or increase hunting effort on other species.

Conclusions

Overall, it appears that the economic predictions made in the 1994 EIS analysis were relatively accurate. Our estimated increase in park visitation (3.7%) due to wolf presence is lower than was predicted in the EIS (4.93%). However, the EIS prediction was based on a survey of only summer visitors; our 2005 study estimated a 4.78% increase in summer visitation due to wolf presence. Regarding increases in visitor spending in the three-state area due to wolf presence, the estimate of $35.5 million (confidence interval of $22.4 to $48.6 million) based on our 2005 study is consistent with the EIS estimate of $27.7 million (2005 dollars).

Projected costs of wolf predation (based on the market value of cattle and sheep taken by wolves) have been in the range predicted by the EIS, and were on the order of about $65,000 per year in 2004 and 2005. The impact of wolves on actual observed hunter harvest in the first 10 years after reintroduction was negligible, in that average hunter harvest and permits issued for big game species were either higher or unchanged compared to pre-wolf averages. However, reflecting in part the influence of a long-term drought, the presence of wolves, and aggressive management policies to reduce elk populations through hunting on the Northern Range, there

Statistic	Spring	Summer	Fall	Winter [1]
Total recreational visitation to Yellowstone	382,598	1,819,798	547,777	85,478
% of visitors from outside the three-state area	70.5%	83.68%	67.59%	82.2%
(A) Recreational visitors from out of the three states	269,770	1,522,807	370,242	70,289
(B) % of visitors who would not have visited without the presence of wolves	1.93%	4.78%	3.45%	3.66%
(C) Average spending per visitor within the three states by visitors from outside the area [2]	$361.89	$369.12	$425.50	$510.84
(A) * (B) * (C) Total estimated annual three-state visitor spending attributable to wolves [3]	$1,885,178	$26,889,668	$5,431,916	$1,314,167
Total estimated annual visitor spending in the three states attributable to wolves	$35,520,929			
95% Confidence interval	$22,404,274 to $48,637,585			

[1] Based on 1999 winter visitor survey estimates (Duffield and Neher 2000).
[2] Average spending for those who specifically came to see wolves was nearly identical, but due to a much smaller sample size, had a much higher variance.
[3] Sample size, by season for the 2005 sample was: 495 for spring, 477 for summer, and 322 for fall. The winter sample from 1998–1999 was 221.

Table 4. Estimated three-state (MT, ID, and WY) direct expenditure impact associated with wolf presence in Yellowstone National Park based on visitors responding to entrance station surveys.

has been recently a substantial reduction in elk permits. There is not a consensus among biologists on the actual impact of wolves on elk populations, but modeling supports the view that the long-term economic impact on big game hunting will be within the range projected by the EIS, of $342,000 to $890,000 per year (2005 dollars).

Weighing the economic impacts of increased tourism against reductions in livestock production and big game hunting participation, one can conclude that the net impact of wolf recovery is positive and on the order of $34 million in direct expenditures. An input-output model of the three state economy (Minnesota Implan Group, 2007) can be used to estimate the effect on economic output, by accounting for indirect and induced expenditures throughout the three-state economy. Including this multiplier effect leads to an estimated total economic impact in the three-state area of about $58 million in 2005 (range of $34 to $80 million).

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Acknowledgements

This research was supported by the Yellowstone Park Foundation, the Turner Foundation, and the National Park Service. Glenn Plumb was Project Director and helped coordinate NPS participation in the project. Many Yellowstone National Park staff members contributed to the research, including Doug Smith, Wayne Brewster, John Varley, and Tammy Wert and the entrance station staff. We are especially indebted to Becky Wyman for her work on the Lamar Valley data collection. Our biggest debt is to the approximately 2,000 Yellowstone National Park visitors who responded to our survey.

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The printing of *Yellowstone Science* is made possible through a generous annual grant from the nonprofit Yellowstone Association, which supports education and research in the park. Learn more about science in Yellowstone through courses offered by the Yellowstone Association Institute and books available by visiting www.YellowstoneAssociation.org.

The production of *Yellowstone Science* is made possible, in part, by a generous grant to the Yellowstone Park Foundation from Canon U.S.A., Inc., through *Eyes on Yellowstone* is made possible by Canon. This program represents the largest corporate donation for wildlife conservation in the park.

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