

UNIVERSITY OF WYOMING

NATIONAL PARK SERVICE RESEARCH CENTER



36th ANNUAL REPORT
2013

**UNIVERSITY OF WYOMING - NATIONAL PARK SERVICE
RESEARCH CENTER**

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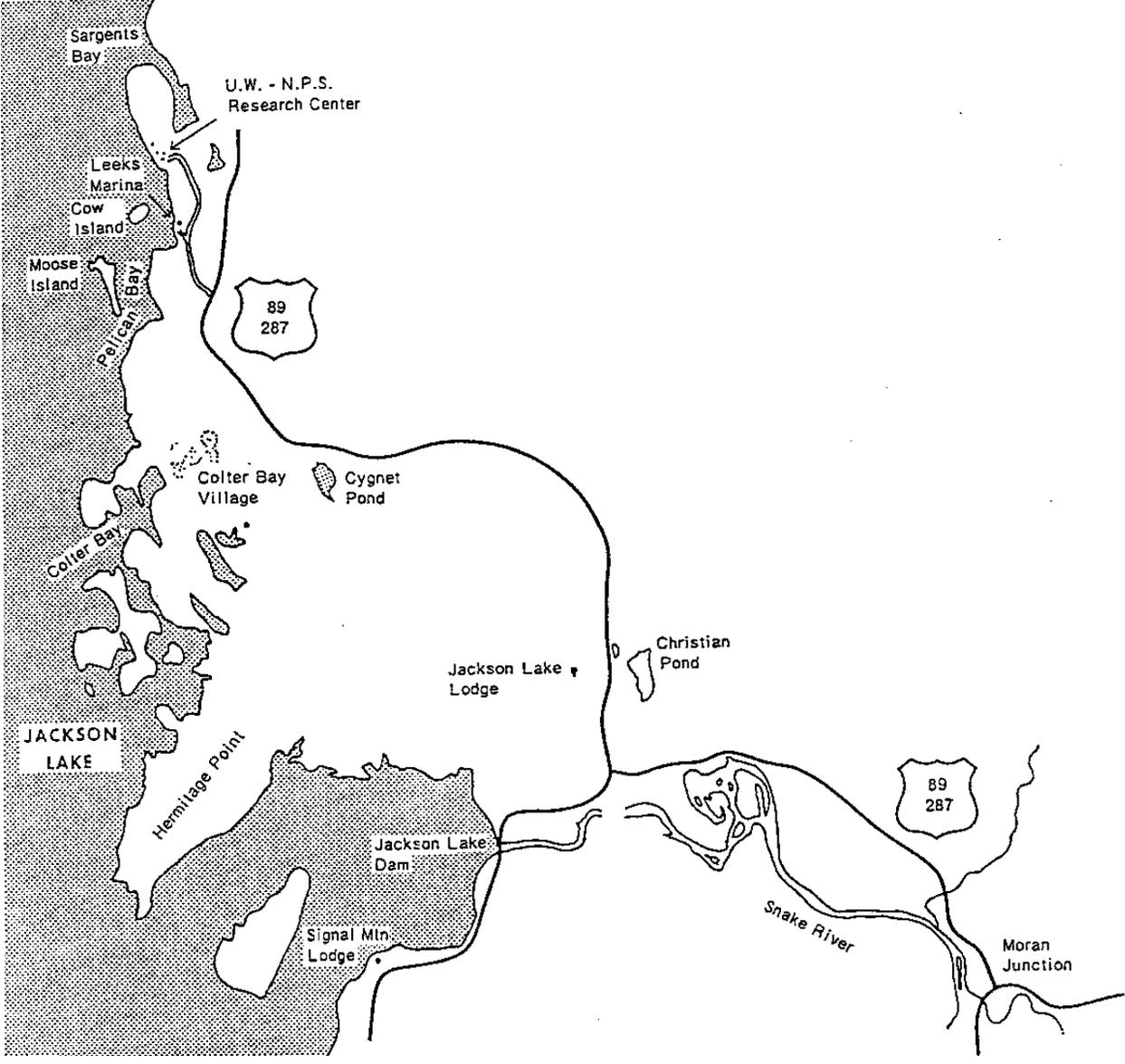
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DIRECTOR'S COLUMN

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During the period of this report the University of Wyoming-National Park Service (UW-NPS) Research Center supported and administered research in the biological, physical and social sciences and cultural resources performed in national parks, national forests and surrounding areas in the Greater Yellowstone Ecosystem. The UW-NPS Research Center solicited research proposals from university faculty, governmental research scientists and non-governmental research organizations throughout North America via a request for proposals. Research proposals addressed topics of interest to National Park Service scientists, resource managers, and administrators as well as the academic community. Studies conducted through the Center dealt with questions of direct management importance as well as those of a basic scientific nature.

The Research Center continues to consider unsolicited proposals addressing applied and basic scientific questions related to park management. Research proposals are reviewed and evaluated by the Research Center's proposal review committee. This committee is composed of University faculty and National Park Service representatives and is chaired

by the Director of the UW-NPS Research Center. Research contracts are usually awarded by early April.

The UW-NPS Research Center also operates a field research station at the AMK Ranch on Jackson Lake in Grand Teton National Park. The research station provides researchers in the biological, physical and social sciences and cultural resources an enhanced opportunity to work in the diverse aquatic and terrestrial environments and the cultural resources of Grand Teton National Park and the surrounding Greater Yellowstone Ecosystem. Station facilities include housing for up to 60 researchers, wet and dry laboratories, a library, herbarium, boats, and shop accommodations. The research station is available to researchers working in the Greater Yellowstone Ecosystem regardless of funding source, although priority is given to individuals whose projects are funded by the Research Center.

More information about the UW-NPS Research Station can be found at the station's web site: <http://www.uwyo.edu/uwnps/>.

RESEARCH PROJECT REPORTS

The following project reports have been prepared primarily for administrative use. The information reported is preliminary and may be subject to change as investigations continue. Consequently, information presented may not be used without written permission from the author(s). Reports from past research at the station (1954–present) are available online and full-text searchable form here: http://repository.uwyo.edu/uwnpsrc_reports

GRAND TETON NATIONAL PARK



MERCURY AND OTHER TRACE ELEMENTS IN GLACIAL MELTWATER AT GRAND TETON NATIONAL PARK, WYOMING

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✦ ABSTRACT

Glaciers are a reservoir of mercury (Hg) and other trace elements that have accumulated in the ice during the industrial era. As glaciers continue to melt at an alarming rate, these potentially toxic metals are released to the environment. In order to evaluate the impact of glacier melt on water quality in high elevation catchments in Grand Teton National Park, we sampled transects along the Teton and Middle Teton glaciers and proglacial streams during early-July and mid-August 2013. The glaciers were snow-covered during July, and thus water samples were primarily melt of snowpack from the previous winter. The glacier ice was exposed during August, and thus samples likely represented true glacier melt. These contrasting sample sets allowed for a determination of the impact of snowmelt versus glacier melt on water chemistry. Ten samples were collected during July and August along the Glacier Gulch transect: four of surface drainage on the Middle Teton glacier, three near the terminal moraine, and three downstream of the glacier. Thirteen samples were collected during July and August along the Garnet Canyon transect: one at the Lower Saddle of the Grand Teton, four of surface drainage on the Middle Teton glacier, two near the terminal moraine, two at the moraine of Teepe Glacier, and four samples downstream of the glaciers. All water samples were analyzed for total Hg, a suite of trace elements (including U, Sr, and Mn), and stable water isotopes ($\delta^2\text{H}$ and $\delta^{18}\text{O}$). Analyses for methyl Hg, solutes, and tritium (^3H) are still underway. Preliminary results indicate that snowmelt and glacier melt was a significant source of total Hg, but additional work is needed to determine the extent of

Hg methylation in the proglacial streams. Other trace elements were found in low concentrations in the melt water, but increased substantially downstream of the glaciers due to water-rock interactions.

✦ INTRODUCTION

The retreat of glaciers worldwide may lead to the rapid release of mercury and other trace metals to high elevation aquatic ecosystems (Barbante et al. 2004, Hong et al. 2004, Schuster et al. 2002). Mercury is a toxic element that is deposited to aquatic systems primarily by atmospheric deposition. Due to enhanced orographic-driven wet and dry deposition at high elevations, glaciers likely receive disproportionately high mercury loads (Carling et al. 2012, Fortner et al. 2011, Reynolds et al. 2010). In an ice core from the Wind River Range in Wyoming, Schuster et al. (2002) found elevated mercury concentrations in ice from the 1700s to present day, with a maximum during the 1960s to 1980s (Figure 1). They attributed the increased mercury deposition to mining and industrialization during the 19th and 20th centuries. Likewise, sediment cores collected from remote, high elevation lakes in Rocky Mountain National Park (Colorado) and Glacier National Park (Montana) showed an increase in mercury concentrations beginning in the 1900s, with a peak sometime after 1980 (Mast et al. 2010). Huang et al. (2012) showed that glaciers on the Tibetan Plateau are currently an important sink in the global mercury cycle, but they hypothesized that with a warming climate the glaciers may become a mercury source that could endanger ecosystems and human health in the region. This may

already be happening in other locations, including the Canadian Rockies, where melting glaciers and snowpack may be a source of mercury to osprey that live at high elevations (Guigueno et al. 2012).

In addition to mercury, glacial melt may be a source of other harmful trace elements (e.g., lead, arsenic, uranium) to pristine high elevation watersheds. Trace elements are deposited to alpine environments via wet deposition, but a majority of these elements are deposited by wind-blown dust. Carling et al. (2012) found that concentrations of mercury, lead, and arsenic increased by a factor of five or greater in Wasatch Mountain (Utah) snowpack after dust deposition. Likewise, Reynolds et al. (2010) measured elevated concentrations of lead in sediment cores from remote Uinta Mountain lakes in northeastern Utah, which they attributed to dust emission from mining areas located >100 km away. In a study at Mt. Hood, Oregon, Fortner et al. (2009) found that trace metals were released from glacier melt, and that a portion of these metals were derived from distal anthropogenic sources. Receding glaciers also expose readily-weathered fresh bedrock and glacial till. For example, retreating glaciers in the Cordillera Blanca of Peru have exposed sulfide-rich bedrock, which has led to acidic runoff with high trace metal concentrations (Fortner et al. 2011).



Figure 1. Worldwide cumulative glacier volume relative to 1850 excluding the Antarctic and Greenland ice sheets—black line (Cogley 2009), and mercury concentrations in the Upper Fremont Glacier, Wyoming from 1900 to 2000—gray line (Schuster et al. 2002). Adapted from Guigueno et al. (2012).

In Wyoming, as in other areas around the world, glaciers are receding at an alarming rate. Wyoming is the second most glaciated state in the lower 48, and glaciers contribute to the headwaters of some of North America's major river systems. The Wind River Range of Wyoming is the most glaciated region in the American Rockies, yet total glacier surface area decreased by 38% from 1966 to 2006 (Thompson et al. 2011). Recent research has shown

that the melt rates have increased even more since 2006 (VanLooy et al. 2012). Glacier melt contributes as much as 50% of total streamflow to high alpine streams in the Wind Rivers, and thus shrinking glacier reserves may lead to water shortages in the future (Cable et al. 2011). Glaciers in the nearby Teton Range have retreated at a similar rate over the past four decades, with the Teton, Middle Teton, and Teepee glaciers losing $17\pm 3\%$, $25\pm 4\%$, $60\pm 3\%$ of their surface area, respectively, between 1967 and 2006 (Edmunds et al. 2012).

As the rate of glacier melt continues to accelerate (Figure 1), the impact that trace metals in the meltwater pulse may have on downstream ecosystems is poorly understood. We hypothesized that water quality downstream of glaciers could be degraded as centuries' worth of contaminants are released over the span of a few decades. Also, we hypothesized that water quality could be negatively impacted due to interactions with fresh bedrock and glacial till that are exposed by the retreating glaciers. To test these hypotheses, we evaluated water chemistry of proglacial streams (i.e., streams that drain glaciers) in Grand Teton National Park (GTNP) in order to develop baseline criteria on concentrations of mercury and other trace elements in glacier melt. Ultimately, this study has implications for water quality and ecosystem ecology of glaciated areas worldwide. Specific objectives of this research were to:

1. Evaluate concentrations of mercury and other trace elements in glacier-dominated catchments at GTNP;
2. Evaluate seasonal variability in the chemistry of snow and glacier melt;
3. Evaluate relative contributions of trace elements from glacier melt, snowmelt, and water-rock interactions.

◆ METHODS

Sample collection

Water samples were collected from supraglacial and proglacial streams in Garnet Canyon and Glacier Gulch during July and August 2013. During the July sampling (July 2 and 5) the glaciers were covered with snowpack from the previous winter. During the August sampling (August 14 and 16) much of the seasonal snowpack was melted and ice was exposed at the surface. This field sampling design allowed for evaluation of water chemistry under snowmelt-dominated conditions during July and ice melt-dominated conditions of August.

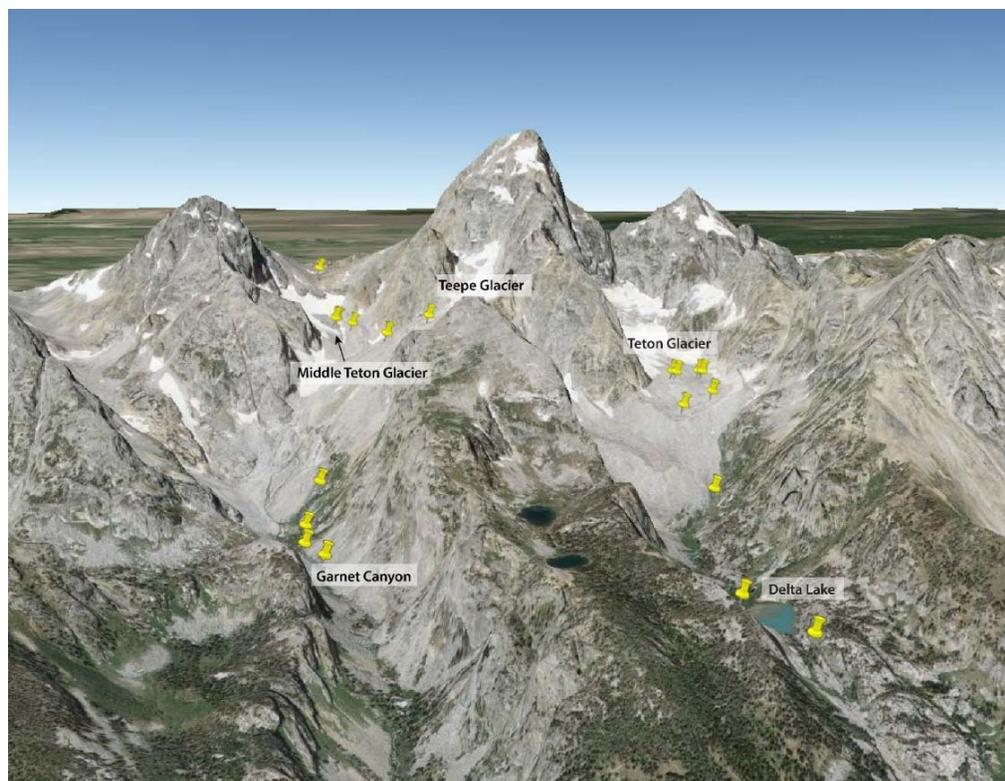


Figure 2. Tilted Google Earth image showing sample sites (yellow pins) on and below the Middle Teton, Teepe, and Teton glaciers. Image taken 3 August 2013, about midway between the two sampling events.

The Garnet Canyon transect included one sample near the Lower Saddle of the Grand Teton, four samples of supraglacial melt channels on the Middle Teton Glacier, one sample of supraglacial melt on the Teepe Glacier, samples at the terminal moraine of each glacier, and four samples downstream in Garnet Canyon terminating below the Meadows campsite (Figure 2). The Glacier Gulch transect included four samples of supraglacial melt on the Teton Glacier, two samples at the terminal moraine of the glacier, and three samples downstream in Glacier Gulch terminating below Delta Lake (Figure 2).

Well-established methods were followed for sample collection and handling (Carling et al. 2011, Carling et al. 2012, Carling et al. 2013a, Carling et al. 2013b). To cover all the sampling sites in each transect in a single day, we divided into two teams of two people to collect the samples. Each team followed strict “clean hands/dirty hands” protocols as outlined in EPA Method 1669. At each site, separate bottles were used to collect samples for mercury (250 mL FLPE), trace elements (125 mL LDPE), and stable water isotopes (1L LDPE). Upon returning to the field station at the end of each sampling day, samples were filtered (0.45 μm) into separate bottles and acidified (1% v/v HCl for mercury samples and 2.4% HNO_3 for trace element samples).

In addition to water samples, each team measured field parameters (pH, water temperature, and conductivity) at each site using a YSI Quatro multi-parameter probe. The probe was calibrated at the field station prior to each sampling day.

On each sampling day, each team collected a field blank by pouring Milli-Q water into empty 250 mL FLPE and 125 mL LDPE bottles. The field blank samples ($n=4$) were used to determine background contamination during sample collection and sample handling. Field blanks showed no significant contamination for any of the measured elements.

Sample analyses

Mercury samples were analyzed using an automated Brooks Rand CVAFS at Brigham Young University. All samples were analyzed for total Hg (THg), but analyses are still underway for methyl Hg (MeHg). THg concentrations were determined according to EPA Method 1631e with BrCl oxidation. At a minimum, matrix spike recoveries and replicates were analyzed for every 10 samples. For the sample run to be accepted, matrix spike recoveries had to fall within 75-125% of the original sample run and replicate analyses had to fall within $\pm 10\%$. Method blanks were analyzed at the beginning of each run in order to calculate a daily detection limit. Typical

values of the detection limit were 0.2 ng/L for THg. To check accuracy, our laboratory participated in the 2014 Brooks Rand Labs Interlaboratory Comparison Study with results within $\pm 10\%$ of the most probable values.

Trace element samples were analyzed using an Agilent 7500ce quadrupole inductively coupled plasma mass spectrometer (ICP-MS) at the University of Utah. Concentrations were measured for the following 40 elements: Ag, Al, As, Ba, Be, Ca, Cd, Ce, Co, Cr, Cs, Cu, Dy, Fe, Gd, Ho, K, La, Li, Lu, Mg, Mn, Mo, Na, Nd, Ni, Pb, Rb, Sb, Sc, Se, Sm, Sr, Tb, Ti, Tl, U, V, Y, and Zn. A calibration solution containing all the elements reported was prepared gravimetrically using 1000 mg/L single-element standards (Inorganic Ventures, Inc.). This solution was used to prepare a calibration curve with six points plus a blank for each sample run. Al, Ca, Cr, Fe, K, Mn, Na, Sc, and V were determined using 4 mL He/min in the collision cell, and As and Se were determined using 4 mL He/min plus 2.5 mL H₂/min. The detection limit was determined as three times the standard deviation of all blanks analyzed throughout each run. A USGS standard reference sample (T-205) and NIST standard reference material (SRM 1643e) were analyzed multiple times in each run together with the samples as a continuing calibration verification. The long term reproducibility for T-205 and SRM 1643e show that our results are accurate within 10% for most elements.

Stable water isotopes ($\delta^{18}\text{O}$ and $\delta^2\text{H}$) were measured on unfiltered aliquots from the 1 L LDPE bottle using a Los Gatos Research Liquid Water Isotope Analyzer (LWIA-24d) at Brigham Young University. All measurements were made relative to Vienna Standard Mean Ocean Water (VSMOW), with a precision of 0.4‰ and 1.0‰ for $\delta^{18}\text{O}$ and $\delta^2\text{H}$, respectively. Analyses for tritium (^3H) and solutes are still underway, but should be completed by the end of August 2014.

◆ PRELIMINARY RESULTS

Stable water isotopes

All water samples plotted on or near the global meteoric water line (GMWL), indicating little influence of evaporation or sublimation during transport from the glaciers to proglacial streams (Figure 3). Samples collected during July and August had substantially different water isotope signatures as a whole, with August samples plotting toward heavier isotopic values on the GMWL relative to the July

samples (Figure 3). This provides evidence that the July and August sampling events successfully captured different hydrologic regimes, with snowmelt-dominated conditions in July and ice melt-dominated conditions in August. The difference in isotopic composition of July and August samples will be investigated more fully in the future. One hypothesis for the heavier isotopic signatures in August relative to July is that the glacial ice is an accumulation of winter (lighter isotopes) and summer (heavier isotopes) precipitation, whereas the snowmelt represents only winter precipitation.

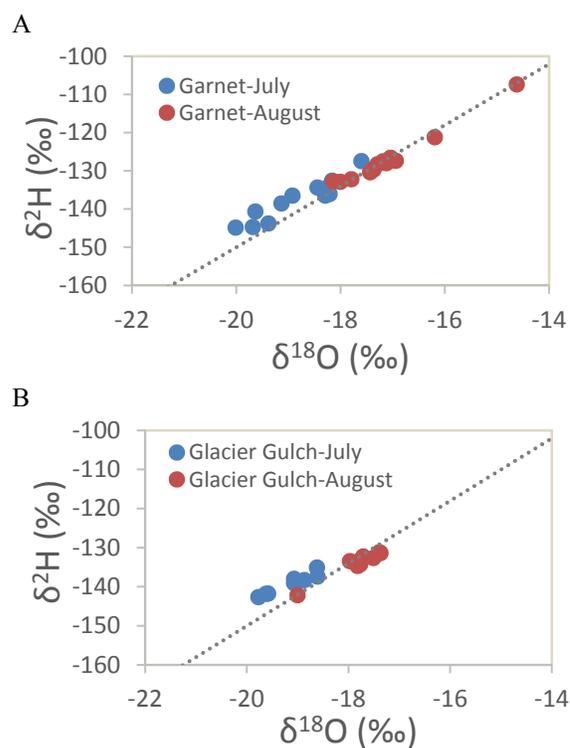


Figure 3. Stable isotopes of water samples collected at (A) Garnet Canyon and (B) Glacier Gulch. July and August data are shown as blue and red circles, respectively. Values are relative to VSMOW. The dotted line is the global meteoric water line.

Mercury and other trace elements

Figure 4 shows concentrations of mercury (Hg) and selected trace elements at the Garnet Canyon transect (Figure 4A) and Glacier Gulch transect (Figure 4B). In order to more easily interpret mercury and trace element results, samples from each transect were grouped according to location. At the Garnet Canyon transect, the groups were the saddle (n=1), supraglacial melt streams on the Middle Teton Glacier (n=4), the Teepe Glacier moraine (n=2), above the Meadows camp site (n=2), and below the Meadows

camp site (n=2). At the Glacier Gulch transect, the groups were supraglacial melt streams on the Teton Glacier (n=4), the terminal moraine (n=2), below the moraine (n=1), above Delta Lake (n=1), and below Delta Lake (n=1).

Hg concentrations were low (<1 ng/L) in both the Garnet Canyon and Glacier Gulch transects. At Garnet Canyon, concentrations were highest in the Saddle and supraglacial melt samples and lowest downstream (Figure 4A). At Glacier Gulch, Hg concentrations were similar at all sample sites (Figure 4B). There were no significant differences in Hg concentrations between July and August, indicating that melt from snowpack and glaciers contribute similar amounts of Hg to the stream systems in both catchments. The similar concentrations in the supraglacial melt channels and downstream samples indicates that atmospheric deposition is likely an important contributor of Hg to the watershed, and that water-rock interactions do not add substantial amounts of Hg to the system.

Although the concentrations of total Hg were low, there still may be a threat to downstream ecosystems if the inorganic Hg has potential to be methylated. Even low methyl Hg concentrations can be toxic to wildlife and cause harm to humans who consume fish from high alpine lakes. Preliminary results show that methyl Hg concentrations are low in the supraglacial melt channels but increase substantially downstream. More samples need to be analyzed in order to confidently show whether the apparent increases are significant. Other elements with interesting trends include uranium (U), strontium (Sr), and manganese (Mn). U concentrations were low near the glaciers but increased dramatically in the downstream samples in both catchments, with similar results during July and August (Figure 4). Low U concentrations in the glaciers and relatively high concentrations downstream indicates that U is dissolved into the stream as a result of water-rock

interactions. Higher concentrations in Garnet Canyon relative to Glacier Gulch are likely a result of increased water-rock contact time. Thus the metamorphic or igneous bedrock likely contain U-bearing minerals that release uranium during weathering processes. More work is needed to determine which rocks and minerals in Garnet Canyon and Glacier Gulch contain U.

Sr showed a similar trend as U, but with some notable exceptions. Sr concentrations were low in the supraglacial melt channels and increased substantially downstream, with higher concentrations in Garnet Canyon relative to Glacier Gulch (Figure 4). This indicates that water rock interactions are likewise controlling Sr distribution. However, Sr concentrations were also relatively high at the Saddle in Garnet Canyon and at the moraine at Glacier Gulch (where U concentrations were low). This indicates that the local groundwater may contain relatively high concentrations of Sr since these sites are likely spring-fed.

Mn concentrations were somewhat of an anomaly compared with the other measured elements. Mn concentrations were relatively high in supraglacial meltwater, especially on the Middle Teton Glacier (Figure 4). This indicates that atmospheric deposition is likely an important source of Mn to these catchments, probably in the form of aeolian dust. Mn was also notable because concentrations were higher in August relative to July at most samples sites (Figure 4). The seasonal differences were most pronounced below the Teton Glacier in Glacier Gulch, where Mn concentrations were a factor of 10 higher in August relative to July. This may indicate that the glacier melt contains higher Mn concentrations relative to seasonal snowmelt, but more work is needed to determine the cause of these trends.

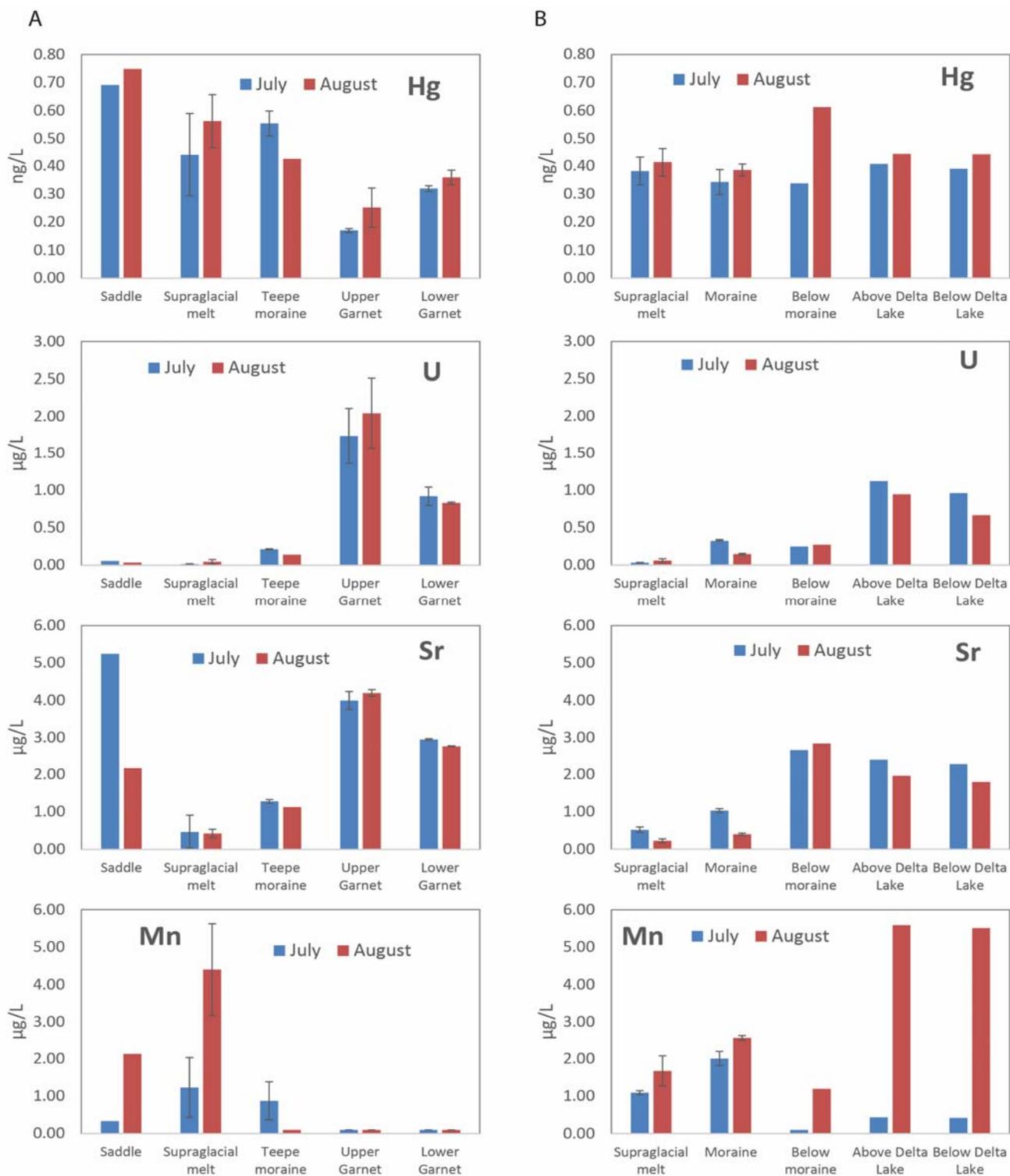


Figure 4. Trace element concentrations in filtered water samples collected at (A) Garnet Canyon and (B) Glacier Gulch. July and August data are shown as blue and red bars, respectively. Concentrations are ng/L for Hg and µg/L for U, Sr, and Mn. Error bars show average and standard deviation for sample types that included more than one sample.

◆ MANAGEMENT IMPLICATIONS

Meltwater from the Middle Teton, Teepee, and Teton Glaciers appears to be a significant source of inorganic Hg to Garnet Canyon and Glacier Gulch. If Hg from the glacier is converted to methyl Hg, it could pose a threat to downstream ecosystems. In contrast, most of the other measured elements were found in low concentrations in the supraglacial meltwater and were contributed mainly from interactions with bedrock downstream of the glaciers. We found no significant differences between the chemistry of snowmelt (July samples) and glacier melt (August samples), indicating that there is no extra source of Hg and other trace elements in the older ice relative to recent snowfall.

Continued monitoring of water quality is necessary to protect wildlife in snowmelt dominated catchments across GTNP under a warming climate. Changes in the timing and extent of snowmelt, shrinking glaciers, and other factors could result in negative impacts on the quality and quantity of water in streams, lakes, and wetlands in the Park. For example, as glaciers continue to recede, seasonal snowmelt will interact with bedrock and glacial till to a greater extent. Increased water-rock interactions could lead to higher concentrations of harmful trace elements such as uranium downstream of the glaciers. A long-term monitoring system at selected locations would allow GTNP scientists to evaluate the impacts of melting glaciers on water quality over the long term.

◆ ACKNOWLEDGEMENTS

In addition to support from the UW-NPS Research Station, this project has received funding from the College of Physical and Mathematical Sciences and the Department of Geological Sciences at Brigham Young University. Design and coordination of the field work benefited greatly from the staff at the Research Station and GTNP. We thank BYU students Cameron Harrison, Joel Johansen, Brian Selck, Dylan Dastrup, Desmond O'Brien, and Timothy Goodsell for field and laboratory assistance.

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DR. JOHN C. REED, JR.: PIONEERING GEOLOGIST, MOUNTAINEER, AND AUTHOR OF *CREATION OF THE TETON LANDSCAPE*

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JOHN C. REED, JR. ✦ U.S. GEOLOGICAL SURVEY ✦ DENVER, CO



The principal investigators on Jackson Lake, July 2013. Left: Jack Reed; Right: Carol Frost

✦ ABSTRACT

Few geologists today possess the mountaineering skills to study rocks exposed in the topographically challenging terrain of the Tetons. Even fewer can claim the accomplishment of making the first geologic map of an entire mountain range. One of these pioneering geologists is John C. Reed, Jr., who joined the U.S. Geological Survey in 1953, and who is now scientist emeritus at the U.S. Geological Survey in Denver (Figure 1). In addition to his field geology expertise, Dr. Reed also has a special talent for communicating complex geologic concepts to the public. The purpose of this project was to profile this pioneering mountaineer-geologist and accomplished writer, and to archive his maps, field notes, and photographs for use by future scientists and for the public, particularly park visitors.

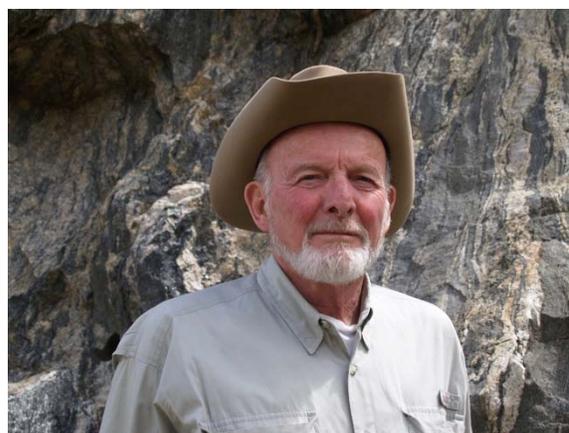


Figure 1. Jack Reed

The products of this project include:

- A bibliography of Dr. Reed's publications on the geology of Grand Teton National Park (see Appendix).

- Oral histories of Dr. Reed’s experiences doing geologic mapping in the park. Video recording was done of Dr. Reed and his wife Linda in July 2013 on site in Grand Teton National Park. From the recordings, four edited, approximately 4-6 minute segments were produced on the geology of the Teton Range, the Teton Glacier, the process of making the geologic map, and the life of the field base camp manager. These have been accessioned into the University of Wyoming American Heritage Center John C. Reed Collection (#12585).
- A profile by Dr. Reed entitled “Thinking back through a lifetime in the U.S. Geological Survey” will be published in the fall 2014 issue of *Rocky Mountain Geology*. The article includes a summary of Dr. Reed’s scientific contributions to Teton geology by Carol Frost.
- Archival quality digital copies of Dr. Reed’s bibliography, CV, and Teton field maps, field notebooks, photographs, and 35 mm slides have been made and have been accessioned into the University of Wyoming American Heritage Center John C. Reed Collection (#12585).

◆ INTRODUCTION

In 1962, when Jack Reed (John C. Reed, Jr.) began his geologic map of the Teton Range, little was known about these basement rocks. Members of the Hayden Surveys had noted their metamorphic character (Bradley 1873, St. John 1879), Horberg and Fryxell (1942) had identified scattered occurrences of metasedimentary rock within the gneisses that compose the high peaks, and Bradley (1956) had published a structure map of Buck Mountain area, but large tracts of the scenic mountain peaks and canyons remained to be explored and described. The U.S. Geological Survey made an excellent choice in assigning Jack to map the Precambrian rocks: not only was he an experienced field geologist but also an accomplished mountaineer and climber who’d first summited the Grand and Middle Tetons in 1953. In the course of his geologic mapping Reed would pioneer routes and make first ascents of eleven peaks in the northern part of the range (Ortenburger and Jackson 1996) (Figure 2). He also contributed the chapter on Teton geology in Ortenburger’s “Climber’s Guide to the Teton Range.”



Figure 2. Jack Reed on the summit of Teewinot.

Jack accomplished the majority of the fieldwork for his geologic map during the summers of 1962, 1963, and 1964, working systematically from north to south. In 1962 he and field assistant Jim Dieterich mapped from Webb Canyon south to Snowshoe Canyon, including Rolling Thunder Mountain, Ranger Peak, and Eagles Rest Peak (Reed 1963). They also surveyed a small area in the vicinity of Lake Solitude and Petersen glacier. In 1963 he and Dave Steller examined and mapped the rocks from Waterfall to Leigh Canyons, including Mount Moran. The area mapped by Jack and his assistant Don Coates in July and August 1964 extended from Paintbrush Canyon to the mountains south of Granite Canyon in the southern part of the range (Figure 3). That fall, he and Don took a series of low altitude oblique stereoscopic aerial photographs that Jack used to help delineate the granite and pegmatite dikes that intrude the older gneissic rocks and to map the sedimentary rocks on the western flanks of the range. In 1965 he and J. David Love returned to the northern part of the Tetons to map in the area of Owl and Berry Creeks, and in 1966 Reed worked in the high country west of the Cathedral Peaks. Finally in 1970, working with Rob Blair, Jack completed the mapping project with geologic fieldwork in the northwestern part of the range. His field notebooks, field map sheets, and photographs record over 1200 sites where he made geologic and structural observations. These data formed the basis of his portion of the final geologic map for Grand Teton National Park, an area in excess of 186 square miles of spectacularly rugged terrain (Love et al. 1992).

Jack’s wife Linda spent some time each season in the Teton Range with her husband. An experienced climber herself, she accompanied Jack on some of his traverses in the first years before their daughter and son were born (Figure 4). Later she managed the base camps at Taggart Creek and on Jackson Lake while looking after their children.



Figure 3. Jack Reed on the outcrop in the Teton Range.

Jack's scientific investigations of the Teton Range were not limited to geologic mapping of the Precambrian rocks. He took time during the field seasons in 1962-1966 to survey and resurvey markers placed across the Teton Glacier to document the rate of ice movement and changes in ice thickness (Reed 1965) (Figures 5-7). Later he and R.E. Zartman conducted the first K-Ar, Rb-Sr, and U-Pb age determinations on the Precambrian rocks of the Teton Range (Reed and Zartman 1973). Along with these scientific pursuits, he and J. David Love, later joined by Kenneth Pierce, wrote the beautifully illustrated popular book, "Creation of the Teton Landscape," for a general audience.



Figure 4. Jack and Linda Reed on the divide above Lake Solitude.



Figure 5. Aerial view of Teton Glacier photographed by Jack Reed in 1964.



Figure 6. Reed's team surveying Teton Glacier.

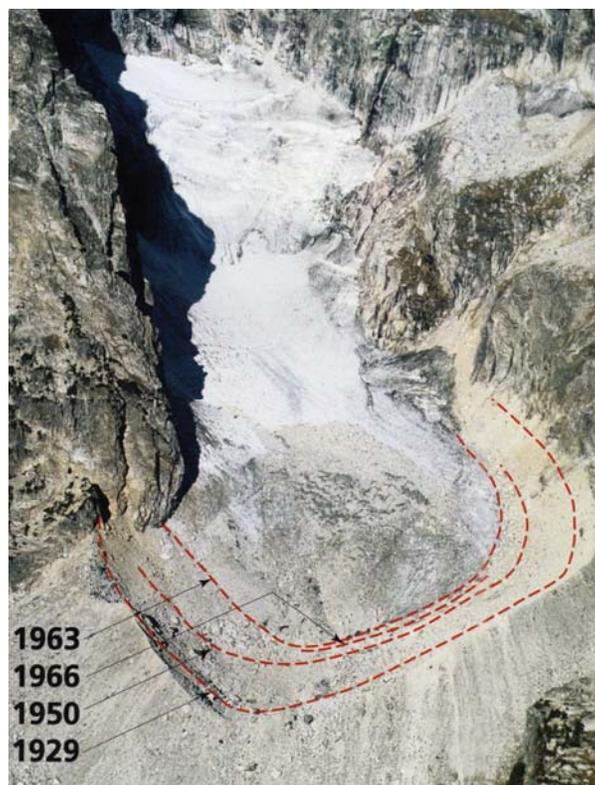


Figure 7. The extent of Teton Glacier as surveyed by Jack Reed in 1963 and 1966 compared to earlier years.

✦ **GEOLOGIC WORK IN THE TETONS, IN JACK REED'S WORDS**

In 1962, I was offered a chance to undertake a project in Wyoming's Teton Range. Dave Love, who was considered the dean of Wyoming geology, had been mapping in and around Jackson Hole for many years. He had requested someone to map the Precambrian rocks of the Teton Range for the geologic map of Grand Teton National Park that he was compiling. Would I like the job? Having done some climbing in the Tetons previously and having led a Colorado Mountain Club outing there in 1959, I jumped at the chance!

I began mapping in the Tetons in 1962 and made good progress for four field seasons (Figure 8, 9). But my idyll in the hills was rudely interrupted in 1965 by a summons back to D.C. to serve as chief of the Eastern States Branch. It was tough for the family to leave our mountain home in Colorado, but a wonderful chance for me to be introduced to the inner workings of a scientific bureaucracy.

I was paroled from my job as branch chief in spring 1969 and the family returned to Denver. That summer, USGS geologist Bob Zartman and I visited the Tetons and collected samples for radiometric dating. I spent much of the following winter learning the techniques of Rb/Sr and K/Ar dating in the laboratories of the Isotope Geology Branch in order to establish general ages on several of the major map units.



Figure 8. Jack Reed in the field, Teton Range.



Figure 9. Jack Reed, reviewing field notes on the flanks of Symmetry Spire.

During the 1970 field season, I completed mapping on the west side of the Teton Range and began final compilation of my part of the Grand Teton National Park geologic map; however, because of delays in other segments of the project and the need to adjust our geologic mapping to a newly published topographic base, the map was not published until 1992.

Early in the Teton project, Dave Love had discussed compiling a general-interest book on the geologic story of the Tetons and Jackson Hole. Bill Dilley, then chief park naturalist, was extremely enthusiastic about the idea and indicated that the Grand Teton Natural History Association (now known as the Grand Teton Association) would be delighted to publish such a volume. I began work on the book in 1965 and continued as time allowed during my stint as branch chief and my subsequent work in the Tetons. Preparation of illustrations and ironing out various disagreements on content and style between the authors dragged on for several years, but the first edition of *Creation of the Teton landscape: The geologic story of Grand Teton National Park* was finally published in 1971. It was well received and has gone through at least a half-dozen printings.

◆ SUMMARY

Field geologist, mountaineer, and skilled scientific interpreter of the natural world: Jack Reed made foundational and enduring contributions to our understanding of the creation and evolution of the Teton landscape. The John C. Reed collection at University of Wyoming's American Heritage Center preserves his contributions and includes digital scans of Reed's field maps, field notes, and photographs, along with video interviews of Reed and his wife Linda made on location in Grand Teton National Park in July 2013.

◆ ACKNOWLEDGEMENTS

In addition to support from the UW-NPS Research Station, this project would not have been possible without the expertise of videographer and editor James S. Costin of UW-TV, and digital collections manager Tyler Cline of the UW American Heritage Center. Thanks also go to Bridgette Guild, Museum Curator, Grand Teton National Park Science and Resource Management.

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CENTRAL PLACE FORAGING CHARACTERISTICS OF BEAVERS (*CASTOR CANADENSIS*) AND HABITAT MODELING IN GRAND TETON NATIONAL PARK

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✦ JUSTIFICATION AND SCOPE

A significant role of the National Park Service in the United States is the preservation of pristine landscapes. The natural landscape offers the visitor the opportunity to enjoy the wonders of nature and its processes to create beautiful vistas, soaring mountains, and the interplay of vegetation communities. The visitor to the park can be a passive recreationist and observe the landscape or be an active recreationist and experience the landscape through hiking, biking, mountain climbing and a range of other activities. The

key linkage between the active and passive recreationist is the landscape that they are experiencing, in one perspective or the other. Any disruption of that natural landscape diminishes the experience. Unfortunately, the perception of the disruption varies with each individual. The trail to get to a scenic vista can be overlooked by some observers, while others believe it is an example of the devastation of human impact.

Figure 1 is an image of the impact of beavers near Spread Creek. To some observers it is nature's natural landscape, to others the beaver is as devastating

to the landscape as a lumber jack is to the forest. The alterations to the landscape made by the beaver are far reaching including not only the cutting down of whole trees for the construction of lodges, but the damming of streams and the creation of ponds and subsequent wetlands. However they are perceived, the importance of beavers to the ecosystem has been identified by a number of authors (Naiman et al. 1986, Naiman et al. 1988, Muller-Schwarze and Sun 2003, and Wright and Jones 2006).



Figure 1. Beaver tree cuttings near Spread Creek.

Research on beavers has a long and varied past with one of the first major works describing and analysing beaver locations, imprint on the landscape, movements, and habitats by Lewis Morgan in 1868. As time has progressed, more in-depth analyses have been completed on a number of aspects of beaver ecology. Two major types of beaver studies focus on their movement and foraging habits. The area of daily and seasonal movements delineates the beaver's territory, which has both a spatial and social component. The size and densities of the territories provide knowledge of the distribution and population of beavers in an area. The social dynamics of the territories can have two dimensions, the intra-colony interactions of parents to their off-spring and sibling relations, and the interaction between colonies that make-up the territories. This research will focus on the spatial aspects of beaver territorial foraging and the determination of beaver movements as they relate to foraging along the Snake River.

The overall problem addressed in this research is to determine the spatial extent and patterns of beaver foraging over the course of a foraging cycle-six to nine months. By using micro-GPS technology, beaver movements can be captured at a high spatial and time

resolution to examine the route, forage-time, and spatial extent of their eating and construction activities. The micro-GPS technology has the ability to collect up to 60,000 locations providing species coordinates and timeline, thus providing accurate information of their movements and time sequencing.

This research is a continuation of the research proposal submitted to the UW-NPS Research Station last year, 2011-2012. The following are our continuing research objectives:

1. Map riparian habitat along the Snake River corridor, focusing on side-channels used by beavers.
2. Document beaver activity and habitat utilization by tracking their movement to and from their lodge, along a particular side-channel, and more broadly within the riverine environment using micro-GPS units.

As mentioned previously, the spatial characteristics of beaver foraging are the main thrust of this project. Beavers that have built lodges, either along a bank or in a pond/lake, radiate out from that location to forage, and thus are considered central place foragers (Jenkins 1980). Studies have found that because of the characteristics of their prey species, beaver foraging changes with distance from water (Jenkins 1980, Belovsky 1984, McGinley and Whitham 1985, Gallant et al. 2004, and Raffel et al. 2009). Generally, the foraged plant species increase in size with distance from water, either a lake or pond. Raffel et al. (2009) along with Pinkowski (1983) and Gallant et al. (2004) found that not only were there size differences with distance, but also species selectivity. Thus, the overall foraging by beavers has an impact on the vegetation density and composition (Donkor and Fryxell 1999, Barnes and Mallik 2001). These changes can then have an overall impact on the ecosystem if sustained over a long period of time.

A typical central place study will locate the lodge that is the home of the beaver colony and survey vegetation species from that location noting type and foraging activity. In the study by Raffel et al. (2009) they completed a survey of beaver activity around the lake and identified eight foraging sites with beaver cuts less than 2 years old. The research team delineated the sites by the extent of foraging and then recorded information on all of the tree species (>1cm in diameter) within the foraging area, distance from shore, cut status and stem/trunk diameter. Their analysis consisted of modelling the preferred foraged species and relating this to size, distance from shore and distance from the lodge. Overall, this aspect of the

Grand Teton NP beaver foraging has been completed for several select sites (Gribb and Harlow 2011).

This research has two major distinctions from the cited research. First, there has only been one central place foraging study along a western US river system. McGinley and Whitham (1985) examined the central place foraging of beavers along the San Juan River, UT. They specifically focused on cottonwoods (*Populus fremontii*) and only in one select location. Breck et al. (2001) were not specifically examining central place foraging, but they did study beaver home range along the Yampa and Green Rivers.

The focus of this beaver research was originally designed to address movements along the Snake River, addressing beaver foraging along a western river, an aspect that has not been fully examined. Second, this study captured beaver movement with the micro-GPS unit, a process that has never been attempted. Not only were the foraging locational patterns recorded, but also foraging times. Fryxell and Doucet (1993) recorded this same type of information with beavers in an enclosure using visual observations, but they provided pre-cut tree stems and embedded them into the soil to determine foraging selection, times and distances. The current study recorded real foraging times and movement coordinates in a natural environment.

◆ SIGNIFICANCE

This project has three points of significance. First, this is a technological innovation project attaching a micro-GPS unit to beavers. This had not been attempted before, and the process and procedures were recorded to provide a framework upon which to build additional research in this technique. In the work of Raffel et al. (2009) the researchers GPS'd the activity areas of the beaver and did their calculations all after the fact. Several studies have fixed a radio telemetry unit to the tail of the beaver and systematically monitored their locations using telemetry (Rothmeyer et al. 2002, McNew and Woolf 2005, and Bloomquist and Nielsen 2010). The shortcoming of this technique is that the location and movements between telemetric readings is unknown, the only location information collected is at the times and days selected by the researchers, thus a biased sampling of activities and movement were collected. The micro-GPS unit has the capability to capture a signal at a set time interval, every 5 minutes, thus allowing a systematic sampling of beaver locations (www.telemetrysolutions.com) over the entire research period. In this case, the research period was only from May 26-June 2, 2013. One known shortcoming of this system is that GPS signals

generally do not penetrate water to a depth of more than 20 cm. In a sample test with a hand-held GPS, locations underwater were collected to a depth of 1m (Gribb, unpublished 2011). However, the hand-held GPS unit had a much larger antenna than the unit attached to our test beaver. The unit used in this study was only 52mm (w) x 78mm (l) x 28mm (h). The signal was lost as the beaver entered/exited the lodge or swam in deeper water. In addition, the signal was lost while the beaver was in the lodge.

The second point of significance for this study is that it provides a detailed record of the extent of beaver foraging, though for only a short time period (May 26-31) in the Spread Creek meadow pond complex in Grand Teton NP. The resolution of the location and movement data provides the detail that is needed to determine home range and colony territory. This study recorded the movement of the beaver in a pond area that encompasses approximately 11ha with a complex of 20 ponds, with 10 greater than 0.03 ha and 10 less than 0.03 ha. The captured location data allows the researchers to calculate the distances travelled, frequency of pond use, the frequency of water way use, and the proportion of time on each pond. This type of information has not been recorded for any western ponds, a dominant feature for beaver habitats in the mountainous western U.S.

The third point of significance is the building of a beaver habitat model that incorporates a range of data for a riverine habitat. Most models utilize either a pond site/situation (Gallant et al. 2004) or a broad area approach (Slough and Sadler 1977, Allen 1983, Howard and Larson 1985, Beier and Barrett 1987, South et al. 2000, Beck and Staley 2005, Maringer and Slotta-Bachmayr 2006, Cox and Nelson 2006, Frantisek and Kostkan 2009, and Bird et al. 2013). This model is based on a combination of remote sensed data of vegetation with digital data on topography, soils, and stream reach delineations. The Snake River has two significant components, the portion above the Jackson Lake Dam and the portion below the Jackson Lake Dam. The portion above the dam is unrestricted and natural, whereas the portion below the dam is significantly impacted by releases of water held by the Jackson Lake Dam. The examination of beaver habitat along a river in the western United States has been limited (Slough and Sadler 1977, Howard and Larson 1985, Breck et al. 2003, Bryan et al. 2013). This habitat model relies on the stream density, vegetation, soils and slope factors to determine the potential habitat along the Snake River stream reaches.

◆ METHODS

The general strategy of the central place foraging investigation is to characterize beaver riparian ecology by an inventory of the foraged vegetation and the monitoring of an individual beaver using a pair of tracking methods, and to integrate these two sources of information to provide insight on physical factors influencing beaver behavior patterns. Our study involved a combination of geospatial data analysis and field work, and each of these components is described in the following sections. The project initially proposed to examine three specific beaver habitats: a segment of the Snake River adjacent to the Bar BC Ranch with backwater tributaries; a segment of the Snake River 5km downstream from the Flagg Ranch bridge without a backwater tributary; and a beaver pond sequence along Spread Creek, 1km east of US26/US98/US191. Each of these locations had active beaver lodges and displayed active foraging.

To understand beaver habitat utilization and movements, a systematic method of collecting beaver locational data was needed. The first task is to locate, live-trap and attach a micro-GPS unit on a beaver. Because this is a pilot project to test the use of a micro-GPS unit, one beaver would be captured at each of the three pilot locations, fitted with the device and released. To make recovery of the GPS unit easier and to test the procedure for capturing, attaching the unit and collecting data afterwards, a beaver was trapped first at the Spread Creek ponds complex. Trapping of the beaver was accomplished by a team composed of experienced wildlife handlers, Dr. H. Harlow (UW Dept. of Zoology and Physiology) and Drew Reed (formerly Wyoming Wetland Society) on May 26, 2013. To facilitate handling and reduce the capture trauma, the beaver was anesthetized using the process described by McNew et al. (2007). A measured dose of ketamine hydrochloride and xylazine hydrochloride was administered with appropriate lag time for recovery before release. All UW, AMS, NPS, and USDA wildlife handling guideline procedures were followed (Appendix A, UW IACUC permit). A portion of a small GPS device (80mm x 10mm x 10mm) was glued to the beaver tail and another part of the unit was belted to the base of the beaver tail. This would allow flexibility of tail movement and the aerodynamic design of the GPS would minimize the possibility of the unit being caught-up on vegetation and underwater debris. In addition, a radio-telemetry device as a component of the micro-GPS was activated at the same time as the GPS unit.

To accomplish our research objectives, the micro-GPS unit attached to an adult beaver can possibly

collect the coordinates of their movements for six months. Because the GPS uses a set time interval between location recordings (every 5 minutes upon connecting to the GPS-satellite network) detailed movements can be documented. Finally, the radio-telemetry antenna assisted in locating the beaver to download the GPS data, allow for re-capture and removal of the micro-GPS. According to Bryan Bedrosian, Beringia South, data can optimally be downloaded within a radius of 400 m from the GPS unit. However, if the beaver has moved from its lodge it will be critical to locate the beaver and retrieve the data from the micro-GPS, thus a vhf radio telemetry unit is built into the micro-GPS unit. All necessary procedures were followed to ensure that the recording devices and study area were not disturbed nor impact recreationists. The pilot study areas were selected because of their locations away from river recreationists- rafters and fishermen and the general public.

To map the terrain and riverine characteristics of the Snake River required combining field data, remote sensed data and digital environmental data. Objective #2 is to examine and analyze the interrelationships between these different data sets to produce the appropriate maps and a new, more robust beaver potential habitat model. The field and remote sensed data have been described previously, the environmental factors were derived from GTNP, USGS, and UW WyGISC data sets on topography, hydrology, vegetation, soils, and geology. The integration of these different types of data sets provided a model that is multi-dimensional and dynamic, parameters that Shenk and Franklin (2001) thought critical to any natural resource management modeling. The remote sensing and river morphological measurements were the main components of the habitat model. This integration of data sets incorporated the use of multi-dimensional spatial analysis to determine the statistical significance of the different field measurements, environmental factors, and remote sensed imagery in the construction of the new habitat model.

◆ RESULTS

Mapping the Snake River corridor for beaver habitat involved compiling the appropriate spatial datasets from a variety of sources. The appropriate datasets for identifying beaver habitat can be categorized into five major components as identified by a number of researchers (Slough and Sadlier 1977, Allen 1983, Howard and Larson 1985, Beier and Barrett 1987, South et al. 2000, Beck and Staley 2005,

Maringer and Slotta-Bachmayr 2006, Cox and Nelson 2006, Frantisek and Kostkan 2009, and Bird et al. 2013): water, landscape, vegetation, soils, and anthropogenic factors. The water component details the characteristics of the water system: water flow, stream order, stream characteristics (width, depth, stream reach length), stream reach, stream gradient, bank height, floodplain width, wetlands, pond size, braiding, and sinuosity. The landscape factors generally relate to topography, slope and orientation. Vegetation has a number of different factors that are examined including species, communities, species/communities a set distance from water, tree and shrub density, tree diameter breast height, tree and shrub canopy cover, shrub height, shrub stem size, and browse/cutting evidence. Soils information is generally texture and depth, especially a set distance from water. Anthropogenic factors are distance to residential/commercial development, river engineering (dams, levees, channelization, and bank stabilization), road density, and farming.

This project did not utilize all of the factors, but did employ parts of four of the five components. The water component consisted of the main hydrology of Grand Teton National Park at the HUC-12-level and the identification of all lakes and ponds (over 0.25ha). Another aspect of the water component entailed using the river reaches delineated by Nelson (2007) and modifying their boundaries to correspond with the Snake River floodplain. The river reaches were used as the main spatial units for analysis because of the geomorphic characteristics they portray. The vegetation component consisted of the spatial distribution of the specific species communities, in this case willows (*Salix spp.*) and cottonwoods/aspens (*Populus spp.*), the two main species consumed by beavers in Grand Teton National Park (Collins 1977). Soil texture is a key for beavers building bank dens along the Snake River channel, but not as important for bank lodges in the backwater tributaries. Finally, the anthropogenic factor that is the most dominant in Grand Teton National Park is the Jackson Lake dam. To accommodate the influence of the dam, the Snake River is divided into two portions, the Upper Snake River (15.9km) and the Lower Snake River (43.4km) with the dam as the separator. The other anthropogenic factors are not considered in the modeling.

General descriptors of the Snake River corridor provide a needed background for the project overall. The topography and slope of the Snake River is not as dramatic as most streams. The northern reach of the Snake River at the southern border of Yellowstone National Park has an elevation of 2091 m and this flows into Jackson Lake with a normal elevation of 2064.6 m, thus the Upper Snake River gradient over this 16.2-km stretch is only 0.17%. The southern reach from Jackson Lake Dam (2064.6 m) to Moose (1969 m) is 42.9 km and has a gradient of 0.23%. The low gradient provides an environment in which the Snake River has the potential to create significant braided streams with a large sinuosity index.

The Snake River was divided into 27 reaches, 7 reaches on the Upper Snake River above Jackson Lake and 20 reaches from Jackson Lake dam to Moose (Nelson 2007). Defining aspects of each reach related to the geomorphic characteristics of the stream channel: sinuosity, braiding, confluence, width/depth, floodplain and gradient. Figure 2 illustrates the delineation of the reaches. The average reach is approximately 121.2 ha, however, there is a significant difference between the area of the Upper Snake River reach and the Lower Snake River reach, 35.5 ha versus 151.2 ha, respectively. The Upper Snake River flows through a narrow canyon for almost one-half of its distance, whereas the Lower Snake River spreads out across the Snake River valley below the dam. Both sections of the river, however, are similar in average reach stream length 2296.9 m and gradient 0.20%.

Vegetation along the Snake River was identified and delineated by the Grand Teton National Park using 2005 NAP photography at a resolution of 1m. This data was up-dated using 2012 NAP photography at the same resolution. The updates were generally associated with the meandering of the Snake River and the increase/decrease or elimination of sand bars and movement of vegetation along cutbanks. Two major categories of vegetation were distinguished, communities of *Salix spp.* and *Populus spp.*. These two major communities were formed by combining the following vegetation classes: *Salix spp.* includes *Salix spp.* shrubland; *Populus spp.* includes *Populus tremuloides* forest, mixed conifer-*Populus spp.*, *Populus angustifolia*-*Populus balsamifer* riparian forest, and *Populus tremuloides* woodland regenerated. Table 1 provides an overview of the proportion of each major beaver habitat vegetation community by reach.

Table 1. Vegetation communities by reach.

Reach	Area(ha)	Salix spp.(ha)	%Reach	%SR Total	Populus spp.(ha)	%Reach	%SR Total
UpperSnake_Reach1	17.02	1.63	9.59	0.74	0.00	0.00	0.00
UpperSnake_Reach2	9.18	0.00	0.00	0.00	0.00	0.00	0.00
UpperSnake_Reach3	11.72	0.57	4.88	0.26	0.00	0.00	0.00
UpperSnake_Reach4	4.86	0.62	12.72	0.28	0.00	0.00	0.00
UpperSnake_Reach5	59.74	17.22	28.83	7.78	0.00	0.00	0.00
UpperSnake_Reach6	159.08	73.67	46.31	33.30	4.22	2.65	100.00
UpperSnake_Reach7	254.89	127.53	50.03	57.64	0.00	0.00	0.00
Upper Snake Total	516.48	221.24		42.84	4.22		0.82
LowerSnake_Reach1	85.81	27.39	31.92	6.44	4.42	5.15	0.48
LowerSnake_Reach2	72.23	7.78	10.78	1.83	4.45	6.16	0.48
LowerSnake_Reach3	131.75	23.99	18.21	5.64	5.96	4.52	0.64
LowerSnake_Reach4	63.31	6.35	10.02	1.49	0.00	0.00	0.00
LowerSnake_Reach5	10.68	1.95	18.23	0.46	0.40	3.70	0.04
LowerSnake_Reach6	14.62	0.46	3.15	0.11	0.66	4.52	0.07
LowerSnake_Reach7	9.23	1.39	15.03	0.33	0.66	7.16	0.07
LowerSnake_Reach8	109.25	15.08	13.80	3.54	0.79	0.72	0.08
LowerSnake_Reach9	3.91	0.00	0.00	0.00	0.00	0.00	0.00
LowerSnake_Reach10	118.53	21.40	18.05	5.03	5.00	4.22	0.54
LowerSnake_Reach11	59.69	29.68	49.72	6.97	10.18	17.06	1.09
LowerSnake_Reach12	24.35	6.57	26.99	1.54	15.01	61.65	1.61
LowerSnake_Reach13	169.67	59.56	35.10	14.00	49.87	29.39	5.36
LowerSnake_Reach14	99.70	3.31	3.32	0.78	64.20	64.39	6.90
LowerSnake_Reach15	788.91	77.37	9.81	18.18	217.59	27.58	23.37
LowerSnake_Reach16	118.69	2.51	2.12	0.59	50.41	42.48	5.41
LowerSnake_Reach17	857.76	86.14	10.04	20.24	367.87	42.89	39.51
LowerSnake_Reach18	89.67	21.70	24.20	5.10	37.53	41.85	4.03
LowerSnake_Reach19	29.38	10.11	34.39	2.37	10.27	34.94	1.10
LowerSnake_Reach20	166.56	22.82	13.70	5.36	85.81	51.52	9.22
Lower Snake Total	3023.70	425.55		14.07	931.06		30.79
Grand Teton NP Total	3540.18	646.79		18.27	935.28		26.42

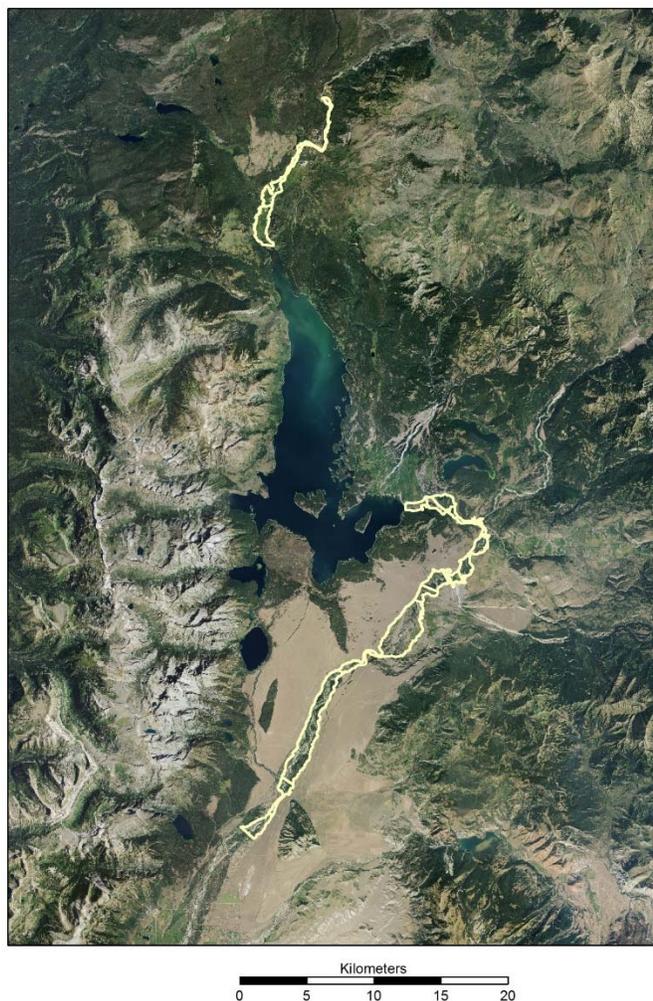


Figure 2. Upper and lower Snake River reaches.

The soil component of the model was derived from the U.S. Soil Service Soil Survey of Teton County, Wyoming Grand Teton National Park Area and the digital SSURGO data files of the Natural Resources Conservation Service. Along the Snake River below the Jackson Lake Dam, the dominant soils are the Tetonville gravelly loam, Tetonville complex, Tetonville-Riverwash complex and assorted Tetonia-Lantonia and Taglake-Sebud associations. As the Snake River meanders through the valley there are cyclical occurrences of sandbars and cutbanks, braided stream and straight bank stream. Intermittently the Snake River cuts into the older stream terraces and creates a high bank, steep slope gravel, cobble and sand embankment.

The overall result of the multi-factored analysis is a map of potential beaver habitat along both portions of the Snake River. The potential beaver habitat accounts for only a small percentage of the

Snake River corridor, limited by the vegetation communities and the extensive braiding in several river reaches (Figures 2 and 3). Major portions of the river's bank conditions are not suitable for bank dens or bank lodges because of the high percentage of cobbles, gravel and sand. In addition, the alternating sand bars and cut banks do not offer areas suitable for dens or lodges.



Figure 3. Lower Snake River potential beaver habitat.

The second objective of this project was concerned with documenting beaver activity areas, central place foraging. The initial intent was to attach a micro-GPS unit to a beaver and track its movements over six months. Three beaver activity areas were selected to conduct this original research: two locations on the Snake River (one on the Upper Snake River and one on the Lower Snake River) and one site in the Spread Creek pond complex. To test the procedure for live capturing, anesthetizing, attaching the GPS and downloading the location data, the Spread Creek pond complex was selected for ease of access and limited range of the beaver. On May 26th the unit was attached to a 21.8kg beaver. The unit stayed attached until May 31st, with the collection of 128 UTM coordinate points.

Table 2. Descriptive statistics of GPS positions -- distance to lodge by day.

Overall Description		May 26-27	May 27-28	May 28-29	May 29-30	May 30-31
Mean	113.12	57.20	154.14	122.87	148.16	137.92
Standard Error	5.82	1.57	18.79	13.25	7.41	13.47
Median	100.81	57.68	135.88	132.07	145.59	146.54
Standard Deviation	65.84	10.28	88.11	57.75	34.74	63.16
Coefficient of Variation	58.20	17.97	57.16	47.00	23.45	45.79
Kurtosis	0.57	0.40	-0.48	-0.87	1.09	-0.26
Skewness	0.93	0.48	0.70	0.13	-0.18	-0.32
Range	311.52	47.26	287.84	193.31	155.55	221.22
Minimum	15.36	39.35	39.04	37.87	64.55	15.36
Maximum	326.88	86.61	326.88	231.17	220.11	236.58
Count	128.00	43.00	22.00	19.00	22.00	22.00

Table 3. Ring-sector analysis, Spread Creek Pond complex.

GPS Location Frequency										
Rings	Sectors								Total	%
	1	2	3	4	5	6	7	8		
1	3	19	16	3	0	0	12	24	77	60.6
2	0	1	38	4	0	0	2	1	46	36.2
3	0	0	4	0	0	0	0	0	4	3.1
Total	3	20	58	7	0	0	14	25	127	
%	2.4	15.7	45.7	5.5	0.0	0.0	11.0	19.7		100

Figure 4 displays the distribution of the recorded positions, with an overall central foraging area of 11ha. There is a complex of 20 ponds with $10 > 0.03\text{ha}$ and $10 < 0.03\text{ha}$. Table 2 provides a listing of the descriptive statistics for each day of activity and the overall descriptive statistics. May 26-27th the beaver did not venture far from the lodge, averaging only 57.2 meters from the lodge. However, from May 28th until May 31st the average distances increased to 122-154m with an average coefficient of variation of 41.42%. On May 31st at 05:30am the micro-GPS unit became detached from the beaver, both the glue and the strap failed. The micro-GPS unit was retrieved using the VHF signal.

Descriptive spatial statistics portray the distribution of foraging by the tagged beaver. Using ring-sector analysis it is possible to analyze the spatial distribution of foraging at the Spread Creek Pond complex. Table 3 displays the number of point locations per ring/sector from the lodge, with element (Ring-2, Sector-3) containing 38 points (29.9%) of the 127 point total. This element has a high density of willows and easy access from one pond to another (Figure 5). A constraint in foraging is a high

embankment (5m) approximately 100m from the lodge and oriented NW-SE. This is evident by the fact that over 80% of the points are in sectors 8, 2 and 3. This embankment separates the meadow-pond complex from the surrounding outwash plain.

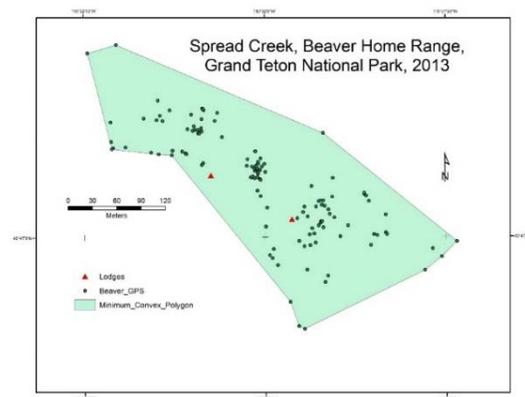


Figure 4. GPS positions and home range, Spread Creek pond complex.

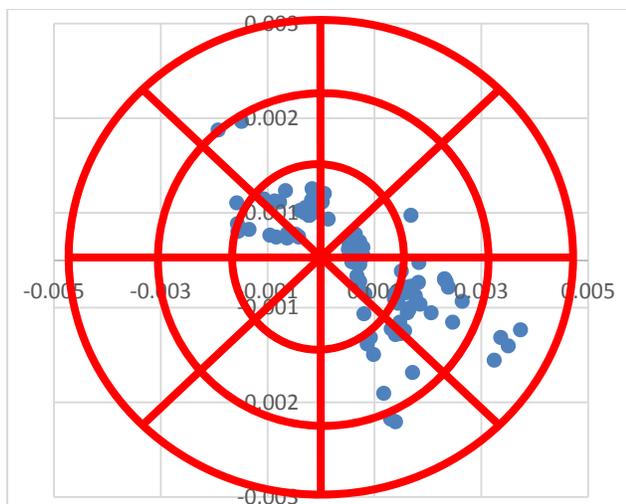


Figure 5. GPS positions, ring-sector analysis, Spread Creek pond complex (scale: 0.001=115m).

On June 26, 2013 another attempt was successful in live-trapping a second beaver (23.2kg) and attaching a micro-GPS unit. A modification was made to the strap to strengthen its attachment to the GPS unit, the point of failure in the first attempt. Unfortunately, the unit was lost within one day of attachment. A VHF signal could not be located, and thus the unit was lost. Two attempts were initiated to recapture another beaver and after ten days the traps were removed. In addition, traps were set up along the Lower Snake River to capture a river beaver, but similarly, after 10 days with no capture the attempts were abandoned.

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HOW CONIFER DIVERSITY AND AVAILABILITY INFLUENCE THE ABUNDANCE AND BIOLOGY OF THE RED CROSSBILL

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✦ ABSTRACT

In order to understand the distributions and abundances of animals, many environmental factors must be considered, particularly the availability of food resources. Food resources are especially important to nomadic species that move in response to the spatial and temporal availability of these specific food resources that are critical to their survival. An example of such nomadic species is the red crossbill (*Loxia curvirostra*), which specializes on conifer seeds, a resource that significantly varies both temporally and geographically. Thus, crossbills will move large distances each year to find areas with abundant conifer seeds. While conifer seeds impact the distribution, abundance, and reproductive rate of crossbills, it is likely not the only factor driving these patterns. To truly understand what drives the distribution and abundance of crossbills across North America, further study is needed not only on how external environmental factors such as food abundance affect these patterns, but how tradeoffs among internal physiological processes such as reproduction and survival related processes such as immune function may affect when crossbills irruptively migrate or whether or not reproduction occurs. Historically, research to understand how organisms orchestrate their annual cycles with respect to these costly and conflicting physiological processes has focused narrowly on seasonal breeders that constrain reproduction to times of year when thermoregulatory demand is low (i.e., summer), which provide limited opportunities to reveal how physiological costs of different processes may interact with environmental conditions to influence the evolution of investment strategies. In this study, we

are examining **how the diversity, abundance, and size of cone crop of conifers influence both 1) the quantity and diversity of red crossbills, as well as 2) their seasonal modulation in investment patterns in reproduction and self-maintenance processes such as immune function** in Grand Teton National Park, where crossbills can be found breeding in both summer and winter. Preliminary results from this study have indicated that both conifer diversity and cone crop size affect overall quantity and vocal type diversity of crossbills in Grand Teton National Park, as well as affecting their investment in reproduction and immunity. Overall, results from this study will provide information on how species in general and crossbills, specifically, respond to rapidly changing environments, which has become increasingly important in light of the effects of anthropogenic change.

✦ INTRODUCTION

There are many interacting factors that may affect distributions and abundances of animals, including tolerances of physical environmental factors (Brown and Fedmeth 1971), competition (Connell 1983), predation (Hahn and Denny 1989), disease (Hochachka and Dhondt 2000), and the availability of crucial food resources (Brown et al. 1995). In particular, it has been well documented that food resource availability has pronounced effects on the distribution and abundance of those nomadic species that move in direct response to the spatial and temporal availability of these food resources (Anderson 1980, Kelsey et al. 2008). One such nomadic species is the red crossbill (*Loxia curvirostra*), which specializes on

extracting seeds from conifer cones (Groth 1993). Further, crossbills can be categorized into ten vocal types that are known to specialize on one or two “key” conifers (Groth 1993). Because most conifers are mast seeders and annually produce erratic quantities of cones and seeds (Koenig and Knops 2000), crossbills will move large distances each year to find areas with abundant conifer seeds (Adkisson 1996). While conifer seed impact on the distribution, abundance, and reproductive rate of crossbills (e.g., during a large cone year, crossbills can have as many as four successful clutches between summer and spring of the following year (Adkisson 1996)), it is not the only factor driving these patterns. For example, even in low cone years, crossbills will still reproduce (Kelsey et al. 2008), but potentially at a cost to survival or self-maintenance processes (Schultz unpublished data). Thus, to truly understand what drives the distribution and abundance of different crossbill types across North America, further study is needed not only on how external environmental factors such as food abundance affect these patterns, but how tradeoffs among internal physiological processes such as reproduction and survival related processes such as immune function may affect when crossbills may irruptively migrate or whether or not reproduction occurs.

Even though much study has been devoted to understanding how organisms allocate limited resources between reproduction and survival-related processes like immune function (e.g., Martin et al. 2008, Zera and Harshman 2001), the majority of this research has focused narrowly on studies of seasonal breeders, those organisms that temporally segregate different components of the annual cycle and restrict the most demanding processes to times when resource availability is high and environmental conditions are benign (Menaker 1971, Gwinner 1986, Nelson and Demas 1996). This focus is problematic because many organisms do not follow these annual schedules and so allocation patterns garnered from just seasonal organisms may not apply to all organisms. Thus, by studying these tradeoffs in an opportunistic breeder such as the crossbill, we will gain new knowledge of how harsh environmental conditions and reproductive effort may interact to shape investment in survival, specifically immune function.

Study species

Red crossbills can be found reliably in Grand Teton National Park every year, although the overall abundance and diversity of vocal types present is highly variable from year to year and is known to be somewhat dependent on the size of the cone crop

(Kelsey et al. 2008, Hahn 1998). In this report, we will provide recent data on **how the diversity, abundance, and size of cone crop of conifers influence both 1) the quantity and diversity of red crossbills, as well as 2) their seasonal modulation in investment patterns in reproduction and self-maintenance processes such as immune function.**

✦ METHODS

Objective 1: how the diversity, abundance, and size of cone crop of conifers influence the quantity and diversity of red crossbills.

Study site and species

In Grand Teton, the dominant conifers are lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsunga menziesii*), Engelmann spruce (*Picea engelmannii*), blue spruce (*Picea pungens*), and subalpine fir (*Abies lasiocarpa*). This area is ideal for studying the diversity and abundance of red crossbill types because Type 5 are present every year due to their specialization on lodgepole pine, which produce cones every year (Burns and Honkala 1990), with periodic invasions of other types (2, 3, and 4) in response to large cone crops on Douglas-fir and spruce (Kelsey et al. 2008). Thus, we have focused on red crossbill types 2, 3, 4, and 5, which specialize, but not exclusively, on ponderosa pine, western hemlock, Douglas-fir, and lodgepole pine, respectively (See Figure 1). We use survey sites that were selected in 2006 as stratified random samples of different coniferous habitats in the Grand Teton region (Kelsey et al. 2008). Specifically, ten areas that varied in the relative dominance of conifers that are important food sources for types 2-5 of red crossbills were selected: lodgepole pine, Douglas-fir, and Engelmann and blue spruce. These areas in the park and National Forest are 1) Leidy, 2) Signal Mountain, 3) String Lake, 4), Shadow Mountain, 5) Death Canyon, 6) Granite Canyon, 7) Mosquito Creek, 8) Saw Mill Ponds, 9) Sheep Creek, and 10) Philips Pass. Within these ten areas, there are 3-5 survey or point-count sites, which were randomly selected to be a random distance between 100-500 meters from the start of a road or trail.

We used 15-minute point counts at each site to quantify the relative abundances of the four different crossbill types, following standard methods used by Kelsey et al. (2008) and outlined in Ralph et al. (1993). During the point counts, we note all detections of each type, including the number of birds detected if seen, distinguishing among types by ear.

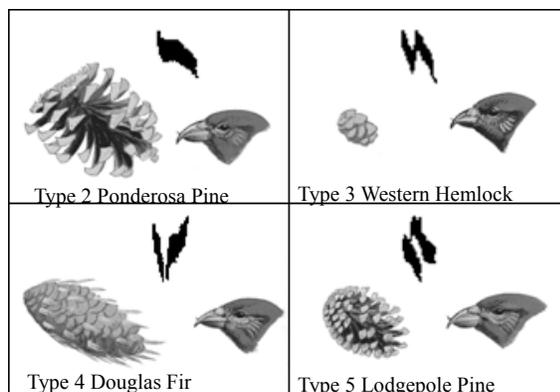


Figure 1. Drawings of the heads, spectrograms of flight calls, and key conifer cones of the four crossbill vocal types studied by Benkman (1993). Crossbills call frequently both while in flight and while perched, reliably call from cages after being captured, and when released after banding. All of these call types are readily identifiable by ear.

Conifer composition and cone crop

To evaluate local habitat selection and diet selectivity of different red crossbill types, we quantified 1) conifer composition by estimating the percent cover and availability of key conifers at each point-count site (site-level percent cover using Quadrat samples of mature trees and calculate percent cover as total number of each species divided by total number of trees across the quadrat), and 2) the availability of key conifers from a cone crop score which ranges from 0-5 (0 having no cones and 5 having large number of cones on cone-bearing section of tree) on 10-20 trees of each species present within 50 meters of the point-count site. Relative abundance of each crossbill type was estimated by reviewing field notes.

Objective 2: how the diversity, abundance, and size of cone crop of conifers influence the seasonal modulation in investment patterns in reproduction and self-maintenance processes such as immune function in red crossbills.

Capture methods

We attract crossbills using live caged decoys. Decoys call loudly when they hear birds of their own type, and birds are caught in mist nets when they approach the decoys (Adkisson 1996). If necessary, we supplement vocalizations from the decoy with playbacks of crossbill vocalizations. From each bird captured, we collect approximately 200 μ L of blood into a pre-sterilized, heparinized capillary tube. We centrifuge the blood and freeze plasma at -20°C until hormone and immune assays (described below).

Measuring reproductive potential

Reproduction is very energetically costly in birds but is essential to fitness (Nelson and Demas 1996). Significant energetic investment is required for attracting and keeping a mate, producing, laying and incubating eggs, and provisioning nestlings (Monaghan and Nager 1997). In addition, investing energy into increased fecundity or parental care in one breeding cycle might subsequently affect survival and future reproduction (Dhondt 2001).

Cloacal protuberance (CP) length in free-living male red crossbills significantly predicts testis length and therefore offers a non-invasive estimation of reproductive status (Cornelius 2009, Wingfield and Farner 1976). Males with cloacal protuberance lengths of 5 mm or larger are categorized as having high reproductive potential; males with cloacal protuberances of 3 to 5 mm are medium, and 3 mm or less are considered low (Cornelius 2009, Wingfield and Farner 1976). In female red crossbills, brood patch (BP) stage significantly predicts ovary condition (Cornelius 2009, Wingfield and Farner 1976). Females with brood patches > 0 are considered high, whereas females with brood patches $= 0$ or below are considered low reproductive potential. Briefly, a dry and fully feathered breast scored a 0; a dry but bare (i.e., without feathers) breast scored a 1; a bare breast with increased vascularization and/or mild edema scored a 2; a bare, vascularized breast with full edema scored a 3; and a bare and wrinkly breast scored a 4 (i.e., post-full edema) (Nolan and Ketterson 1983). Because estimations of cloacal protuberances and brood patches are not a perfect prediction of reproductive condition, we have supplemented this data with 1) lavage of the cloacal protuberance to collect semen and measure presence of sperm, and 2) utilizing hormone profiles (androgens and estradiol) extracted via a competitive binding radio-immuno assay (RIA) from blood samples.

Measuring immune function (survival-enhancing process)

Immune function contributes to survival by detecting pathogens and limiting infection, but because maintenance of immunity can be costly (e.g., Schmid-Hempel and Ebert 2003), many environmental and physiological variables have been hypothesized to cause investment in immunity to vary (Buehler et al. 2008, Martin et al. 2008, Nelson et al. 2002). Broadly, the immune system can be divided into two main components: innate and adaptive. Innate

immune function provides an immediate and non-specific response to a pathogen and can be further categorized into constitutive and induced responses. Adaptive or acquired immunity is activated by the innate response to produce specific antibodies against the pathogen (Martin et al. 2008, Lee 2006).

We specifically measured constitutive immunity because it provides a first line of defense against many pathogens and must always be maintained on some level, which create costs that may be important in mediating physiological trade-offs (Martin et al. 2008). To measure constitutive immunity in crossbills, we utilized 1) complement and natural antibody activity via a hemolysis-hemagglutination assay (Matson et al. 2005), 2) bacterial-cidal assay that measures the capacity of whole blood to limit a bacterial/microbial infection (Millet et al. 2007), and 3) differential white blood cell counts, a simple, gross measure of innate immunity obtained from a simple blood smear (Campbell 2007).

◆ PRELIMINARY RESULTS

Objective 1: How the diversity, abundance, and size of cone crop of conifers influence the quantity and diversity of red crossbills.

As demonstrated by Kelsey et al. (2008), the crossbill types may be specialized for general resource classes (groups of conifer species) rather than single resources. In Grand Teton, type 2s most frequently occur in areas dominated by spruce (both blue and Engelmann) and Douglas-fir, type 3s with Engelmann spruce, type 4s with Douglas-fir, and type 5 with lodgepole pine (Kelsey et al. 2008). Additionally, type 2s will selectively forage on Douglas-firs, type 3s will selectively forage on Engelmann spruce in summer and Douglas-fir in winter, while types 4 and 5 will selectively forage on Douglas-fir to avoid lodgepole pine (Kelsey et al. 2008).

Recent data collected from 2010-2013 (Figures 2 and 3) further demonstrate that both conifer diversity and cone crop abundance significantly contribute to crossbill type quantity and diversity in Grand Teton National Park (see Figure 4). To clarify, cones begin to develop on the trees in early summer (June-July) and are typically harvested by crossbills and other animals up until late spring of the following year (Koenig and Knops 2000). Thus, a heavy cone year like 2011 would last from June/July 2011 through late spring of 2012. Our data suggest that type 5 crossbills are present in years with both low and heavy

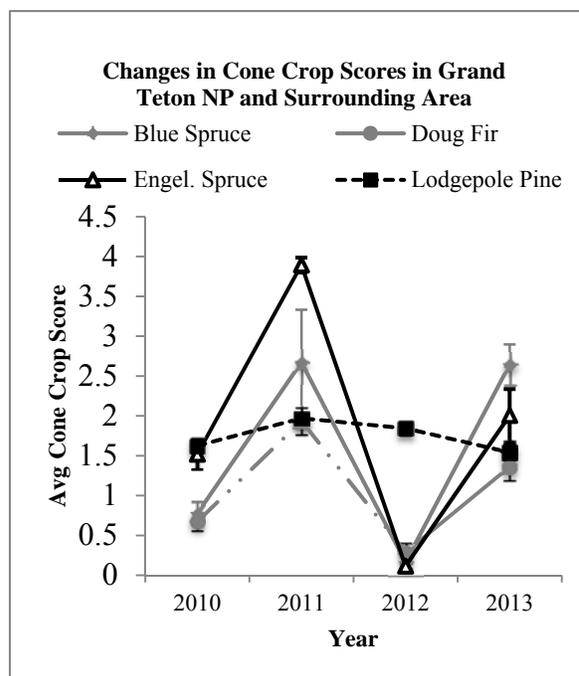


Figure 2. Average cone crop abundance in Grand Teton National Park in 2010, 2011, 2012, and 2013. Lodgepole pine cone abundance appears to be fairly consistent, averaging around 1.5 (out of a max score of 5) every year, whereas the other conifer species fluctuate more dramatically from year to year. 2011 saw the highest cone abundance across all key conifer species, with Engelmann spruce having the largest crop (average score of 3.9). Bars represent standard error of the mean (SEM).

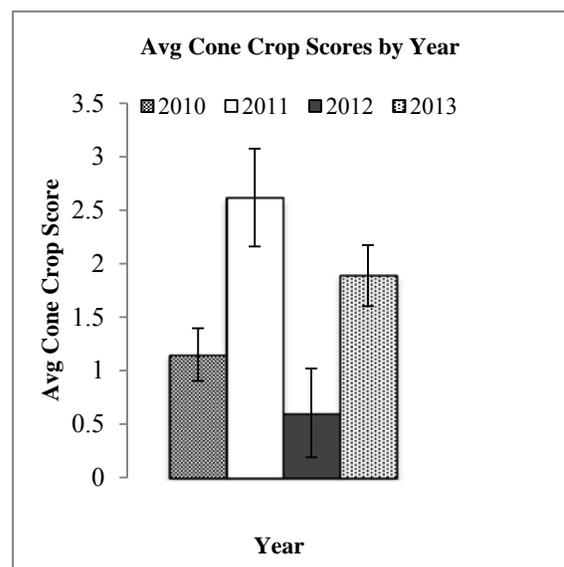


Figure 3. Average cone crop abundance (combining averages of blue spruce, lodgepole pine, Engelmann spruce, and Douglas-fir). 2011 saw the overall highest cone abundance, with 2010, 2012, and 2013 showing significantly lower overall cone abundances. Bars represent standard error of the mean (SEM).

conifer cone crops, whereas other vocal types (2,3, and 4) are only present in heavy cone years such as 2011 (Figure 4). However, juveniles (hatch year) of vocal types (2, 3, and 4) were numerous in summer of 2012 (a low cone year), and were likely born in winter or spring of 2012.

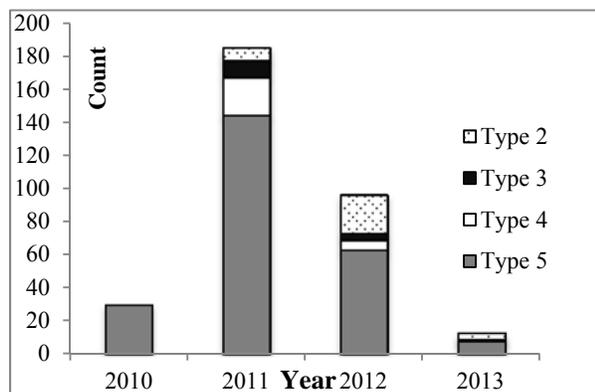


Figure 4. Red crossbill type abundance by year. In 2010 (low cone year), the only crossbill types caught via mist net were type 5. In 2011, types, 2, 3, 4, and 5 were all caught, with type 5 being the most abundant. We caught primarily type 5s in 2012, but did catch young (hatch year) type 2s, 3s, and 4s. Only 14 birds were caught in 2013, mostly type 5s and 2s.

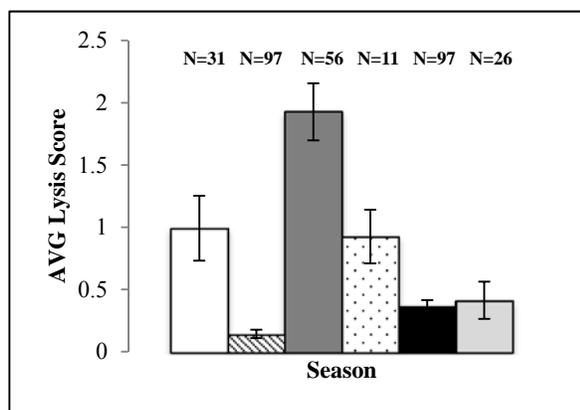


Figure 5. Seasonal pattern of lysis scores (complement level) in red crossbills. Highest lysis scores are seen in the summer, with declining scores during fall, winter, and spring. Lysis scores are also higher in years with heavier cone crops (2011). Bars represent S.E.M.

Objective 2. How the diversity, abundance, and size of cone crop of conifers influence the seasonal modulation in investment patterns in reproduction and self-maintenance processes such as immune function in red crossbills.

Data from 2010-2013 have demonstrated that years in which the cone crops of key conifers are more abundant, crossbills have higher reproductive potential and immune function (as measured by two different immune assays), which is most likely the result of having more food resources available to invest in multiple competing, energetic processes.

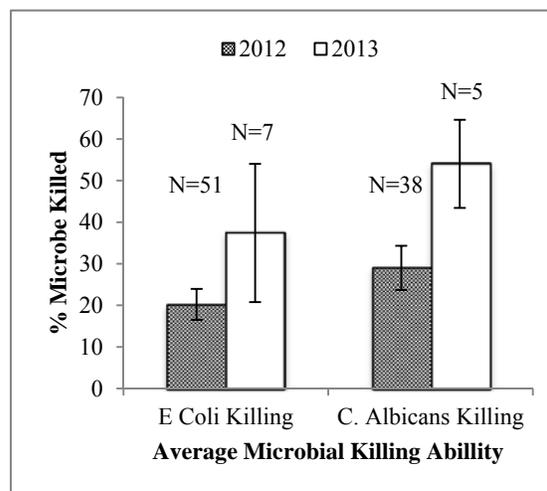


Figure 6. Average microbial killing ability of red crossbills summer of 2012 and 2013. The killing of both microorganisms is mediated by different mechanisms: *E.coli* killing is mediated by complement proteins, whereas *C.albicans* killing is mediated by white blood cell phagocytosis.

How size of cone crops affects overall crossbill immunity: 1) Results from hemolysis-hemagglutination assay: The hemolysis-hemagglutination assay uses a serial dilution of plasma and rabbit red blood cells to measure the activation of humoral component of constitutive innate immunity, specifically measuring complement levels via lysis ability and natural antibodies via agglutination level; higher lysis and agglutination scores typically equate to higher levels of immune function (Matson et al. 2005). When comparing seasonal and annual variation of both lysis scores (complement level) and agglutination scores (natural antibody level), average lysis scores exhibit distinct annual and seasonal patterns (Figure 5). Agglutination scores did not exhibit annual or seasonal variation (figure not shown). 2) For this assay, we measured the ability of crossbill whole-blood (not just plasma) to eliminate (or “kill”) two species of microbe: *Escherichia coli* and *Candida albicans*. *E. coli* killing is primarily mediated by complement proteins, whereas *C. albicans* killing is primarily mediated by white blood cell phagocytosis, thus probing two different mechanisms of immunity with this assay. The overall average of *C. albicans* and *E.coli* killing were both significantly higher in 2013 than in 2012, which may

be related to the heavier cone crop in 2013 (Figure 6).
 3) Results from white blood cell differentials: From the blood smears, we were able to detect distinct

annual variation of average white blood cell levels in red crossbills (Figure 7).

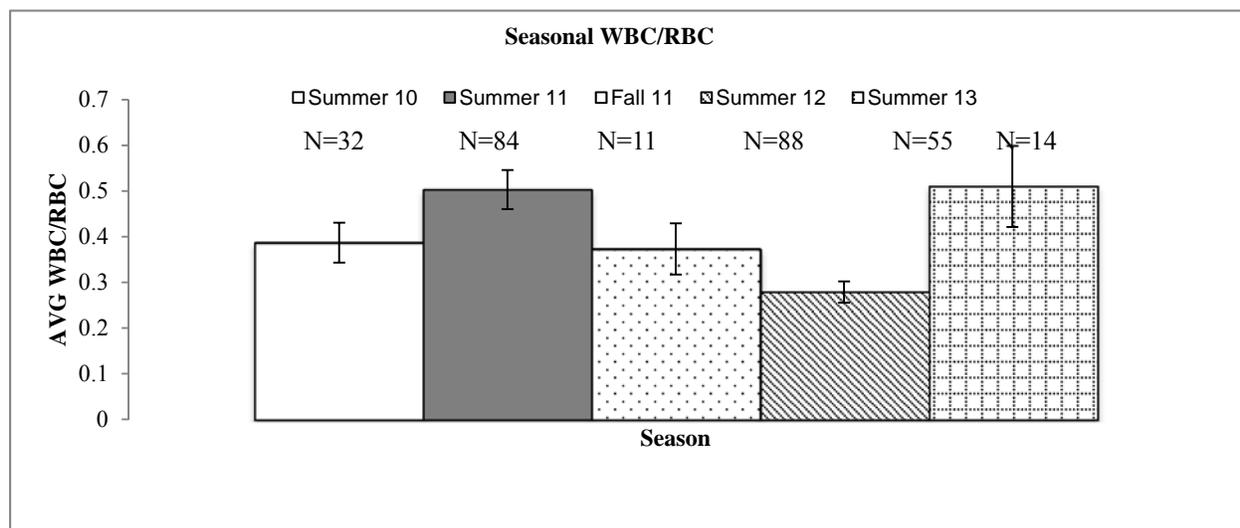


Figure 7. Seasonal pattern of white blood cell/ red blood cell ratios. Highest WBC/RBC ratios are seen in the summer, with declining scores occurring in fall, winter, and spring. WBC/RBC ratios are also higher in years with heavy cone crops (2011, 2013). Bars represent S.E.M.

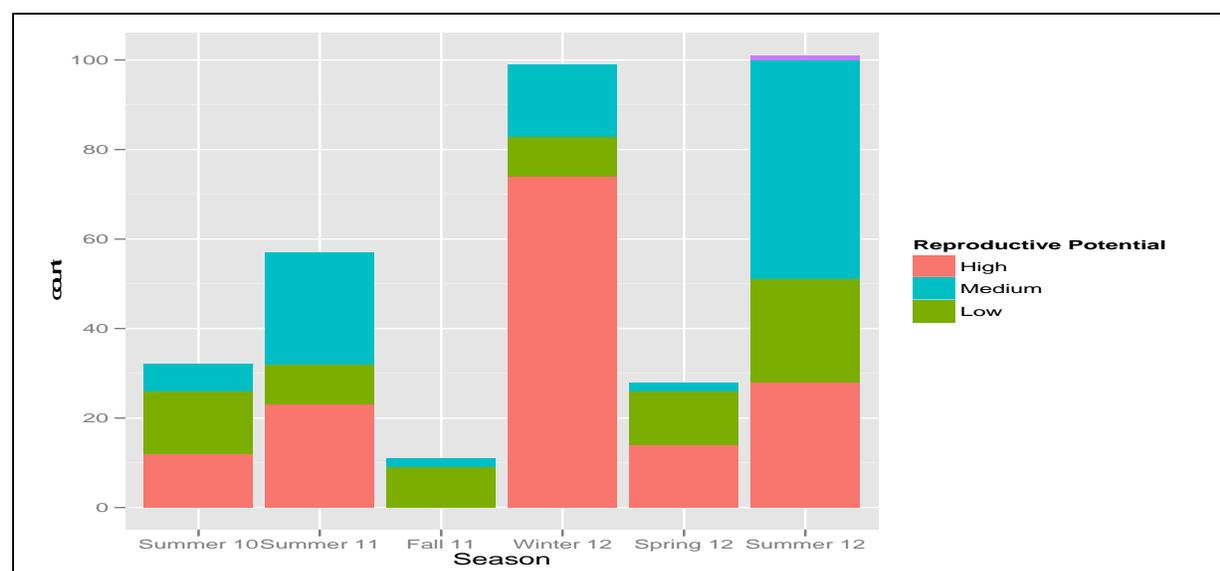


Figure 8. Crossbill reproductive potential (both males and females) across seasons. The largest proportion of crossbills categorized as having high reproductive potential was seen in the winter of 2012 (heavy cone year), and lowest generally seen in the fall and in summers of low cone years (2010, 2012). Data from 2013 not shown.

How size of cone crops affects crossbill investment in reproduction

Overall, crossbills invest more in reproduction (higher reproductive potential as measured by larger cloacal protuberances and presence of spermatozoa in males, and brood patch appearance in females), when cone crop levels are

high, regardless of the other environmental conditions (temperature, precipitation levels) (Figure 8). As demonstrated above, in heavy cone years, crossbills are able to maintain high levels of immunity as well as investing significantly in reproduction, suggesting that with adequate resources, crossbills are able to maintain both physiological processes without exhibiting any tradeoffs.

Overall conclusions

Based on our data collected in 2010-2013 we have augmented our 20 year field data set on red crossbills, further confirming that fluctuations in conifer cone crop size and the overall conifer species diversity affect multiple aspects of red crossbill physiology. Heavy cone years like 2011 that saw large cone crops specifically on Douglas-firs, Engelmann and blue spruces (lodgepole pine saw relatively static cone crops from year-to-year), positively affected two aspects of immunity (lysis scores and white blood cell counts), as well as increasing reproductive potential in both males and females. Additionally, red crossbills had overall higher immunity and higher reproductive potential during heavy cone years, suggesting that when food resources are plentiful, crossbills are able to sustain both costly physiological processes without tradeoffs. According to our model-selection approach, the highest-ranking model predicting seasonal variation in lysis score and white blood cell counts included positive effects of cone crop scores (heavier cone crops increased scores) and temperature.

✦ BROADER IMPACTS

Because crossbills are not entirely dependent on conifer seed abundance to maintain survival and even reproduction, food scarcity may not be the only driving factor influencing selection on their adaptive radiation. Thus, it is important to investigate how the diversity and abundance of conifer species may influence resource allocation to reproduction and self-maintenance in different vocal types of red crossbills. Additionally, how dependent red crossbills are on conifer species in Grand Teton National Park will have conservation implications as conifer species composition changes within the park. Landscape scale changes in age structure and composition of the forests could have major influences on crossbill populations, both in overall numbers and diversity of vocal types in the park (Kelsey et al. 2008).

In addition, the timing and investment in reproduction and survival have been more extensively investigated in seasonally breeding organisms, with most of these studies focusing on captive animals. Thus, we are limited in our ability to answer questions that involve how demanding environmental conditions such as low food availability may affect investment decisions, specifically in regards to reproduction, because seasonally breeding animals typically breed only when environmental conditions are benign. By studying organisms such as crossbills that are able to reproduce in harsh environmental conditions, we will gain more insight into potentially alternative

physiological mechanisms that regulate the timing and investment in survival and reproduction. This information can be applied to understanding how organisms effectively allocate resources to competing physiological processes, which is becoming increasingly important in light of recent anthropogenic changes (Wuethrich 2000, Hughes 2000).

✦ ACKNOWLEDGEMENTS

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IDENTIFYING AVIAN COMMUNITY RESPONSE TO SAGEBRUSH VEGETATION RESTORATION IN GRAND TETON NATIONAL PARK

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✦ ABSTRACT

Approximately 50-60% of native sagebrush steppe has been lost to non-native grasses, which has contributed to population decreases for sagebrush-associated songbirds. Removal of non-native grasses and restoration treatments may return structure and function of sagebrush steppe and ultimately benefit songbirds, but their responses must be evaluated. To determine breeding songbird community responses to sagebrush restoration treatments, in 2013 we conducted bird surveys at restored plots at the Kelly Hayfields restoration area in Grand Teton National Park, Wyoming. We compared bird communities and vegetation characteristics in restored plots to plots that were unrestored and to areas of native sagebrush steppe as starting and endpoints for restoration, respectively. Unrestored plots were dominated by non-native grasses; restored plots were dominated by forbs and bare ground and had very little shrub cover (< 0.1%). Native sagebrush plots were dominated by shrubs and native bunchgrasses. Bird community composition was distinct among the three types of plots. Abundance of grassland birds was highest in unrestored plots, and was positively related to cover of non-native grass and litter depth. Abundance of shrubland birds was highest in native sagebrush, and was positively associated with shrub cover. There were very few detections of birds in restored plots, and most species were negatively associated with the high levels of bare ground that characterized these plots. Restored areas may initially (≤ 5 yrs) provide little breeding bird habitat, which should be accounted for when determining schedules of restoration treatments at Kelly Hayfields.

✦ INTRODUCTION

Invasive, alien plant and animal species are one of the greatest threats to global biodiversity (Butchart et al. 2010). The effects of invasive aliens on ecosystems are mixed, but they can contribute to disruption of ecosystem functioning, habitat loss and degradation, and extinction of native species (Brooks et al. 2004, Clavero and Garcia-Berthou 2006). Given the potentially negative effects of invasive alien species, control often becomes a priority for conservation and management efforts.

Management of alien plant species may depend on the resilience of the ecosystem into which aliens are introduced. In ecosystems that are resilient, introduction of alien plants often results in temporary changes in relative dominance of plants (Briske et al. 2006). Ecosystems lacking resilience may cross ecological thresholds resulting in permanent dominance of alien species and alternative communities that differ substantially in structure and function from the original community. Returning communities to original structure and function will not likely occur without significant human effort, including alien species control or restoration of native species (Briske et al. 2006). However, restoration of original communities to an original or undisturbed state is often very difficult or unlikely (Van Haveren et al. 1997). A more feasible option may be to restore communities to functional surrogates of their past states, and one way to evaluate the functionality of restored systems is to determine whether the restoration provides suitable conditions for native fauna (Block et al. 2001).

One system in North America that has been highly converted range-wide is sagebrush steppe. The sagebrush biome, once covering nearly 63 million ha in western North America (Miller and Eddleman 2001), currently comprises almost 300,000 km² (Miller et al. 2011). This ecosystem provides substantial services to the nation's economy, including livestock grazing, renewable and non-renewable resources, and recreational opportunities. It also serves as habitat for more than 350 species of wildlife for at least part of their life cycle (Hanser et al. 2011). However, sagebrush systems are among the most threatened in North America (Noss and Peters 1995), largely because of conversion to exotic, annual grasslands (West 2000). Approximately 50-60% of native sagebrush steppe has been lost to non-native grasses, primarily to provide forage for livestock. Altered plant communities can result in concurrent changes in animal communities as a result of habitat changes. Not surprisingly, the loss of native sagebrush steppe has resulted in decreases of several species of wildlife associated with sagebrush habitat (Knick et al. 2003).

To determine whether restoration efforts in sagebrush steppe can provide functional wildlife habitat similar to original, native habitats, many

attributes of wildlife populations using restored areas should be measured, including resource selection and demography (Block et al. 2001). However, an important first step in determining whether restored areas can serve as functional habitat for sagebrush-associated wildlife species is to evaluate occurrence, density, and community composition at restored sites relative to unrestored habitats, and to areas of native, undisturbed vegetation. Including unrestored habitats as restoration starting points and native, undisturbed habitat as restoration endpoints will help determine whether restored habitats are on appropriate trajectories in terms of community composition, and how far restoration goals are from being attained. We focus on breeding songbird responses because grassland and shrubland birds associated with native sagebrush steppe have experienced steep population declines over the last four decades (Sauer et al. 2012), and thus represent taxa that could benefit from successful restoration of sagebrush steppe. The objectives of this study were to evaluate short-term effects of current restoration treatments on 1) the abundance and community composition of birds associated with native sagebrush steppe, and 2) habitat variables important in determining the composition of these bird communities.

Table 1. Restoration plots and associated schedule of restoration efforts at Kelly Hayfields at Grand Teton National Park, Wyoming, USA. Glyphosate treatments are intended to kill smooth brome (*Bromus inermis*). Milestone treatments are used to treat exotic forbs such as houndstongue (*Cynoglossum officinale*) and musk thistle (*Carduus nutans*). Cover crops of winter wheat (*Triticum aestivum*) and cereal rye (*Secale cereale*) are used initially instead of native seed mixes to allow for the suppression of annual exotic plants. All bird and vegetation sampling were completed before 2013 treatments.

Restoration Unit	Acres	Restoration Method		
		Sprayed	Burned	Seeded
Aspen Ridge	89	Glyphosate June 2008 Glyphosate July 2009 Milestone summer 2010	September 2008	October 2009 ^a
Hunter East/West	64/122	Glyphosate June 2009 Glyphosate June 2010	September 2008	September 2009 ^b September 2010 ^c October 2011 ^a
Elbo West*	43	Glyphosate June 2010 Glyphosate July 2010	September 2010	September 2010 ^c October 2011 ^a
Elbo East	225	Glyphosate June 2011 Glyphosate June 2013	May 2010	September 2012 ^c
Henrie	324	Glyphosate June 2013		

* not included in vegetation or avian monitoring

^a Native seed mix

^b Winter Wheat; did not sufficiently suppress invasive annuals, so plots were treated with a second cover crop.

^c Cereal Rye

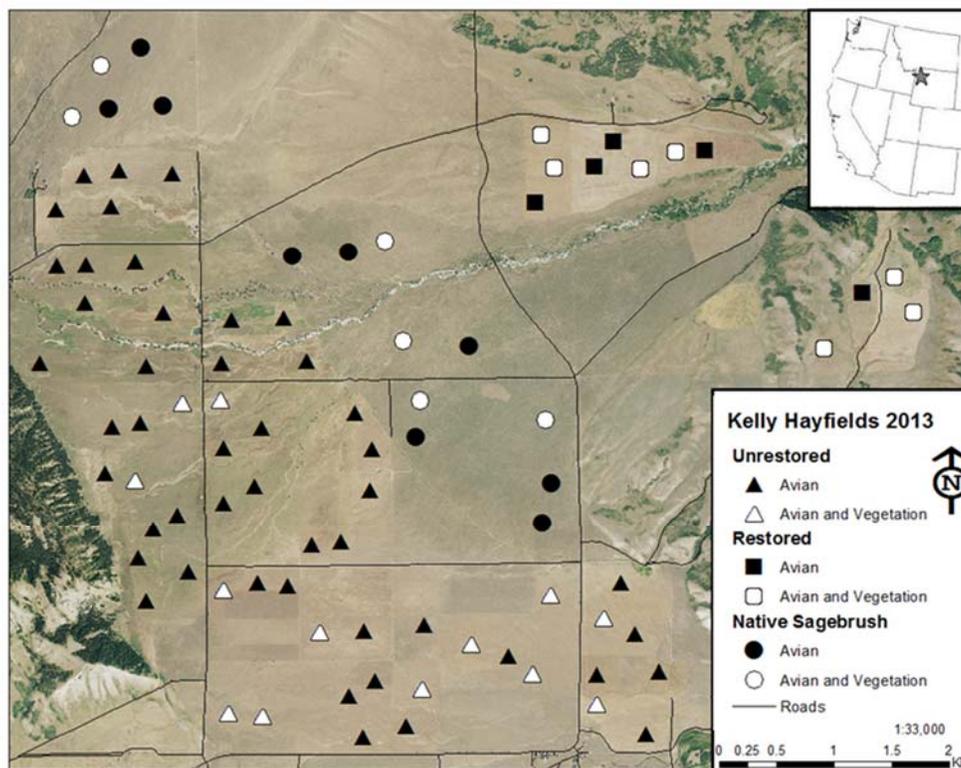


Figure 1. Avian and vegetation survey locations within Kelly Hayfields Grand Teton National Park, Wyoming, USA.

STUDY AREA

To assess whether restored sites provide functional habitat for sagebrush-associated songbirds, we conducted surveys for breeding birds at unrestored and recently-restored plots already established by National Park Service (NPS) personnel in Grand Teton National Park (GTNP), Wyoming, USA. Additionally, we identified and surveyed areas of native sagebrush steppe that represented a restoration end goal in order to make comparisons to restored and unrestored plots (Figure 1). Although GTNP lands are characterized by a number of different ecological zones, lower elevations are primarily conifer and deciduous forests intermixed with extensive sagebrush steppe in drier upland areas. Prior to establishment of GTNP, land now known as the Kelly Hayfields was settled by homesteaders who converted native sagebrush steppe vegetation to non-native pasture for agricultural use. Since the NPS acquired the land in the 1960s, agricultural use has been minimal. However, non-native vegetation in areas previously used as pastures remains dominant. In 2007, in cooperation with the US Fish and Wildlife Service, the NPS committed to restoring the Kelly Hayfields to native sagebrush steppe with the “Bison and Elk Management Plan”. Restoration treatments began at

Kelly Hayfields in 2008 (Table 1). The total restoration goal is 1790 ha. At the time of data collection, restoration treatments had been completed on 36 ha, and an additional 184 ha were being actively treated. We conducted surveys on plots ($n = 4$) that were in various stages of restoration (either very recently completed or being actively treated in the year of our surveys; Table 1). In addition to data collection at restored plots, bird surveys were conducted at plots ($n = 9$) in the Kelly Hayfields that have not undergone any restoration treatments (Figure 1); these units serve as a baseline point of comparison. Finally, to serve as a restoration endpoint of comparison, bird surveys were conducted in plots ($n = 3$) of native sagebrush steppe near the Kelly Hayfields (Figure 1). These plots were established by visual inspection of dominant vegetation, and by avoiding areas intersected by road, areas potentially influenced by changes in topography or soil type, and an area near the Hayfields that had been affected by a recent fire (NPS personnel, personal communication). Including non-native, unrestored plots and native sagebrush-dominated plots in the sampling design with restored sites provides us with a continuum of vegetation characteristics that will allow us to assess avian community responses to restoration treatments throughout the restoration process.

✦ METHODS

Avian surveys

To quantify bird abundance and community composition, 5 min fixed radius point count surveys were conducted in all 16 plots using the removal method (Farnsworth et al. 2002). Counts were divided into five, 1-min intervals, and all birds detected within 100 m were recorded only once and subsequently 'removed' (ignored) from the sample population after initial detection to estimate detection probability. Five-minute counts also help minimize the likelihood that individual birds are mistakenly thought to be multiple birds and counted more than once (Fuller and Langslow 1984). Surveys were conducted from 3-14 June 2013 to minimize the likelihood of including migrants during counts (Rehm-Lorber et al. 2010). We established 2-5 survey points within each plot depending on plot size (Figure 1). Points were located a minimum of 150 m from features that might influence vegetation or detection of birds (e.g., roads, fences, or riparian zones) and 250 m from each other. Surveys began within 15 min of dawn and continued until 0930 Mountain Standard Time. Surveys were not conducted during periods of continuous rain, or wind causing tree tops to bend (Beaufort Wind Scale 5). Each survey point was visited twice throughout the sampling period.

Vegetation surveys

Vegetation surveys were conducted at two of the points in each plot used for bird surveys. We used a 90-m line transect originating at the point and extending in one direction determined by a radial degree chosen at random. Vegetation characteristics were recorded along three distance intervals from the origin (0-10 m, 40-50 m, and 80-90 m). Within each 10 m distance interval, measurements were made on the shrub canopy (if present) and understory at 1 m intervals ($n = 30$ points along each transect). Percent shrub cover was assessed by recording and summing the linear distances along each transect directly intercepted by shrub canopy, and dividing by 30. Height of each shrub intersecting the transect line was also measured, and the species recorded. Understory characteristics were assessed using point intercept along the same transect: species intercepted first (top canopy), second (lower canopy), and soil surface characteristics were evaluated at each 1 m interval. Functional cover types were recorded, which included native and non-native grasses, forbs, and standing dead material, and live plants were identified to genus or species when possible. Soil surface was characterized as a functional type or species if a plant's

base was intercepted, or litter, bare ground, rock, or cryptogam. Vegetation height (cm) and litter depth (mm) was measured at each 1-m interval.

Statistical analyses

We attempted to estimate songbird densities using the Farnsworth removal model (Farnsworth et al. 2002) which allows estimation of detection probabilities and adjusts estimates of abundance based on detection rates. However, sparse numbers of observations for any species at restored plots precluded use of this method. So, for the remainder of our analyses, we used the maximum count of each species from two visits within a plot as our response variable. We recognize there are limitations to inferences we can make from our data because we have not accounted for differences in detection probability among species or habitats. However, during initial modeling of songbird density, we estimated very high detection probabilities (p) for species that occurred in sufficient numbers to be modeled for native and unrestored treatments, which included Brewer's Sparrow ($p > 0.92$), Savannah Sparrow ($p > 0.97$), Green-tailed Towhee ($p > 0.91$), Vesper Sparrow ($p > 0.69$), and Western Meadowlark ($p > 0.98$), suggesting low detection probabilities and large differences among species may not have strongly influenced our results.

To compare songbird community composition among native sagebrush steppe, restored, and unrestored areas, and to describe relationships among songbird community composition and vegetation characteristics, we used a multivariate approach. To determine whether there were differences in community composition among plot types, we conducted a Multi-Response Permutation Procedure using abundance of each species (MRPP; Mielke 1984). Plot types were used as a priori groups for comparison of community composition. Distances were calculated using the Euclidian measure and groups were defined by plot type (native sagebrush steppe: $n = 3$; restored: $n = 4$; unrestored: $n = 9$).

Non-metric multidimensional scaling (NMS) was used to elucidate results of the MRPP analysis and to evaluate the relationship between songbird community composition and habitat characteristics (Kruskal 1964, Mather 1976). Euclidian distance measure was used for the NMS. Final dimensionality of the data was evaluated using final stress versus the number of dimensions, where stress is a measure of departure from monotonicity between distance in original species space and distance in ordination space, and by performing 225 runs of a randomization

test (McCune and Grace 2002). To describe habitat factors influencing patterns of breeding songbird community composition, habitat measurements were overlaid onto the final ordination. These measurements included: percent cover of shrubs, native and non-native grasses, and bare ground, as well as litter depth and understory height. We determined which habitat measurements to include based on a review of the primary literature for species-habitat associations. Correlation coefficients of vectors from the habitat matrix represent the strength and direction of relationships with axes. We conducted all multivariate analyses in PC-ORD Version 6.08 (McCune and Mefford 2011).

◆ RESULTS

We observed 24 bird species, eight of which have established associations with some component of native sagebrush steppe habitat (Table 2; Rich et al. 2005). The most common species were shrubland and grassland-associated species, including: Brewer's Sparrow (*Spizella breweri*), Brewer's Blackbird (*Euphagus cyanocephalus*), Green-tailed Towhee (*Pipilo chlorurus*), Long-billed Curlew (*Numenius americanus*), Savannah Sparrow (*Passerculus sandwichensis*), Vesper Sparrow (*Pooecetes gramineus*), Western Meadowlark (*Sturnella neglecta*), and Sage Thrasher (*Oreoscoptes montanus*). Mean number of species ranged from 1-6 for all plots (Table 3). Similar numbers of species were observed in native and unrestored plots, and the fewest species were detected in restored plots. Savannah Sparrow and Western Meadowlark were most abundant at unrestored plots (Table 4). Brewer's Sparrow, Green-tailed Towhee, and Sage Thrasher were most abundant at native sagebrush steppe plots. Vesper Sparrow abundance was relatively low and similar among treatments.

Vegetation composition and structure was substantially different among the three plot types. Native plots were characterized by relatively high percent cover of shrubs, native bunchgrasses and forbs, and litter cover (Table 5). Restored plots had relatively high percent cover of native and non-native forbs and bare ground, and low cover of shrubs or grasses. Unrestored plots were dominated by non-native grass (primarily *Bromus inermis*) and had high percent litter cover relative to restored plots. Depth of the litter layer and height of the understory (grasses+forbs) was lowest in restored plots (Table 6). Shrub height was greatest in native sagebrush plots, and although some unrestored plots had a shrub

Table 2. Total number of detections for all species observed during point count surveys in native sagebrush steppe ($n = 3$), restored ($n = 4$), and unrestored ($n = 9$) plots in the Kelly Hayfield area of Grand Teton National Park, Wyoming, USA in 2013.

Common Name	Latin name	Total Detection
Savannah Sparrow	<i>Passerculus sandwichensis</i>	134
Brewer's Sparrow	<i>Spizella breweri</i>	112
Vesper Sparrow	<i>Pooecetes gramineus</i>	69
Western Meadowlark	<i>Sturnella neglecta</i>	41
Green-Tailed Towhee	<i>Pipilo chlorurus</i>	32
Brewer's Blackbird	<i>Euphagus cyanocephalus</i>	10
Long-billed Curlew	<i>Numenius americanus</i>	10
Common Raven	<i>Corvus corax</i>	8
Sage Thrasher	<i>Oreoscoptes montanus</i>	7
American Robin	<i>Turdus migratorius</i>	3
Tree Swallow	<i>Tachycineta bicolor</i>	3
Barn Swallow	<i>Hirundo rustica</i>	2
Canada Goose	<i>Branta canadensis</i>	2
Mountain Bluebird	<i>Sialia currucoides</i>	2
Sprague's Pipit	<i>Anthus spragueii</i>	2
American Kestrel	<i>Falco sparverius</i>	1
Black-billed Magpie	<i>Pica hudsonia</i>	1
European Starling	<i>Sturnus vulgaris</i>	1
Lincoln's Sparrow	<i>Melospiza lincolnii</i>	1
Merlin	<i>Falco columbarius</i>	1
Northern Flicker	<i>Colaptes auratus</i>	1
Turkey Vulture	<i>Cathartes aura</i>	1
Violet-green Swallow	<i>Tachycineta thalassina</i>	1
White-crowned Sparrow	<i>Zonotrichia leucophrys</i>	1
Total Number of Detections		446

Table 3. Mean number of species (\pm SE) observed within native sagebrush steppe ($n = 3$), restored ($n = 4$), and unrestored ($n = 9$) plots at the Kelly Hayfield area of Grand Teton National Park, Wyoming, USA during 2013.

Treatment	Mean no. species
Native	4.67 (± 0.67)
Restored	2.33 (± 0.67)
Unrestored	4.42 (± 0.53)

component (Table 5), average shrub height was much lower (difference = 48.41 cm) compared to native plots (Table 6).

The MRPP test using songbird abundances in native sagebrush, restored, and unrestored plot types as a priori groups yielded a large A-statistic ($A = 0.36$, p -value < 0.0001), reflecting distinct songbird community composition in each plot type and high within-group homogeneity. Pairwise comparisons revealed that all three plot types had unique species composition (Table 7). Based on examination of T-values, native versus unrestored plots had the strongest differences in species composition, while native versus restored and restored versus unrestored had similar magnitudes of difference between them.

Table 4. Mean number of observations (\pm SE) of sage brush steppe-associated songbird species in native sagebrush steppe ($n = 3$), restored ($n = 4$), and unrestored ($n = 9$) plots at the Kelly Hayfield area of Grand Teton National Park, Wyoming, USA. Values reported are means of the maximum number of observations of each species from two visits to each plot during 2013.

Species	Treatment		
	Native	Restored	Unrestored
Savannah Sparrow	0 (± 0.00)	1.00 (± 1.00)	7.33 (± 1.00)
Brewer's Sparrow	16.0 (± 2.65)	0.25 (± 0.25)	1.67 (± 0.86)
Vesper Sparrow	2.33 (± 1.20)	3.25 (± 1.49)	2.50 (± 0.58)
Western Meadowlark	1.00 (± 0.58)	0.50 (± 0.50)	2.42 (± 0.62)
Green-Tailed Towhee	6.67 (± 2.85)	0 (± 0.00)	0 (± 0.00)
Sage Thrasher	2.00 (± 1.15)	0 (± 0.00)	0 (± 0.00)

Table 5. Mean percent cover (\pm SE) by functional type in native sagebrush steppe ($n = 3$), restored ($n = 4$), and unrestored ($n = 9$) plots at the Kelly Hayfields area of Grand Teton National Park, Wyoming, USA.

Treatment	% Shrub cover	% Native grass	% Non-native grass	% Native forb	% Non-native forb	% Bare ground	% Litter
Native	11.23 (± 2.25)	5.78 (± 2.71)	0.10 (± 0.10)	15.16 (± 1.83)	0.56 (± 0.56)	6.79 (± 2.03)	81.23 (± 7.33)
Restored	0.05 (± 0.05)	2.64 (± 3.73)	5.0 (± 3.92)	11.81 (± 5.25)	12.36 (± 6.76)	43.61 (± 14.32)	50.14 (± 15.81)
Unrestored	0.89 (± 0.47)	1.98 (± 1.13)	30.65 (± 3.59)	1.91 (± 0.74)	4.44 (± 2.07)	15.56 (± 3.36)	80.62 (± 2.92)

Table 6. Average (\pm SE) vegetation height and litter depth in native sagebrush steppe ($n = 3$), restored ($n = 4$), and unrestored ($n = 9$) plots at Kelly Hayfields area of Grand Teton National Park, Wyoming, USA in 2013.

Treatment	Litter depth (mm)	Understory height (cm)	Shrub height (cm)
Native	14.34 (± 3.47)	13.11 (± 2.69)	62.42 (± 2.65)
Restored	3.22 (± 1.66)	6.15 (± 0.98)	0.4 (± 0.4)
Unrestored	13.28 (± 3.38)	13.67 (± 1.23)	14.01 (± 7.29)

Table 7. Results of a multi-response permutation procedure comparing breeding songbird community composition sampled in native sagebrush steppe ($n = 3$), restored ($n = 4$) and unrestored ($n = 9$) plots during 2013 at the Kelly Hayfield area of Grand Teton National Park, Wyoming, USA.

Comparison	T^a	A^b	P -value
Native vs. restored	-3.67	0.46	< 0.01
Native vs. unrestored	-5.77	0.33	< 0.01
Restored vs. unrestored	-3.72	0.15	< 0.01

^a $T = (\delta - m_\delta)/s_\delta$, where δ = the weighted mean within-group distance, m_δ = mean of δ under the null hypothesis, and s_δ = standard deviation of δ under the null hypothesis. The more negative the value of T , the larger the difference between groups (McCune and Grace 2002).

^b Chance-corrected within-group agreement, describing within-group similarity. The highest possible value for A is 1 (McCune and Grace 2002).

Ordination of the untransformed data yielded a 2-dimensional solution (final stress = 3.52, instability < 0.0001) and total $R^2 = 0.98$ (axis 1: $R^2 = 0.89$, axis 2: $R^2 = 0.09$). The R^2 value represents the variance in the original distance matrix represented in ordination space. Cover of shrubs and native grasses and cover of non-native grass are at opposite ends of axis 1, suggesting that axis 1 represents a gradient of plant species composition where higher shrub and native grass cover is correlated with less cover of non-native grass (Figure 2, Table 8). Axis 2 separates cover of non-native grass and litter depth from extent of bare ground and represents a gradient of vegetation structure where higher values of non-native grass cover are positively correlated with litter depth and negatively correlated with extent of bare ground. Sage

Thrasher, Green-tailed Towhee, and Brewer's Sparrow had strong, positive associations with higher cover of shrubs and native bunchgrasses (Table 8, Figure 2). Savannah Sparrow, Western Meadowlark, and Vesper Sparrow had positive associations with a deeper litter layer and higher cover of non-native grass, and negative associations with higher cover of bare ground (Table 8, Figure 2).

Table 8. Correlations of each variable with axes obtained from a non-metric multidimensional scaling ordination of breeding songbird abundance in native sagebrush steppe ($n = 3$), restored ($n = 4$), and unrestored ($n = 9$) plots at the Kelly Hayfield area of Grand Teton National Park, Wyoming, USA.

Variable	Correlation coefficient	
	Axis 1	Axis 2
<i>Species</i>		
Sage Thrasher	0.77	0.31
Green-tailed Towhee	0.68	-0.24
Brewer's Sparrow	0.97	0.23
Vesper Sparrow	0.22	-0.16
Savannah Sparrow	-0.64	0.70
Western Meadowlark	0.03	0.32
<i>Habitat</i>		
% shrub cover	0.94	0.10
% native grass	0.51	-0.19
% non-native grass	-0.67	0.52
% bare ground	-0.20	-0.51
litter depth	0.27	0.63
understory height	0.24	0.33

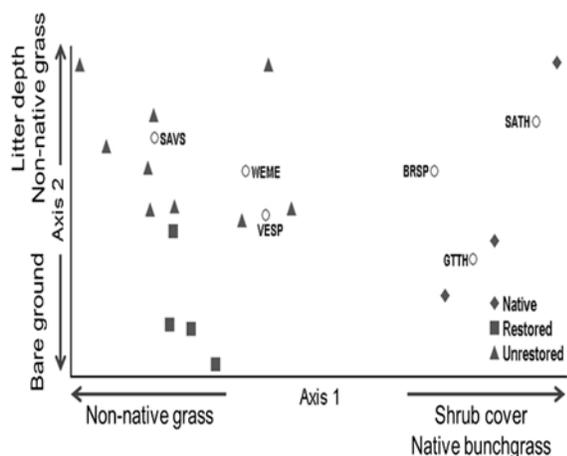


Figure 2. Ordination of native sagebrush steppe, restored, and unrestored plots (2013) in species space using non-metric multidimensional scaling. Arrows beside axes represent relationships of habitat variables with each axis. Cover of shrubs, native and non-native grasses, and bare ground are presented as percentages, litter depth in mm, and understory height in cm. Species codes: SATH = Sage Thrasher; GTTH = Green-tailed Towhee; BRSP = Brewer's Sparrow; VESP = Vesper Sparrow; SAVS = Savannah Sparrow; WEME = Western Meadowlark.

◆ DISCUSSION AND MANAGEMENT IMPLICATIONS

This study evaluated the short-term response of songbirds to sagebrush restoration treatments, and our results will contribute to a better understanding of the effects of restoration treatments on sagebrush steppe birds and their habitats. Currently, there is little information available in the primary literature on bird responses to restoration in sagebrush steppe ecosystems. In fact, a recent review of published articles by Ortega-Alvarez and Lindig-Cisneros (2012) of the effects of ecological restoration on birds yielded no studies focused on sagebrush steppe habitats. Although there are studies reporting restoration treatments of sagebrush steppe with the aim of creating or improving Greater Sage-grouse (*Centrocercus urophasianus*) habitat, the actual effects of restoration of sagebrush habitat on sage grouse populations seemingly have also not been evaluated (e.g., Wisdom et al. 2002, Baker et al. 2009). We found songbird communities of distinct composition among native sagebrush steppe, restored, and unrestored plots. Unsurprisingly, native sagebrush plots with high shrub cover were occupied by sagebrush-associated species including Sage Thrasher, Green-tailed Towhee, and Brewer's

Sparrow (Figure 2). Recently- and actively-restored plots were characterized by a large forb component, sparse shrubs or grasses, and low numbers of bird detections. Thus, restored plots were not associated with the abundance of any bird species (Figure 2). Unrestored plots were dominated by non-native grasses and primarily occupied by grassland-associated species like Vesper Sparrow, Savannah Sparrow, and Western Meadowlark.

Sparse detections of birds during and shortly after restoration treatments (≤ 5 yrs) suggest that restored plots provide little breeding habitat for birds of any species. Restored plots in this study no longer provided breeding habitat for many grassland birds, as grass cover was low and bare ground too extensive (Table 5). Moreover, restored plots also still had very little shrub cover ($< 0.1\%$), thereby precluding shrub-nesting birds. To provide adequate breeding habitat for sagebrush-associated birds (including Greater Sage-grouse), shrub canopy should be approximately 15-30%, or higher (Connelly et al. 2000, Chalfoun and Martin 2007, Holmes and Altman 2012). The shrub species included in restoration treatments in this study (e.g., *Artemisia tridentata vaseyana*, *Chrysothamnus* spp.) may immediately begin to establish following seeding, but it may take *A. tridentata* as many as 10 years to dominate a site (Tirmenstein 1999). Grass cover will likely increase before shrub cover, and in the near-term, restored plots may again provide habitat for grassland birds once the extent of bare ground is reduced and an acceptable grass canopy and litter layer develops (Fisher and Davis 2010). However, consideration of our reported patterns of breeding bird abundance and community composition is important for managers when considering schedules for restoration treatments, as many hectares of potential breeding habitat may be removed from the local landscape for ≤ 10 yrs or more following initial sagebrush restoration treatments.

Although unrestored plots were occupied by grassland birds, we did not evaluate whether they provided high-quality breeding habitat. Unrestored plots were dominated by non-native grasses, which may differ from native habitat in phenology, cover, and invertebrate abundance or species composition (Lloyd and Martin 2005, Kennedy et al. 2009, Johnson and Sandercock 2010, Litt and Steidl 2010), all of which may influence the reproductive success of breeding birds. Thus, without habitat-specific demographic rates, we cannot conclude that removal of breeding habitat via restoration of plots dominated by non-native grasses is detrimental to breeding birds.

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PRELIMINARY STUDY OF THE INFLUENCE OF CONDUCTIVITY AND CALCIUM CONCENTRATIONS ON THE DENSITY AND SPECIES RICHNESS OF NATIVE AND INVASIVE GASTROPODS IN GRAND TETON NATIONAL PARK, WYOMING

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◆ INTRODUCTION

Freshwater gastropods are a diverse taxa that inhabit a wide variety of freshwater habitats (Lydeard et al. 2004, Strong et al. 2008). Freshwater gastropods often form narrow endemic ranges (Strong et al. 2008) with many species restricted to a single drainage or an isolated spring (Brown et al. 2008). In North America, over 60% of freshwater snails are listed as imperiled or presumed extinct (Lysne et al. 2008). The main factors for the reduction in snail biodiversity are habitat loss, water pollution, and the introduction of invasive species (Strong et al. 2008).

Invasive species can dramatically alter the native community by reducing biodiversity and changing ecological processes (Alonso and Castro-Diez 2008). The effects of invasive species on aquatic ecosystems are often permanent and lead to reductions in biodiversity due to predation and competition with native species (Alonso and Castro-Diez 2008, Lysne et al. 2008, Strayer 1999). Invasive gastropods impact native ecosystems by altering carbon and nitrogen levels (Hall et al. 2003, Arango et al. 2009), consuming large amounts of primary producer biomass (Hall et al. 2003, Riley et al. 2008, Strayer 2010), and changing native macroinvertebrate community composition (Kerans et al. 2005, Riley et al. 2008, Cross et al. 2010, Brenneis et al. 2011).

Some invasive gastropods tolerate a wide range of abiotic environmental conditions including temperature and salinity (Alonso and Castro-Diez

2008). However, other environmental factors have received less attention, but may be important in determining the range of invasive snails and their impact on native gastropod populations. Conductivity and environmental calcium levels are important for growth and reproduction in gastropods (Kefford and Nugegoda 2005, Zaluzniak et al. 2009) because decreased levels of calcium and other ions results in decreased shell strength, reduced locomotion, and increased metabolic demands (Hunter et al. 1967, Dalesman and Lukowiak 2010). A few studies have shown a direct relationship between conductivity and growth and reproduction in invasive snails. Herbst and colleagues (2008) reported that the invasive New Zealand mud snail, *Potamopyrgus antipodarum*, is tolerant of medium and high levels of specific conductivity and only showed decreased survival when conductivity was below 100 $\mu\text{S}/\text{cm}$. In Australia, the invasive snail *Physa acuta* had lower growth and egg production in water with conductivity below 100 $\mu\text{S}/\text{cm}$ (Kefford and Nugegoda 2005). However, few studies have examined the impact of conductivity on the distributions of native and invasive snail populations or the possible interactions between native and invasive snails for limited calcium ions.

Conductivity can also affect the species richness of gastropods. High conductivity is positively correlated with species richness of mollusks worldwide (Dillon 2000). In a study of 31 lakes in Northern Wisconsin, conductivity below 36 $\mu\text{S}/\text{cm}$ resulted in lower snail species richness while lakes with higher than 50 $\mu\text{S}/\text{cm}$ exhibited higher snail

diversity (Hrabik et al. 2005). Yet, little research into the relationship between conductivity and gastropod species richness has been conducted in stream ecosystems.

Due to the impacts that invasive gastropods may have on native gastropod populations, it is important to identify the environmental factors that affect invasive gastropod populations. We conducted a preliminary field survey to test the hypothesis that conductivity is directly correlated with gastropod density and species richness.

◆ METHODS

We conducted a preliminary field survey along Polecat Creek in the John D. Rockefeller, Jr. Memorial Parkway. Sampling locations occurred above, at, and below the geothermal hot spring which corresponds to three conductivity levels (low, intermediate and high, respectively) in the stream. Geothermal springs increase the minerals available and conductivity of waters at and below their inputs (Herbst et al. 2008). To assess snail richness and abundance, we collected gastropods using a stovepipe sampler (20.4 cm diameter) from a single channel transect at each location. Gastropod samples were collected at five locations along each channel transect. We preserved samples in 70% ethanol immediately after collection and later counted and identified all snails to the lowest taxonomic level. We also counted the abundance of bivalves in each sample as bivalves may compete for calcium ions in areas where this mineral is limited. We also measured temperature, conductivity, total hardness, and salinity using a YSI probe and water quality test kits.

For our preliminary field study, we used a one-way ANOVA tests to determine whether abiotic factors (temperature, conductivity, etc.) and gastropod density (total snail density, the density of individual families, and snail richness) differed significantly among the three locations along Polecat Creek (Quinn and Keough 2002).

◆ PRELIMINARY RESULTS

Of the abiotic factors measured between the three locations in Polecat Creek, temperature differed significantly among locations ($df = 2$, $F = 35.014$, $p < 0.001$) while conductivity was nearly significant ($df = 2$, $Kruskal-Wallis = 5.132$, $p = 0.077$; Table 1). The highest temperatures occurred at the site below the hot

spring which was significantly different from the temperatures at the hot spring and above the hot spring. Conductivity was higher at the hot spring and below the hot spring than at the location above the hot spring (Table 1). Although water hardness did not differ significantly among locations ($df = 2$, $F = 1.465$, $p = 0.303$), the overall trend was a reduction in total water hardness as locations moved downstream. Salinity was constant at all locations and therefore we did not assess statistically.

Table 1. Average abiotic factors for Polecat Creek, Wyoming at three sampling location. Standard deviation is shown in the parentheses.

Location	Temperature (°C)	Salinity (ppt)	Conductivity (µS)	Total Hardness (mg/L)
Above Spring	22.567 (0.321)	0.10 (0.00)	172.767 (0.666)	2.566 (0.192)
At Hot Spring	23.233 (0.153)	0.10 (0.00)	192.167 (30.277)	2.334 (0.667)
Below Spring	24.433 (0.321)	0.10 (0.00)	195.267 (6.503)	2.000 (0.000)

Table 2. Analysis of Variance results for snail abundance for Polecat Creek, Wyoming. The degrees of freedom (df), sum of squares (SS), mean squares (MS), f-ratio (F) and p-value (P) are given for each statistical test. Bold numbers indicate significant p-values.

Abiotic Factor	df	SS	MS	F	P
<i>P. antipodarum</i>	2	14,418.53	7,209.26	1.351	0.296
Native Snails	2	115.73	57.87	2.52	0.122
Clams	2	136.13	68.07	4.932	0.027
Snail Family Richness	2	1.73	0.87	1.3	0.308

Table 3. Mean abundance of mollusks as well as mean snail family richness for each location on Polecat Creek, Wyoming. Standard deviation is shown in the parentheses.

Location	Mean Mollusk Abundance			Mean Snail
	<i>P. antipodarum</i>	Native snails	Clams	Family Richness
Above Spring	36.2 (29.2)	0.8 (0.4)	0.4 (0.5)	2.0 (0.7)
At Hot Spring	19.2 (17.7)	7.2 (8.1)	7.6 (5.8)	1.8 (0.4)
Below Spring	91.8 (121.9)	2.0 (1.9)	2.6 (2.7)	2.6 (1.1)

There were no significant results among locations for snail abundance and family richness (Table 2). Although the abundance of *P. antipodarum* was not significantly different among locations ($p = 0.296$) the overall trend was for higher abundance of this invasive snail below the hot springs (Table 3). Alternatively, the native snails showed a slight, but non-significant ($p = 0.122$) increase in abundance at the hot spring location. Family richness ranged from one to four families of snails with the highest richness at the below hot spring location (Table 2), however these results were not statistically significant ($p = 0.308$). Additionally, we collected data on native clam abundance at each location as bivalves may compete with snails for calcium resources. We found that clam abundance were significantly higher at the hot spring location than above the hot spring ($p < 0.03$).

◆ DISCUSSION

Because we only sampled one stream on one occasion and found high variance in conductivity and *P. antipodarum* density within locations, interpretation of our data is difficult. However, based on these preliminary data, we found that temperature and to a lesser extent conductivity follow the expected pattern of increased levels at and below the hot spring. The presence of a gradient in both temperature and conductivity is consistent with other research (Herbst et al. 2008) and validates the use of these locations (above, at, and below the hydrothermal spring) for our different conductivity levels in future studies. We will use more detailed water testing procedures in future studies to have more definitive results for different ions (Ca, Mg, Cl, etc.).

Both native snail abundance and *P. antipodarum* abundance were not significantly different among locations, however, we found higher abundance of the invasive snail below the hydrothermal spring which is consistent with prior research (Herbst et al. 2008). Mean snail family richness was also found to be higher at the below hot springs location, however, these results were not significant, but may indicate that higher conductivity, temperature, or other factors may increase the richness of snails below hot springs. In our preliminary study, we found that both native snails and clams had higher abundances at the hot spring location while *P. antipodarum* abundance was lowest at this location (Table 3). These results may indicate that the hot spring provides a refuge for native mollusks by excluding *P. antipodarum* from the area. The underlying mechanism(s) for the low abundance of *P. antipodarum* cannot be determined based on our

preliminary study; however, a wider range of water quality testing in future studies may provide insights into the underlying cause for the low abundance of *P. antipodarum* at hot spring locations.

◆ ACKNOWLEDGEMENTS

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THE ROLE OF DENDROCHRONOLOGY IN UNDERSTANDING THE MODERN DECLINE OF WHITEBARK PINE IN GRAND TETON NATIONAL PARK, WYOMING

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✦ ABSTRACT

Whitebark pine (*Pinus albicaulis*) is the only pine keystone species found in North America. Although it is considered a keystone species in high elevation ecosystems in the northern Rockies, it occupies a relatively restricted range and its future is uncertain. In modern times, it has experienced a significant decline in population due to pine beetle infestations, blister rust infections, fire suppression, and climate change. Despite the knowledge that the species is severely threatened, little is known about its paleoecology. More specifically, much remains unknown about how the distribution and stability of whitebark pine were affected by past climate change.

The purpose of this study is to determine in great temporal and spatial detail the demographics of the current stand of whitebark pine trees in the watershed surrounding an unnamed, high-altitude pond (known informally as Whitebark Pine Moraine Pond) located approximately 3.06 miles NW of Jenny Lake in Grand Teton National Park (GTNP). The main objectives of this study are:

- 1.) To obtain the precise GPS locations of the current stand of whitebark pine trees in the watershed to generate a GIS map detailing their locations.
- 2.) To obtain increment cores of a subset of the trees in the watershed to estimate age and date of establishment for the current stand of whitebark pines, with particular attention to fire history.

- 3.) To analyze ring widths from core samples to identify climatic indicators that may influence the regeneration and survival of whitebark pine.

✦ INTRODUCTION

Whitebark pine is a long-lived, moderately shade tolerant species found only at high elevation sites occurring in subalpine ecosystems of the Northern Rocky and Cascade Mountains in the United States (Keane and Parsons 2010). In modern times, the most pressing mortality event in subalpine forests of western North America is occurring in whitebark pine (Millar et al. 2012). In addition to biotic factors such as blister rust and pine beetles, there is some preliminary data indicating increased mortality in whitebark pine due to a warming climate (Bower and Aitken 2008). Historical climate data, based on records from NOAA dating from 1949-2012, indicates that the average yearly temperature in the Greater Yellowstone Ecosystem is increasing, while the yearly amounts of both overall precipitation and snowfall are decreasing. A significant portion (10-15%) of these rapidly vanishing trees are found in the Greater Yellowstone Area (GYA) and GTNP (Figure 1). Of these 10-15% of whitebark pine trees, it has been suggested that only a slight increase in global atmospheric temperature (4.5° C) would completely remove whitebark pine from the GYA and GTNP ecosystems (Schrag et al. 2008).

Whitebark pine is considered to be a keystone species of the particular ecological niche it occupies in the United States for three reasons. First, more than one hundred animal species, including the endangered

grizzly bear (*Ursus arctos horribilis*), depend on its high-energy seeds for survival (Felicetti et al. 2003). If whitebark pine should vanish from its niche, endangered species would be forced to lower elevations in search of food, thus increasing the potential for contact with humans and human-caused casualties. Second, the presence of whitebark pine in subalpine ecosystems helps to slow the melting of accumulated snow, resulting in reduced flooding occurrences. And third, by slowing the melt of snow, whitebark pine provides a high quality source of water to plants and animals during the summer melting season (Keane and Parsons, 2010).

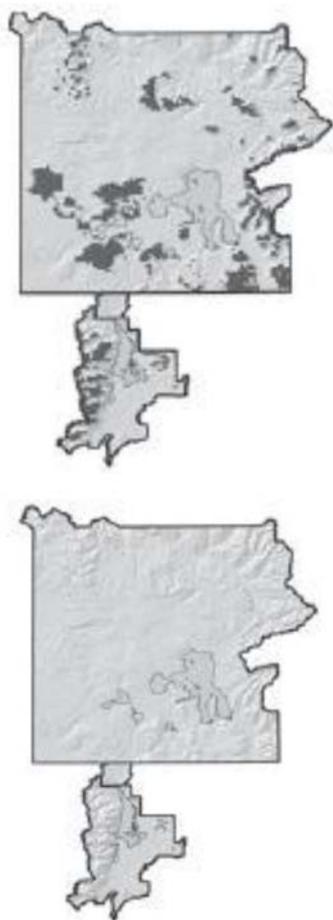


Figure 1. The current range and distribution of whitebark pine in GTNP and GYA (top), and the predicted range and distribution of whitebark pine in GTNP and GYA given a projected 4.5C temperature increase (bottom). From Schrag et al. 2008.

In addition to its importance as a keystone species, whitebark pine also has value as a recreational resource. Whitebark pine has many aesthetic qualities that make it a potential attraction to park visitors. Tree

species that thrive at high altitudes generally have unusual morphological characteristics resulting from the harsh conditions provided by high altitude conditions. One of the most striking characteristics of high altitude species, including whitebark pine, is the twisted formations of trunks and branches. Additionally, whitebark pine has value as a recreational resource because communities tend to form very open, park-like forests ideal for adventurous hikers (Keane and Parsons 2010). Lastly, whitebark pine forests offer value as a recreational resource for avid birdwatchers. Whitebark pine is the only species of pine in North America that does not disperse its seeds utilizing wind. Rather, whitebark pine relies on a mutualistic relationship with a bird—the Clark’s Nutcracker—to disperse its seeds. In the late summer and fall, Clark’s Nutcrackers harvest seeds from the whitebark pinecones and carry them up to ten kilometers away and bury them (Tomback 1982). The nutcrackers will eventually return for the seed stocks, but those seeds left unclaimed will eventually begin to germinate (Tomback et al. 2001). This mutualistic relationship with the Clark’s Nutcracker would provide avid birders the opportunity to see this high-altitude bird in action during the summer and fall months, that, without the presence of whitebark pine, they would likely never see.

Demographics about the current stand gained from this study will provide two key pieces of evidence. First, results from the proposed study will provide an indication of how the current stand of whitebark pine trees came to exist in the watershed by providing both estimated ages and dates of establishment. Should the results indicate that all whitebark pine trees in the watershed are roughly the same age, it can be inferred that they grew as the result of a stand-replacing fire, thus indicating the importance of fires to the survival of the species. There is some preliminary data indicating that stand-replacing wildfires are important for establishing whitebark pines (Peterson 1999). If trees are vastly different in age, this would indicate that fire plays a less significant role in survival than past research suggests.

Second, results from analyzing tree ring widths would provide information as to how whitebark pine responded to past climate change. It is known that during times of climate change, zones of vegetation tend to respond by shifting their ranges (Whitlock 1993). Upper treeline in mixed spruce-fir communities in the Rocky Mountains has been shown to be especially dynamic to climate change (Elliott 2011). However, nothing is known specifically about how these past changes in climate altered the range or

stability of whitebark pine in the United States. Given the narrow elevational zone occupied by whitebark pine, this proposed research would be valuable in forming conservation plans because one of the main concerns associated with the disappearance of whitebark pine is range shift due to climate. The most effective way to establish a solution for the current crisis is to understand how the species, and ecosystem as a whole, responded to climate change in the past.

Much of the high-elevation wildlife and scenery in Grand Teton National Park exist only because of whitebark pine's role as a keystone species. Understanding how climate change has affected, and continues to affect, this threatened and disappearing species will help park conservationists develop new strategies for maintaining and restoring the current stands of whitebark pine trees.

◆ STUDY AREA

Fire, vegetation, and dendrochronological histories were examined at a small, un-named subalpine lake (known informally as Whitebark Moraine Pond; 43.79° N, 110.110.79° W; elevation 2800 m; Figure 2) and the surrounding watershed in Grand Teton National Park, WY, USA (Jones 2013). The lake and surrounding watershed are located at treeline in the uppermost reaches of Paintbrush Canyon, approximately 5 km NW of Jenny Lake. The lake has a maximum depth of 4 m and a watershed of 0.76 ha. The watershed contains no inlet or outlet systems, and the majority of hydrologic input is provided by summer snowmelt.

Whitebark Moraine Pond, a moraine-dammed lake, was produced by late Pinedale glacial activity (Jones 2013, Pierce 2003). Moraine-dammed lakes generally form when glacial meltwater collects behind terminal moraine debris as a glacier retreats (Richardson and Reynolds 2000). Whitebark Moraine Pond resulted from the retreat of a Pinedale glacier which reached its maximum extent in Grand Teton National Park approximately 9000 yr BP (Marston et al. 2005). As the Pinedale glacier retreated, resulting meltwater became trapped by terminal moraine debris and was prevented from flowing downslope, resulting in the formation of a dammed lake. The terminal moraine and rocky debris are still present in the south-east section of the study site.

The modern vegetational ecosystem of the study area can be characterized as a subalpine conifer forest. Canopy species dominate the watershed and consist primarily of whitebark pine (*Pinus albicaulis*),

subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*). Shade produced by the dense canopy results in a sparse understory including a small number of grasses and forbs. However, likely due to environmental constraints, vegetation approaching watershed boundaries (i.e. higher in elevation) is almost exclusively composed of whitebark pine.



Figure 2. Photo of the study site location showing vegetation of the watershed. Photo courtesy of Dr. Sarah Spaulding.

Typical of most high-elevation ecosystems, soils in the watershed generally lack well-developed horizons (Tomback et al. 2001). The lack of soil profile development is primarily caused by a combination of steep slopes and high rates of eolian erosion (Weaver 2001). As a result of poor development, soils in the watershed have a relatively low water-holding capacity; it has been estimated that approximately 35-60% of all annual precipitation becomes surface runoff in high elevation watersheds, though soil drought is uncommon (Tomback et al. 2001). Soils in the watershed contain a large portion of organic matter (>20%; Jones 2013) due to the high annual production of conifers and slow decomposition characteristic of cold climates.

Annual growing season (May-July) precipitation at the site from 1895-2012 averaged 310 mm, and showed no significant trends during the time period. Annual growing season maximum temperature averaged 14.68 °C for the same time period, and annual growing season minimum temperature averaged -1.94 °C. The average annual range in temperature for the time period was 12.74 °C and has been steadily decreasing since the mid 1980's. This decrease in annual temperature range is attributed to an increase in average growing season minimum temperatures. Average growing season minimum

temperature has increased rather significantly since the mid 1980's, increasing a total of 6.12 °C. More specifically, annual July minimum temperatures have increased 8.89 °C since the 1980's.

◆ METHODS

Where necessary, project methods have been approved by the respective permitting authority or oversight committee.

GPS locations to determine demography

The location of each whitebark pine in the watershed was recorded using a high-quality GPS unit. The latitude and longitude coordinates of each tree location were recorded and stored in the unit. All recorded coordinates were ultimately used to create a map depicting the exact location of each whitebark pine in the watershed as it relates to other features such as the pond. This map was generated using the latest available version of ArcGIS software. A map of whitebark pine locations would be valuable from a conservation standpoint because such maps seldom exist because whitebark pine has never been used as a timber resource.

Increment cores

From the total number of whitebark pines in the watershed, twenty were selected to core to establish ages and dates of establishment. Cores from the selected subset of trees were taken using standard dendro-chronological techniques with a 5.15 mm diameter increment bore 30 cm above the soil surface (Elliott 2011). Diameter at breast height (dbh) was also recorded. Once the cores were in a laboratory setting, they were sanded and scanned, and rings on each individual core were counted to establish chronologies, using crossdating protocols and software. Pith estimators and age-to-coring-height equations were applied as in Elliott (2011). The dates and spatial patterns of establishment were then used to determine if the current stand grew in response to a stand-replacing fire or if each tree grew independently.

Response to modern climate

Tree ring widths of each core were measured and recorded. An analysis of tree ring widths provided important information about the magnitude of climate change events experienced by each tree, as well as how climate change events impacted the growth and stability of each tree on a local scale. Methods generally followed those of a larger study of climate

and local scale factors on upper treeline in the Rocky Mountains (Elliott 2012). Because climate stations are rare at higher elevations in the Rocky Mountains, Precipitation-elevation Regressions on Independent Slopes Model (PRISM) data were used for the study site (Daly et al. 2008). This climate analysis allows for the comparison between climate conditions in the past and the current climates in order to predict the response of the current stand of whitebark pine.

◆ PRELIMINARY RESULTS

Demography of current stand

The average date of establishment for the current stand of whitebark pine is 1751 C.E., however, individual dates of establishment range from 1324 C.E. to 1919 C.E. Of the 16 trees that were cored to the center, 75% were established between 1600 C.E. and 1800 C.E. (Figure 3A). With the exclusion of the oldest individual, dbh is inversely related to date of establishment ($R^2 = 0.62$); that is, older individuals are typically larger than younger individuals (Figure 3B). Transect data indicate that only 14% of the current stand is composed of whitebark pine, with subalpine fir and Engelmann spruce occupying 81% and 5%, respectively. All new growth within the survey area consisted of subalpine fir.

Ring widths and modern climate

Average yearly ring widths ranged from 1.23 mm in 1950 to 0.60 mm in 2011 for the period of available climate data (1895-2012) (Figure 4A). A breakpoint analysis confirmed the presence of change point at 1949 (± 4.5 years) and further indicated that average ring widths increased until 1949, and then began to decline to their current widths.

Average July minimum temperature (T_{min}) was identified as the most statistically significant variable affecting annual ring widths ($p < 0.001$) (Figure 4B). Other temperature and precipitation variables had no significant effect on the growth of whitebark pine at this site. Until 1991 (± 2 years), average July T_{min} values experienced no significant variation and remained relatively constant through time. A maximum value of 37.38 F was reached in 1945, with a spread in data of 8.07 F. After 1991, however, average July T_{min} values exhibited more variability and increased to temperatures higher than any other time during the record. Values reached a maximum in 2011 with an average July T_{min} of 45.7 F with a spread of 13.34 F from 1991-2011.

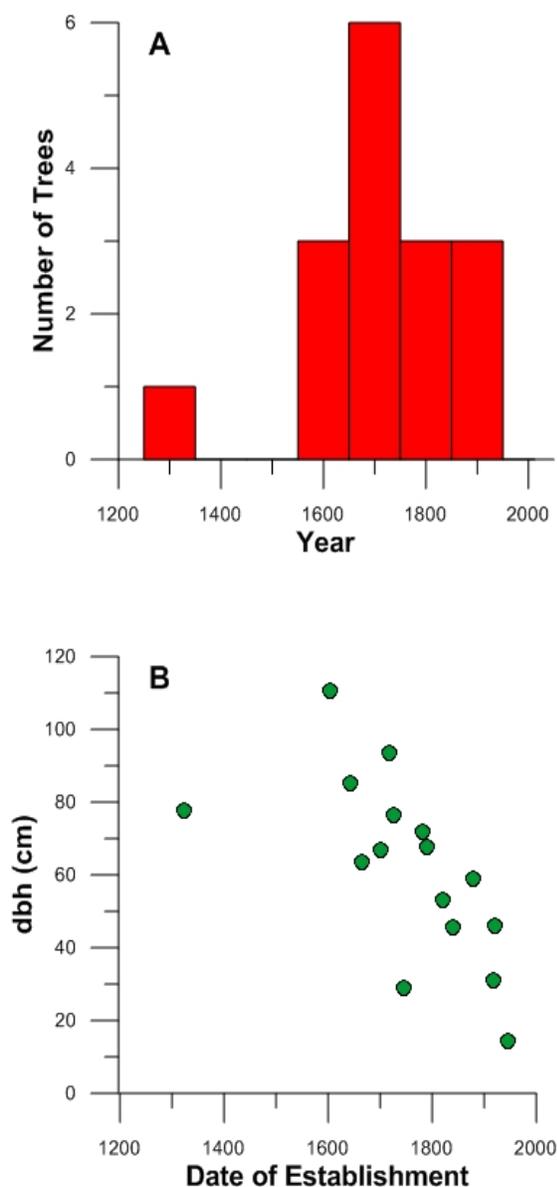


Figure 3. (A) Trends in estimated dates of establishment for all cored trees. (B) Relationship between dates of establishment and measured dbh values.

Average July T_{min} values were plotted against average annual ring widths to determine the effect of climate on tree growth (Figure 4C). Analyses indicated that average July T_{min} values were a significant ($p < 0.001$) predictor of whitebark pine growth. The resulting relationship between the two variables reveals that the modern decline in whitebark pine growth at the study site can be attributed to increasing July minimum temperatures.

Increasing July minimum temperatures have aided in the displacement of whitebark pine by subalpine fir. The initial onset of declining ring widths around 1949 may have been triggered by an unknown ecological event which subsequently increased the stand's sensitivity to later temperature changes beginning in 1991, thereby amplifying its effect on the population. *Abies* and *Picea*, competitors of whitebark pine, are better adapted to survive in warmer climates than whitebark pine. While July minimum temperatures were discovered as the most significant variable at this site, Perkins and Swetnam (1996) observed a significant inverse relationship between ring widths and May temperatures in the Sawtooth-Salmon River region of Idaho. This discrepancy in climate variables may be caused by the geographic difference in site locations. In both cases, increased growing season temperatures have resulted in altered subalpine conifer communities by allowing warm temperature-adapted species to invade the niche normally occupied by whitebark pine. Because subalpine fir tends to grow much faster than whitebark pine, it acts as a competitor for resources and ultimately restricts the growth of whitebark pine through out-shading.

◆ MANAGEMENT IMPLICATIONS

Our results indicate that whitebark pine populations are decreasing in GTNP as a direct result of warming July temperatures. This modern decline of whitebark pine poses several management and conservation challenges. The fundamental risk associated with the loss of this species centers around whitebark pine's role as a keystone species. Because the endangered grizzly bear depends so heavily on whitebark pine seeds for survival, the disappearance of whitebark pine has the potential to increase human-bear mortality events as bears are forced to lower elevations in search of alternative food sources.

The central challenge associated with mitigating this modern decline of whitebark pine is that climate change (the main driver of this decline) is not an environmental problem with a simple solution. Climate change is a global phenomenon acting on a long timescale. Because this driver of whitebark pine decline is not easily managed, the best management option will be to focus on more locally-driven processes contributing to the decline, such as fire suppression.

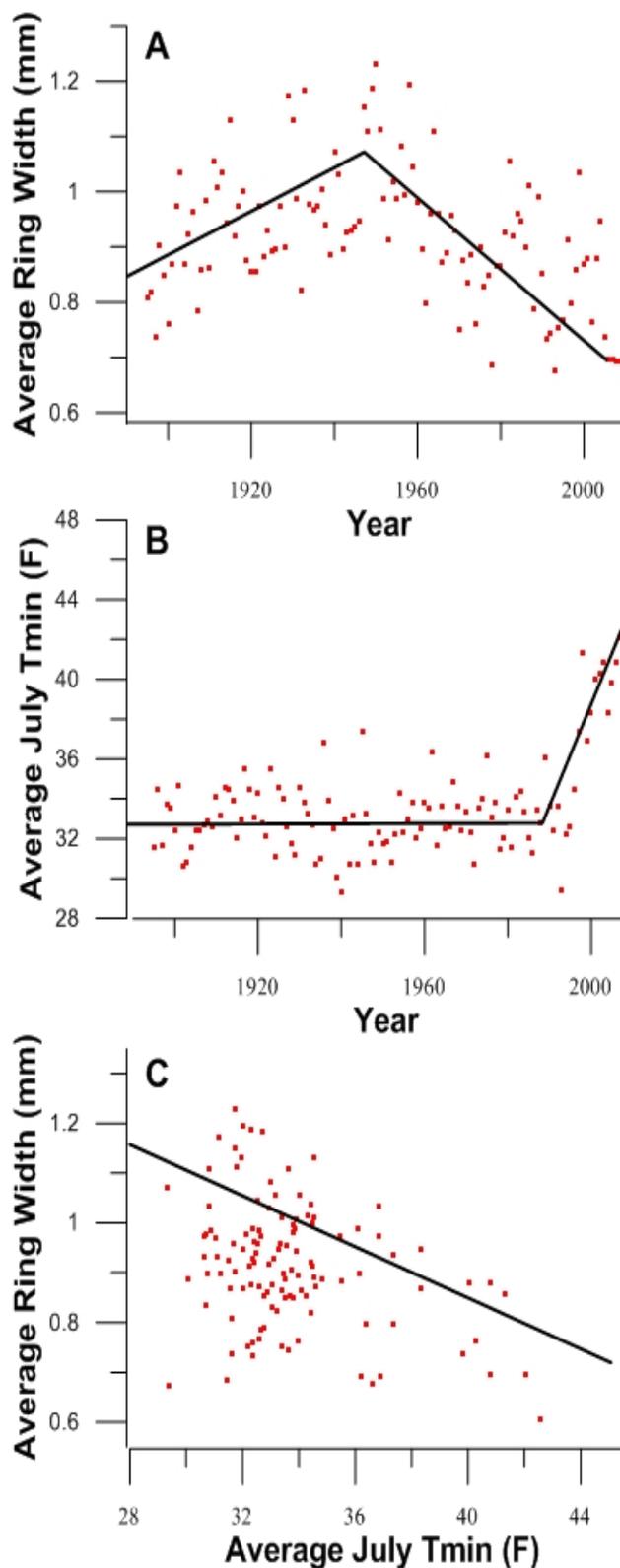


Figure 4. (A) Average ring widths by year. (B) Average July minimum temperatures by year. (C) Relationship between ring widths and July minimum temperatures ($p < 0.001$).

◆ ACKNOWLEDGEMENTS

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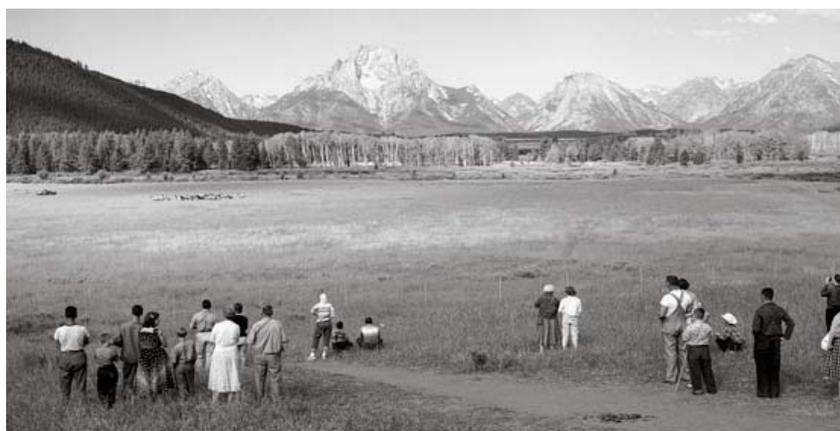
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JACKSON HOLE WILDLIFE PARK: AN EXPERIMENT TO BRIDGE TOURISM AND CONSERVATION

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Observing elk in Buffalo Meadow, 1950. Photo courtesy of the National Park Service.

✦ INTRODUCTION

From a vantage point on a rise above the Snake River, the valley below is shrouded in darkness. A faint glow on the eastern horizon heralds the dawn. The only sound comes from the river as water gurgles over rocks and other impediments. As the sky grows brighter, the shadows in the valley begin to take form, revealing numerous small streams that braid through dense thickets of willows and other shrubbery before returning to the main river channel. Small dark shapes dart among the trees and shrubs, filling the air with a variety of birdsongs. As the rising sun gradually illuminates the valley a herd of elk rise, one-by-one, in a distant meadow and begin grazing on the spring grasses. Moments later a cow moose and her calf emerge from behind the willows at the water's edge, scattering the birds. This area, with its mosaic of

habitats, teems with wildlife. It is not surprising, then, that this upper part of Jackson Hole became the chosen site for the Jackson Hole Wildlife Park (JHWP) and became the Park's main animal viewing area for tourists and scientists alike.

Anticipating a changing economy at the close of World War II, Wyoming Governor Lester C. Hunt initially conceived the idea of a wildlife museum in Jackson Hole to draw more tourists to the state. That idea quickly morphed into the concept of the JHWP, a facility for the exhibition of the predominant game animals of the West. Without an appropriate tract of land under state control Governor Hunt turned to Laurance S. Rockefeller (Rockefeller), president of Jackson Hole Preserve, Inc. (JHP), which held title to over 33,000 acres of land outside the boundaries of Grand Teton National Park (GTNP) in the upper Snake River Valley of Jackson Hole. The two men

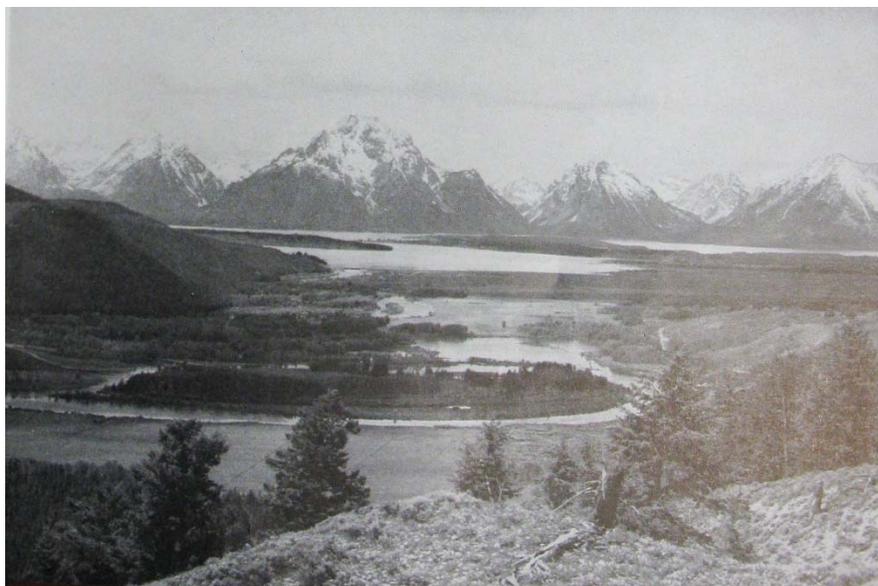


Figure 1. This view, looking west toward Jackson Lake and the Teton Mountains, shows the majority of the JHWP. Buffalo Meadow, the large open area below the rise from where the photograph was taken, was the primary animal viewing area. The original Park headquarters was located in front of the line of trees at the far end of the smaller meadow to the west. Photo acquired from an article published in *Animal Kingdom* magazine.¹

shared the belief that commercial development and conservation were not mutually exclusive. They envisioned a wildlife park with an animal viewing area convenient for tourists. As the concept of the park developed they discussed having on-site interpretive guides and printed materials to educate visitors about the animals and the importance of maintaining their habitats to ensure the animals' survival. Early in the process planners also advanced the idea of the wildlife park having the capacity to host a variety of scientists to conduct studies in wildlife life cycles and behavior, and other ecological studies. For support and guidance they enlisted the New York Zoological Society (NYZS), perhaps the world's foremost authority on wildlife conservation at the time.²

Many people within the conservation community vehemently opposed the proposed wildlife park. Most conservationists supported tourism development when it did not interfere with the natural activities and movements of the area's animals. Therefore they argued against the unnatural conditions of confining migratory animals such as elk, deer,

antelope, and other ungulates within fenced areas. Many spoke passionately about the artificiality of viewing animals in strategically placed pens, regardless of the pen's size, simply for the convenience of tourists. Even the National Park Service (NPS), which remained mute on the project so as not to offend the Rockefellers, had eliminated almost all artificial wildlife viewing areas from the national parks before Hunt proposed the JHWP. Just a year before NPS Director Newton Drury directed Yellowstone to remove the fencing around its bison pastures. Applying the findings of wildlife ecologists and other scientists Drury worked to end the practice of managing national parks as "zoological park[s] or game farm[s]."³

However, many of these same people supported the idea of an area for scientific study. Conservationists, especially wildlife biologists and ecologists, strongly advocated a renewed emphasis on the scientific study of wildlife, something that had diminished during the war years. Conservation could only move forward as the breadth of information about wildlife and their habitats expanded. Yet they also

¹ "The Inauguration of the Jackson Hole Wildlife Park," *Animal Kingdom: The Magazine of the NYZS*, Vol. LI, No. 5, October 1, 1948, Box 5, Series 13, Folder 1, RG5: Jackson Hole Wildlife Park, Grand Teton National Park, Moose, Wyoming (hereafter referred to as RG5 GTNP).

² Fabian to Laurance S. Rockefeller (LSR), August 6, 1945, Box 2, Folder 1945, Richard Winger Papers, American Heritage Center (AHC), Laramie, WY (hereafter referred to as Winger Papers); "Big Wildlife Exhibit to Be Set Up," *Wyoming Tribune*, October 2, 1945, Box 2, Folder 1945, Winger Papers.

³ Richard West Sellars, *Preserving Nature in the National Parks: A History* (New Haven: Yale University Press, 1997), 156-158.

understood the necessity of conducting such research only under natural, unconstrained conditions. They believed that any scientific studies conducted under artificial confinement would produce unusable, false data.

Despite the opposition, the JHWP opened in 1948. Within two years the importance of wildlife and habitat research resulted in the formal establishment of a biological research station within the Park. Very quickly the research station gained priority over the tourist facilities. Early studies contributed greatly to the management of the Jackson Hole elk herd and increased understanding of vegetation degradation and regrowth. Yet visitors to the JHWP did gain an appreciation for animals they otherwise might never have seen except in a traditional zoo enclosure. In that mission, Rockefeller and others viewed the park as a success. Governor Hunt and Rockefeller had correctly foreseen the compatibility of tourism and conservation.

What eluded the men behind the wildlife park was the growing impact of the science of ecology on evolving wildlife management practices. Following the expansion of GTNP, the NPS took over the operation of the JHWP. NPS management policies gradually fell in line with those advocated by Olaus Murie and the other conservationists who had objected to the artificial containment of wild game animals. Funding for the JHWP gradually dwindled, its miles of fencing were allowed to deteriorate. It slowly disappeared into the landscape; but for twenty years it had introduced visitors to some of the most magnificent animals of the West—bison, elk, moose, and antelope. What remains, the lasting legacy of the JHWP, is the Biological Research Station. Now operated by the University of Wyoming in cooperation with the NPS, it hosts scientists from across the country and around the world. Their work continues to advance our understanding about the region's plants and animals, the impacts of climatic change and a host of other topics of pivotal importance to the conservation of our planet and all of its inhabitants.

◆ PRECEDENT

The idea of staged wildlife exhibits was not new or novel. As early as 1894 a private concessioner operated a zoo-type facility in Yellowstone that housed elk, bison, and bighorn sheep as well as a

variety of domestic livestock. Poorly managed, in 1907 Park Superintendent S. B. M. Young ordered the owner to close the complex and release the animals. However, several very popular bear feeding grounds located near Yellowstone's major hotels continued to entertain guests for several decades. When the NPS took over the management of the national parks in 1916, the agency's first director, Stephen Mather, and his assistant Horace M. Albright, who became Yellowstone's superintendent in 1918, enthusiastically endorsed wildlife exhibits. While the initial purpose for the establishment of the nation's parks was to protect unique, majestic landscapes, Mather and Albright knew that visitors placed equal emphasis on observing native wildlife.⁴

Pragmatic men, Mather and Albright understood that Congressional funding for the fledgling new agency would be directly related to the number of tourists who visited the parks. To lure tourists and garner their lasting support for the NPS the men adopted a philosophy of aesthetic conservation. This approach to sustainable development focused on protecting the land and its animals for recreational and sightseeing opportunities versus utilitarian conservation practices that endorsed extractive activities such as hunting, mining and lumbering. Almost immediately the NPS promoted the establishment of zoos and wildlife preserves within the national parks for their entertainment value. To impress upon the public the importance of the national parks, the NPS combined conservation education with the animal exhibits. Park rangers taught onlookers about the animals and their natural habitats. They also informed visitors of the NPS's mission of protecting both the animals and the landscapes for generations to come in an attempt to get the public involved in conservation.⁵

By 1924, under Albright's direction a new staged exhibit, or zoo, opened near the existing buffalo show corral in Mammoth Hot Springs. It displayed a variety of animals caught within Yellowstone's boundaries including black-tailed deer, elk, badgers, a coyote, an aviary, and a pair of black bears. The semi-tamed animals proved very popular with park visitors who were encouraged to get close to the animals for memorable photo opportunities. Combined with the ongoing bear feeding exhibitions, the ability to observe wildlife at close range developed into a major entertainment experience for park visitors.⁶

⁴ Alice Wondrak Biel, *Do (Not) Feed the Bears: The Fitful History of Wildlife and Tourists in Yellowstone* (Lawrence: University of Kansas Press, 2006), 8-11, 18.

⁵ *Ibid.*, 11-13, 20.

⁶ *Ibid.*, 11-16.

Yellowstone was not alone. Other national parks utilized wildlife to lure tourists. Since the caverns hidden underground constituted the main attraction of South Dakota's Wind Cave National Park it drew additional tourists by establishing a game preserve in 1913 as a sanctuary for bison. The NYZS and the American Bison Society donated the preserve's original fourteen animals. The variety of game animals expanded the following year with the introduction of antelope and elk. Western game animals delighted visitors of this prairie environment. At the same time tourists in Rocky Mountain National Park enjoyed close encounters with unusually docile bighorn sheep.⁷

◆ ORIGINS AND CONTROVERSY SURROUNDING THE JHWP

As the nation began looking forward to the end of World War II during the summer of 1945 Governor Hunt, former Wyoming Governor Leslie Miller and the State Game Commissioner, Lester Bagley, pondered ways to contribute to the State's economic development by bolstering tourism. Hunt's initial idea of a wildlife museum quickly expanded into that of a wildlife preserve and exhibition ground. The precedent for such a facility having already been established and proven popular, the challenge they faced was finding a suitable site. They turned to the one family and man known to be dedicated to conservation and who owned an appropriate tract of land, Laurance S. Rockefeller.

The men traveled to Jackson Hole on August 5, 1945 to sell their idea to Harold Fabian, Rockefeller's legal representative in the valley. The meeting lasted through the afternoon and into the evening. The discussion included the need of a sufficiently large enough tract of land to minimize, if not avoid, habitat degradation by the number and variety of animals the complex would house; the need to hide containment fencing to maintain a natural appearance; and possible sources of opposition. Fabian enthusiastically drafted a letter explaining the project to Rockefeller the following day. His letter

also documented the public's genuine interest in game animals, describing cars stopped along Jackson Hole roadways for hundreds of yards while tourists observed and photographed wild animals in their natural habitats.⁸

Hunt, Miller, and Bagley's decision to pursue Rockefeller was well considered. Laurance first visited Jackson Hole with his father, John D. Rockefeller, Jr. and two of his brothers in 1924. A return trip two years later led to an alliance between his father, already involved in conservation projects throughout the country, and Albright to save Jackson Hole from undue commercialization and to create Grand Teton National Park.⁹ Soon thereafter Mr. Rockefeller founded the Snake River Land Company to begin purchasing private landholdings in the valley with the ultimate goal of donating the land to the federal government for inclusion in the yet to be established park. Within a decade the company held title to over 33,000 acres in Jackson Hole.

In 1941, the Snake River Land Company evolved into JHP whose purpose was to hold and manage the properties. Of all of the Rockefeller children, Laurance most avidly pursued his father's interest in conservation. In 1945, he assumed control of JHP, thereby committing himself to bringing his father's vision of Jackson Hole to fruition. Through JHP he also completed other projects begun by his father while greatly expanding the family's dedication to conservation activities.¹⁰

Convinced of the merits of the project, Rockefeller swiftly contributed his unqualified support. Less than two months after the initial meeting with Fabian the concept had expanded to include not only economic development based on a new tourist attraction but also the desire to provide for wildlife research. The *Wyoming Tribune* published an article describing the fundamentals of the proposal, touting its potential to attract thousands of tourists and an "area for scientific study...on a scale unparalleled in the nation." The article revealed that Rockefeller had pledged the needed land, that the wildlife park would be managed by a non-profit entity, and that the New York Zoological Society, "doubtless the outstanding

⁷ "Wildlife Management – Creating a Game Preserve," *Wind Cave National Park*, National Park Service, <http://www.nps.gov/wica/parkmgmt/wildlife-management-creating-a-game-preserve.htm>, accessed March 13, 2014; Biel, *Do (Not) Feed the Bears*, 14.

⁸ Fabian to LSR, August 6, 1945, Box 2, Folder 1945, Winger Papers.

⁹ Marion Albright Schenk, "One Day on Timbered Island: How the Rockefellers' Visits to Yellowstone Led to

Grand Teton National Park," in *Montana: The Magazine of Western History*, Vol. 57, No. 2 (Summer 2007), 28-29, 32-33; Nancy Newhall, *A Contribution to the Heritage of Every American: The Conservation Activities of John D. Rockefeller, Jr.* (New York: Alfred A. Knopf, 1957), 110.

¹⁰ Robert W. Righter, *Crucible for Conservation: the Struggle for Grand Teton National Park* (Boulder: Colorado Associated University Press, 1982), 130-131.

organization in live animal conservation and management in the world,” would assist with the project.¹¹ Several weeks later another *Wyoming Tribune* article reported the unqualified support of Hollywood actor Wallace Beery who first visited Jackson Hole in 1900 and owned a cabin on Jackson Lake. Beery professed there was no better place for such an extensive display of Wyoming wildlife.¹²

Yet Fabian had been correct to express concern about potential opposition. Perhaps the most distressing critique of the wildlife park came from another Jackson Hole resident, renowned wildlife biologist Olaus J. Murie. Murie critically echoed a *New York Herald Tribune* article that referred to the proposed park as a zoo. The article made no mention of the possibility of any biological research, instead focusing on its function as a tourist attraction. Murie publicly voiced his disapproval of the plan, explaining that confining game animals in a specific area created the “antithesis” of a natural, healthy habitat. He claimed that the public could be provided the opportunity to readily view wildlife without the use of enclosures. Stunned by the fact that the project had been approved without receiving input from all of the members of the Jackson Hole Preserve board of directors, of which he was one, and that they were not informed prior to disclosure of the planned project by the press, Murie resigned from the board.¹³

A highly regarded conservation organization, the Isaac Walton League of America (IWLA), also opposed the “zoo.” As chairman of the Committee on Conservation of the national organization, John W. Scott wrote to Richard Winger, president of the Jackson Hole chapter of the League regarding the proposed JHWP. Scott acknowledged the educational value of zoological gardens when located near urban areas but questioned the placement of such a facility in Jackson Hole. He argued that “it [the proposed wildlife park] would be out of place, highly expensive with no important worthwhile function and even highly grotesque and ridiculous.” He professed that when Gov. Hunt had presented the plan in early August to the State Convention of the Wyoming Division of the League that it received a “cool reception” and that most delegates did not take the

governor seriously. Scott also expressed concern about Wyoming’s continued financial commitment to maintaining the facility considering the volatility of state and local politics.¹⁴

However, Winger’s interest in conservation went beyond his association with the IWLA. As an agent of the Snake River Land Company he had been involved with the purchasing of the properties in Jackson Hole. He had also been involved in the establishment of the JHNM. Winger was still working for Rockefeller at JHP when this new venture arose. He felt that the prospective benefits of the proposed wildlife park far outweighed the possible negative aspects that concerned its detractors. Winger’s intimate knowledge of the valley enabled him to counsel Rockefeller and the other board members of the soon to be created Jackson Hole Game Park, Inc. regarding the selection of the site for the preserve as well as other important aspects.

◆ EARLY PLANNING

The tract of land chosen for the JHWP ran along Highway 287 between Jackson Lake Junction and Pacific Creek, with the primary viewing area located on the south side of the highway, southeast of Oxbow Bend. The plan Winger suggested called for erecting fencing at the south end of the property that would funnel animals into the Park as they left the National Elk Refuge and lower elevations of the valley during the spring migration. During the spring and fall, fencing at the northern and southern boundaries would be lowered, allowing most animals to pass through. At the right time during the spring migration the fencing would be reset in order to contain a minimum number of animals for the summer tourist season. Winger hoped that any calves born inside the JHWP grounds would voluntarily return to the Park, the only summer range they knew, after being allowed to leave during the fall migration. He envisioned the development of a JHWP herd that would always summer in the park, allowing all fencing to be removed.¹⁵

¹¹ “Big Wildlife Exhibit to Be Set Up,” *Wyoming Tribune*, October 2, 1945, Box 2, Folder 1945, Winger Papers.

¹² “Wildlife Park Plan Praised,” *Wyoming Tribune*, November 12, 1945, Box 2, Folder 1945, Winger Papers.

¹³ Olaus J. Murie to Vanderbilt Webb, November 4, 1945, Box 2, Folder 1945, Winger Papers; “Jackson Hole Wildlife Park,” National Park Service,

<http://www.nps.gov/grte/historyculture/jhwp.htm> [accessed February 18, 2013]; “Zoo in Bronx Given a Home on the Range,” *New York Herald Tribune*, November 2, 1945, Box 2, Folder 1945, Winger Papers.

¹⁴ John Scott to Winger, December 5, 1945, Box 2, Folder Wildlife Park, Winger Papers.

¹⁵ Winger to LSR, July 10, 1946, Box 1, Series 2, Folder 5, RG5 GTNP; also in Box 2, Folder Wildlife Park, Winger Papers.

Winger's plan addressed two problems. He understood the concerns of many people regarding the artificial confinement of wild animals, in fact he agreed. And he believed that any necessary fencing should be placed where it would have the least visual impact in order to maintain the natural appearance of the landscape. Keeping both of these concerns in mind, his plan called for the eventual removal of almost all fencing. He believed that this strategy would mitigate the main objection to the JHWP by the conservation community. The expense of artificial feeding during the winter created another problem. By enabling the animals to migrate out of the Park, the cost of feed for the animals as well as salaries and housing costs for staff during the winter could be minimized, if not eliminated.¹⁶

Another individual instrumental to the development and initial success of the JHWP was James R. Simon. Backed by a degree in zoology and experience both as a ranger in Yellowstone National Park and as a commissioner with the Wyoming Game and Fish Department (GFC), Simon became the first director of the wildlife park in October, 1946. More than anyone else he articulated the purpose, goals, and challenges of the JHWP. He understood that quelling opposition to the park relied on communicating all of its potential benefits to the public.¹⁷

Even at this early stage of development, almost two years before the park opened, Simon comprehended the importance of education and research to the future success of the project. Simply displaying game animals was not enough; he advocated a multi-faceted approach to inform visitors about the animals' unique characteristics and the importance of each species to the entire ecosystem of Jackson Hole. Yet he also wanted areas that would demonstrate the negative consequences of having too many animals in a given area – overgrazing, highlining of trees, soil depletion, and erosion. Through such displays he hoped people would gain an understanding of the importance of natural resource and wildlife management to the survival of the animals and the conservation of the landscape. Simon gave equal consideration to the development of research programs.¹⁸

Simon also appreciated the dire need of state and federal agencies for verifiable information on which to base hunting and fishing policies. He knew

that the demands of WWII caused many studies to be abandoned before their completion. With the support of Governor Hunt, Commissioner Bagley, the NYZS, and the board of the JHWP, Simon sought to revive some of the old, unfinished research projects and to launch new ones. He envisioned three different approaches to wildlife research. First, he wanted to support independent scientists who would conduct studies of the animals and plants that occupied the various habitats found within the wildlife park. Second, Simon sought to establish a cooperative relationship with state and federal agencies. He wanted the capability of offering the expertise of a resident biologist to take over smaller-scaled studies that such agencies were not able or willing to undertake for themselves. He also wanted to be able to offer to the scientists of those same agencies the use of the research facilities within the park. To that end he called on the board to order a comprehensive facilities development plan that would include a fully-equipped laboratory, dormitories and other accommodations for guest researchers and staff, an office, library, and an information/education center for tourists. Finally, Simon wanted to develop relationships with educational institutions by providing opportunities for students to conduct much needed fieldwork studies to enrich their academic experience. He hoped to attract students from a variety of disciplines – plant biology, aquatic studies, and any number of other animal sciences – in addition to wildlife management. As committed to conservation as Rockefeller and Fairfield Osborn, head of the New York Zoological Society, Simon joined in their vision of the Jackson Hole Wildlife Park as a leader of wildlife and ecological scientific research.¹⁹

These two men contributed significantly to the planning and development of the wildlife park and its facilities. Winger, having lived in the valley for over thirty years, provided invaluable knowledge of the migration movements and behaviors of Jackson Hole's wildlife. Simon drew on his educational and professional experiences. Both of them worked diligently to overcome obstacles in order to create something more than a roadside tourist trap, to realize Rockefeller's goal of educating the public about the importance of habitat and wildlife conservation through visual engagement with the majestic animals of the West.

¹⁶ Ibid.

¹⁷ Simon, "The Jackson Hole Wildlife Park," Box 2, Folder 1945, Winger Papers; also located in Box 1, Folder 17, Lester C. Hunt Collection, American Heritage Center,

University of Wyoming, Laramie, Wyoming (hereafter referred to as the Hunt Papers).

¹⁸Ibid.

¹⁹ Ibid.

✦ PLANNING FOR THE WILDLIFE PARK CULMINATES IN REALITY

Almost three years of planning and development transpired before JHWP became a reality. Aside from the creation and staffing of a business to oversee the operation of the park, the actual boundaries needed to be determined, fencing installed, structures built, and animals acquired. As with any project, each task generated additional questions and challenges.

Establishment of the administrative structure occupied much of the winter of 1945 and 1946. The most immediate task, accomplished in December, entailed the incorporation of a non-profit entity called Jackson Hole Game Park led by a nine member Board of Trustees. The original trustees, also called directors, included Rockefeller, Fairfield Osborn (president of the NYZS) and Alfred Ely (vice president of the NYZS) who represented the NYZS; Lester Bagley, Carl Jorgenson, Foster S. Scott and Gilbert O. Housley represented Wyoming; Kenneth Chorley and Harold Fabian represented JHP.²⁰

Article 2 of the Certificate of Incorporation clearly identified the purposes of the corporation:

“The purposes for which the corporation is formed are exclusively charitable, educational and scientific; for promoting the diffusion of knowledge and useful information concerning wild fowl and game native to the State of Wyoming and other localities...; for providing and maintaining a suitable place or places for the collection, exhibition and preservation of such wild fowl and game; to provide, establish and maintain parks, roads and trails; and for the preservation of the history and tradition of the country, particularly with respect to the Jackson Hole area; and in general to promote, manage and conduct such other and further activities as are germane to these general purposes.”²¹

As delineated, determining the best location for the housing and exhibition of the animals, and acquiring the chosen land (see Figure 2) demanded an analysis of terrain, including existing roads, streams, and trails,

a process that began almost immediately after Rockefeller approved the plan in August. Following incorporation, executing a lease for the selected land from Jackson Hole Preserve and acquiring a permit from the federal government for use of adjoining public lands in the Jackson Hole National Monument became two of the board’s most important tasks. The Department of the Interior issued the lands use permit on March 22, 1946. The Board of Trustees finalized a lease for the majority of the needed land from JHP a few months later. Below is a simplistic map showing the location of the 1,500 acre JHWP.²²

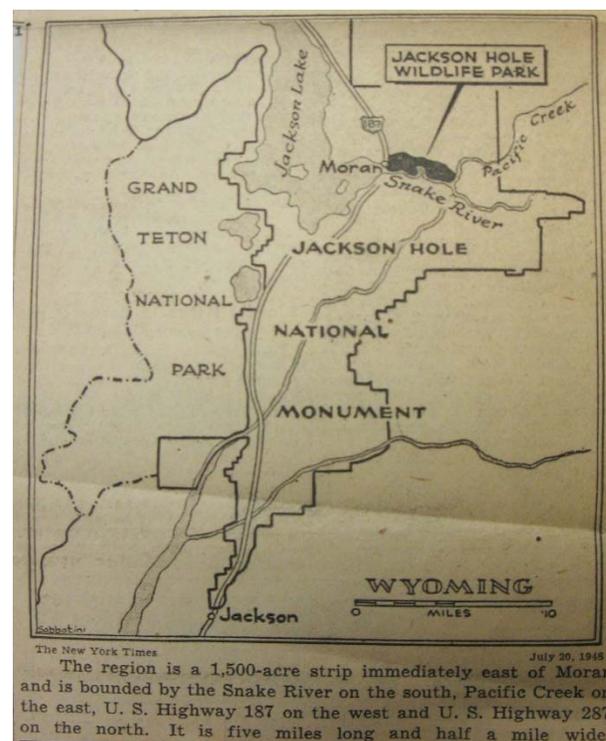


Figure 2. Location of the JHWP relative to GTNP and JHNM.²³

The summer of 1946 witnessed one other significant administrative action. On June 26th the name of the park officially changed from Jackson Hole Game Park to Jackson Hole Wildlife Park.²⁴ No verifiable explanation for the change has been located. However, it can be assumed that since the park and its affiliated research program intended to include fish,

²⁰ Certificate of Incorporation, November 26, 1945, Box 1, Series 1, Folder 2, RG5 GTNP; Fabian to Winger, November 9, 1945, Box 2, Folder Wildlife Park, Winger Papers.

²¹ Certificate of Incorporation, RG5 GTNP.

²² News Release, January 2, 1946, Hunt Papers; Revocable Permit, March 22, 1946, and JHP lease to JHWP, July 1, 1946, Box 4, Series 10, Folder 2, RG5 GTNP.

²³ This map, taken from a July 20, 1948 New York Times article covering the dedication ceremony of JHWP, shows the approximate boundaries of the park; missing is Highway 287 which runs east from Moran along the northern edge of the park. Box 1, Folder 17, Hunt Papers.

²⁴ Certificate of Incorporation, and Proof of Publication, RG5 GTNP.

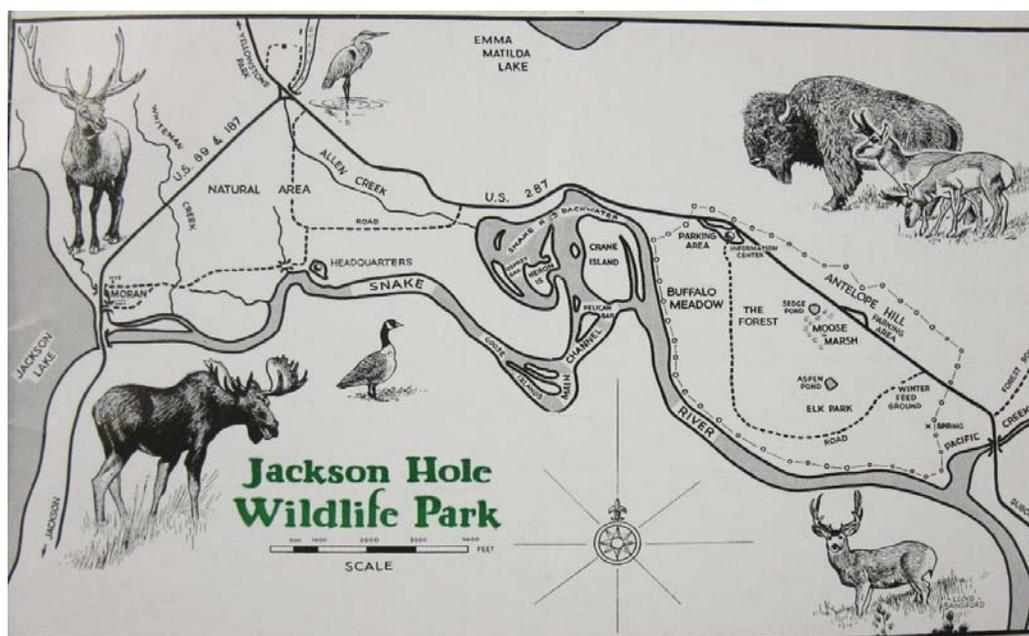


Figure 3. Attendants of the opening ceremony received a booklet that included this map.²⁵

birds, and other animals as well as plants in addition to game animals the choice of “Wildlife” was deemed more representative of the functions of the park.

The critical issues of where to locate the public viewing area and placement of fencing followed. As agent of the JHWP responsible for the daily activities and management of the Park, Winger assumed the task of assisting Dr. Jean Delacour in establishing the physical arrangement of the facility as soon as weather and snow levels permitted late in the spring of 1946. Once the plan was approved, Winger was to oversee construction of the fencing.²⁶ When Delacour’s proposed layout appeared at odds to Winger’s vision and goals for the Park, he communicated his concerns to Rockefeller and other members of the Board of Trustees. Time taken to

consider his alternative recommendations delayed the first phase of fencing installation by several months. The delay ultimately caused the postponement of the park opening from 1947 to 1948.²⁷ Installation of other control measures such as cattle guards in the adjacent highway required approval by and cooperation with the Wyoming Highway Commission and/or the Game and Fish Commission.²⁸

Following completion of the fencing and cattle guards surrounding the exhibition area late in 1947, JHWP scheduled the introduction of its game animals for early 1948. Simon secured numerous elk and three moose from the Park’s grounds. Commissioner Bagley made arrangements for the State Game and Fish Department to provide the other desired game animals. After making inquiries with the

²⁵ *Jackson Hole Wildlife Park*, July 1948, Box 5, Series 13, Folder 1, RG5 GTNP.

²⁶ Fabian to Winger, November 9, 1945, Box 2, Folder Wildlife Park, Winger Papers. Dr. Jean Delacour, a renowned ornithologist, served as a technical advisor and researcher affiliated with the NYZS during the 1940s. See Delacour obituary, *New York Times*, November 29, 1985, <http://www.nytimes.com/1985/11/29/world/dr-jean-delacour-95-leading-ornithologist.html> and Jean Théodore Delacour, Wikipedia, http://en.wikipedia.org/wiki/Jean_Th%C3%A9odore_Delacour.

²⁷ The delay, combined with different approaches to the design of the park, may also have been a contributing factor in Simon being appointed director of the corporation during a meeting of the Executive Committee held on August 12, 1946. The following summer the trustees terminated Winger’s positions as Superintendent of Construction and legal Resident Agent of the JHWP, Inc. Simon was named Resident Agent and as Director he assumed responsibility for all construction projects. Report to the Board of JHWP, February, 1947, Box 1, Folder 17, Hunt Papers; Certificate of Appointment of Agent, August 26, 1947, Box 4, Series 10, Folder 5, RG5 GTNP.

²⁸ Fabian to Winger, November 9, 1945, and Fabian to Bagley, June 26, 1946, Box 2, Folder Wildlife Park, Winger Papers; “Report to the Board of JHWP,” February, 1947, Box 1, Folder 17, Hunt Papers.

superintendents of both Wind Cave and Yellowstone National Parks, twenty bison were delivered from Yellowstone. The State also provided seventeen antelope, nineteen mule deer, and ten white-tailed deer.²⁹

When the Jackson Hole Wildlife Park finally opened on July 19, 1948, like any large scale enterprise it was still a work in progress but much had already been accomplished. In addition to the erection of fencing and the installation of the game animals a visitor information center stood at the primary exhibition area overlooking Buffalo Meadow and interior observation roadways had been constructed to allow visitors close access to the animals. A hayshed to store feed had been erected near the winter feeding ground. And in consideration of motor tourists Simon had enlisted the assistance of the State Highway Department with the installation of highway turn-outs and parking areas. The map in Figure 3 shows the location of some of these key features.

However, the changing public perception of JWHP proved to be equally as important as the physical developments. As the endeavor took shape, moving beyond just a vague concept to tangible reality, many people began to appreciate the park's potential not only as a tourist attraction but also its capacity to advance conservation. As early as February 1947 Simon reported that the National Park Service Association³⁰ withdrew its disapproval and the JWHP had garnered the support of the Dude Ranchers Association.³¹ In September the American Society of Mammologists expressed its desire for the park to "abandon plans for any unnatural presentation of wildlife" but fully endorsed the "emphasis on research"³² The JWHP received another unqualified endorsement from the Wyoming Federation of Sportsmen's Clubs in March, 1948.³³

To measure the opinions of the general public living in and visiting Jackson Hole as compared to special interest groups, Osborn commissioned a survey conducted during the summer of 1947. Carried out by Dr. C. R. Carpenter of Pennsylvania State

College (now Pennsylvania State University), it showed broad support for the park. Of those interviewed, 74.7 percent approved of the development of the wildlife park and an overwhelming 88.0 percent endorsed an affiliated research and training center.³⁴ As the JWHP took shape and people learned more about it opposition diminished and support expanded.

Dedication of Jackson Hole Wildlife Park

As reported by Fabian, the dedication was a classic Rocky Mountain summer event held on a beautiful day, in a beautiful setting, with an afternoon thunderstorm that threatened but held back until the conclusion of the ceremony. Surprisingly, only a handful of the approximately five hundred people who attended hailed from the nearby town of Jackson.³⁵ Rockefeller delivered the keynote address. His speech chronicled the origins and development of the JWHP, identifying key participants and their contributions. He also told of his family's first visit to Jackson Hole in 1924, of his father's desire to protect the area from over development and of his land purchases, suggested by then Yellowstone Superintendent Horace Albright, which resulted in the availability of the land for the JWHP. Rockefeller clearly stated the goal of the new Park: "In short, our objective is to have the scenery, the wildlife, and the historic past of Jackson Hole conserved for, not from, the people who live and visit here...We believe that the JWHP, dedicated here today, will prove to be another important step toward the realization of the general objectives of the Jackson Hole project. The people who come here will see wildlife, they will learn to identify the various animals and birds, to appreciate them, understand the problems involved in their protection, the need for preserving forests, safeguarding watersheds, saving the wilderness – in effect, the people will see what they are asked to conserve."³⁶ Reprinted in full by the Jackson Hole Courier, the public enthusiastically embraced Rockefeller's commitment to the valley. They especially appreciated his comments about the JWHP and the

²⁹ Simon, "Report to the Board of the JWHP," April 1, 1948, Box 1, Folder 17 Hunt Papers.

³⁰ The NPS Association is not to be confused with the NPS, which remained mute regarding the JWHP.

³¹ Report to the Board of JWHP, February, 1947, Box 1, Folder 17, Hunt Papers.

³² Donald F. Hoffmeister to Newton Drury, September, 16, 1947, NPS: Grand Teton National Monument, Box 2, Folder 201-Correspondence, National Archives and Records Administration (NARA), Broomfield, Colorado.

³³ "Resolution by Wyoming Federation of Sportsmen's Clubs," Game and Fish/Administration, Director Files, 1946-49, S-Z, Wyoming State Archive, Cheyenne, Wyoming.

³⁴ Osborn to Fabian, November 21, 1947, and attached report, "Information Schedule on Jackson Hole Region," Box 4, Series 4, Folder 3, RG5 GTNP.

³⁵ Fabian to Boyer, July 20, 1948, Box 5, Series 13, Folder 1, RG 5 GTNP.

³⁶ LSR, "Remarks Made at the Opening Ceremonies of the JWHP," July 19, 1948, RG5 GTNP.

entire JHP strategy of conservation and preservation being for everyone's benefit. Fabian believed that "his [Rockefeller's] talk at the opening of the Wildlife Park did more than any single thing that has happened to bring local public good-will to the entire Jackson Hole Preserve effort."³⁷

Little real advertising of the JHWP has been discovered. Most publicity and information about the Park appears to have been disseminated through newspaper articles. The local newspapers of Jackson Hole, the Salt Lake Tribune, and the New York Times often printed updates about the activities of the Park.³⁸ Those and other papers such as the Denver Post printed informative pictorial layouts, often paired with informative articles.³⁹ *Animal Kingdom*, published by the NYZS, printed several articles informing its readers about current happenings.⁴⁰ And the Wyoming Commerce and Industry Commission produced booklets and brochures called *Wonderful Wyoming* similar to today's tourism pamphlets, advertising the wonders of the Wyoming, including the Teton Mountains, but did not specifically mention the JHWP.⁴³ Simon, presumably with the Boards approval, apparently preferred a targeted approach of localized marketing.

Several of Simon's reports to the Board of Directors and the Advisory Board discussed other means of drawing visitors to the Park. In cooperation with the Jackson Chamber of Commerce, JHWP staff hosted guided tours of the Park to attendees of conventions held in Jackson. GTNP included the Park in its offerings of guided tours and JHWP staff often informed campers about the Park and its animals during NPS campfire programs. A taxi service provided transportation from Moran for those travelling by bus who wanted to see the exhibit. Simon also reported that two saddle horse outfits near the Wildlife Park prioritized visiting the facility during guided rides. He seemed most pleased by the attendance of visitors and residents of Jackson Hole to talks given by researchers about their work. He also let it be known that travel agents across the country

had requested information about the JHWP to include in their travel brochures.⁴¹



Laurence S. Rockefeller made one of the dedicatory addresses. Other speakers were (left to right): Lester Bagley, Wyoming Game and Fish Commissioner; Fairfield Osborn, president of the New York Zoological Society; Carl Jorgensen, president of the Wyoming Game and Fish Commission; Charles Moore, president of the Wyoming Dude Ranchers' Association; the Hon. Lester C. Hunt, Governor of Wyoming; and James R. Simon, Director of the Jackson Hole Wildlife Park.

Figure 4. Rockefeller delivering the keynote address. Photo acquired from the same *Animal Kingdom* article as Figure 1.⁴²



Figure 5. Elk passing through a meadow in the JHWP. Photo acquired from the same article as Figure 1. During the dedication ceremony a horseman kept elk and bison behind the speakers' platform within view of the spectators.⁴³

³⁷ Fabian to Boyer, July 30, 1948, Box 5, Series 13, Folder 1, RG5 GTNP.

³⁸ Multiple newspaper clippings located in several collections – Winger Papers, Hunt Papers, RG5 GTNP, and the Rockefeller Family Papers, Rockefeller Archive Center (hereafter referred to as RAC), Sleepy Hollow, New York.

³⁹ Kenneth Chorley Papers, Box 2, Folder 21, RAC.

⁴⁰ Ibid.; *Animal Kingdom: The Magazine of the NYZS*, Vol. LI, No. 5, October 1, 1948, Box 5, Series 13, Folder 1, RG5 GTNP.

⁴¹ Simon, Reports, 1950-52, Box 18, Folders 15 and 16, Neal Blair Papers (hereafter referred to as the Blair Papers), AHC.

⁴² "The Inauguration of the Jackson Hole Wildlife Park," *Animal Kingdom: The Magazine of the NYZS*, Vol. LI, No. 5, October 1, 1948, Box 5, Series 13, Folder 1, RG5 GTNP.

⁴³ Fabian to Boyer, July 20, 1948, Box 5, Series 13, Folder 1, RG5 GTNP.

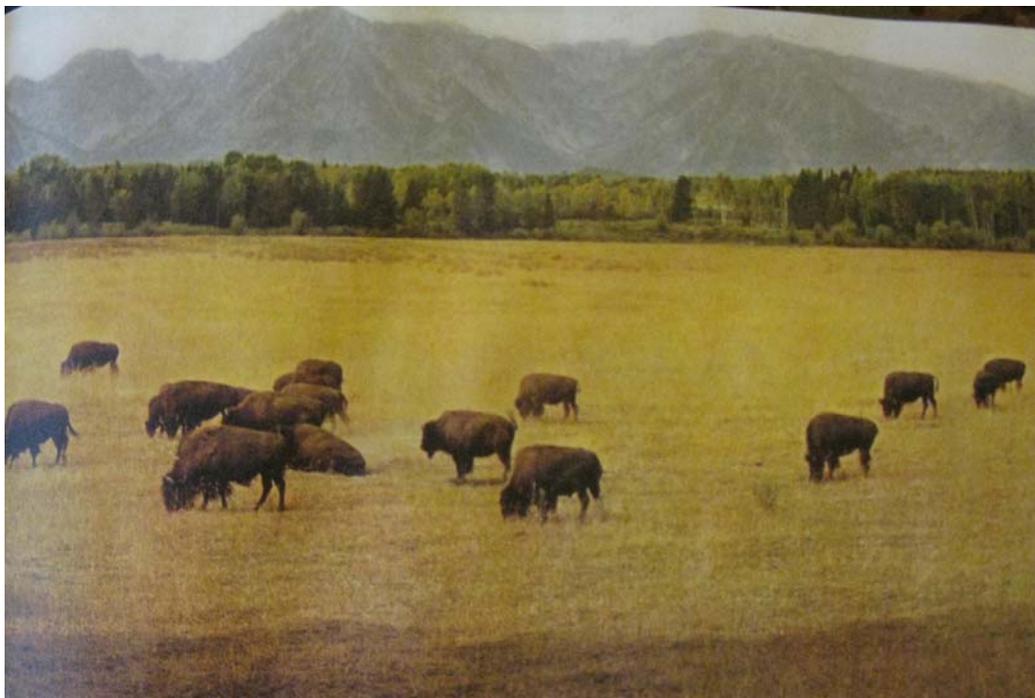


Figure 7. Bison grazing in JHWP, c. 1955.⁴⁴

The State Game and Fish Commission reported that during 1949, the JHWP's first full summer season in operation, approximately 86,000 persons visited the Park. They came from twenty-four foreign countries and almost every state in the nation.⁴⁵ The following year (measured from September 15, 1949 to September 15, 1950) saw only a modest increase of just 3,000 visitors. But attendance skyrocketed during the 1950-51 period with the total number of visitors estimated at over 105,000. The JHWP typically opened for the tourist season on June 15th and closed on September 15th. Therefore Simon had to estimate the total number of visitors, adding to the count recorded at the Visitor Information Center and the antelope enclosure to account for those who stopped to observe the animals during the rest of the year. Visitors enjoyed the experience of seeing elk, bison, white-tail and mule deer, and antelope all in one central location, the

Buffalo Meadow. By all accounts, as a tourist attraction, the JHWP was amazingly successful.⁴⁶

It was equally successful at establishing and growing its bison herd. In January 1948, twenty bison arrived at the JHWP, including fourteen females between one and four years of age. That spring four of the cows produced calves. The following year eight of them gave birth to one calf each.⁴⁷ The Game and Fish Department had provided the original seed herd on the provision that any offspring could be claimed by the Department. The first documentation of the possible removal of excess bison occurred in October 1949.⁴⁸ The State did remove six bison in the fall of 1950 but it is not known if they were delivered to Mr. Faulkner. However, in August 1951, Simon reported that the herd had grown to forty-five and that Game and Fish Department personnel removed twenty-three of those to start two new herds for the State.⁴⁹ Once again the JHWP could claim success, this time through a productive breeding program.

⁴⁴ Newhall, *A Contribution*, 111.

⁴⁵ Game and Fish Commission 1949 Annual Report, Box 18, Folder 13, Blair Papers.

⁴⁶ Simon Report, June 15, 1950 and October 15, 1951, Box 18, Folder 15, Blair Papers.

⁴⁷ Norman C. Negus, "Breeding of Three-Year-Old Females in the Jackson Hole Wildlife Park Buffalo Herd," *Journal of Mammology* 31, no. 4 (1950), 463.

⁴⁸ Lester Bagley to Art Faulkner, October 7, 1949, Game and Fish/Administration, Director's Correspondence, 1946-49, A-F, Wyoming State Archives.

⁴⁹ Simon Reports, October 15, 1950 and August 15, 1951, Box 18, Folder 15, Blair Papers.

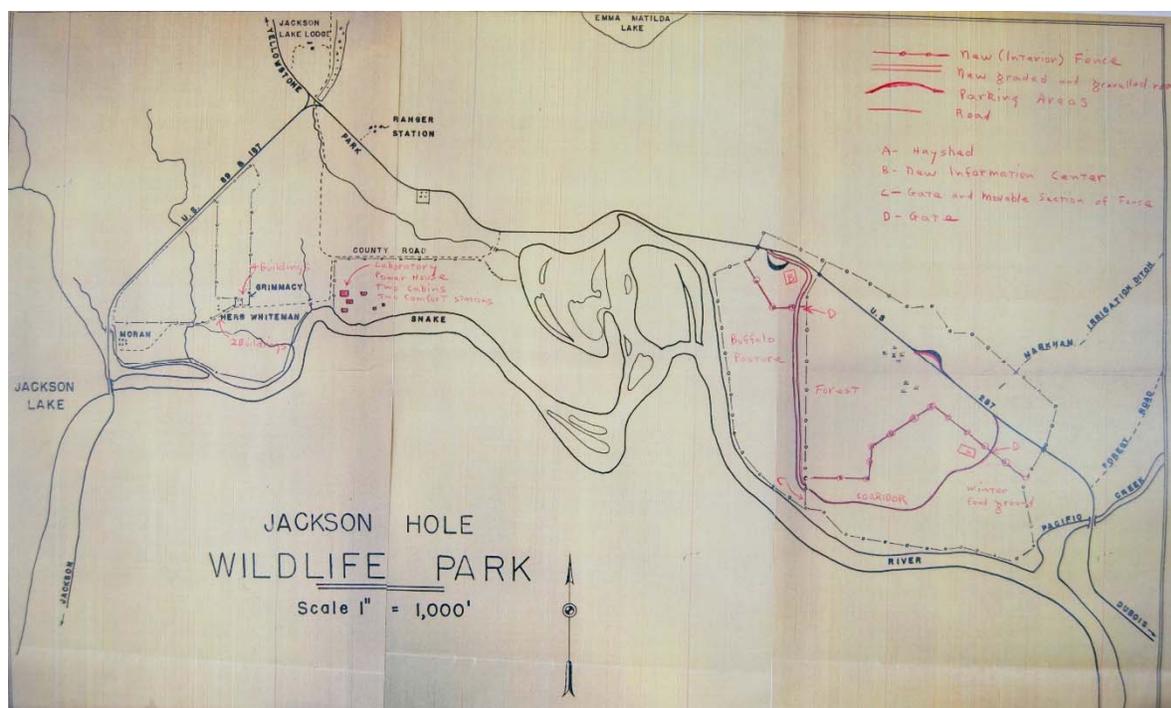


Figure 8. Map of the JHWP at the end of 1948 showing the location of the research field station complex near the west end of the Park, new interior fencing, and the new information center.⁵⁰

◆ EARLY DEVELOPMENT OF THE BIOLOGICAL RESEARCH STATION

The early demand for use of the park as a research facility surprised everyone. The first formal scientific study conducted on the grounds took place in September, 1946 as construction on the first sections of fencing began. Dr. E. Raymond Hall led a group of mammalogists from the University of Kansas who investigated the migration patterns of elk through the park. Information gleaned from their study helped determine the location of later phases of fencing.⁵¹ During the summer of 1947, a year before JHWP formally opened to the public, twenty-three individuals, including sixteen students, from seven different institutions conducted research at the park. The Park hosted another twenty researchers the following summer. As demand grew so did a complex of buildings designed specifically to house and support researchers and their work.⁵²

Simon's contractors kept very busy during the summer of 1948 hoping to complete as much work as possible before winter descended on the valley. The plans included the construction of a laboratory, three cabins, a powerhouse, and two outhouses. Later in the summer, after the completion of the JHWP visitor information center, a small cabin was moved to the research complex to serve as a library. Simon stocked the new laboratory with new scientific and photographic equipment. He also added to the small library collection. Each year the facility expanded, gaining additional housing for staff and researchers, a bath house, and a mess hall. Rockefeller and the NYZS funded the vast majority of these capital improvements.⁵³

Simon and Osborn in particular took great pride in the volume and quality of scientific studies conducted at the Park. However, it created conflict and concern for Bagley and the other members of the Game and Fish Commission on two fronts. First, the original concept as envisioned by Bagley, Hunt, and

⁵⁰ 1948 Map, Map Folder C-1, File 9, Grand Teton Lodge Company, RAC.

⁵¹ Simon Report, February, 1947, Box 1, Folder 17, Hunt Papers.

⁵² Meeting Minutes, August 26, 1947, Box 1, Folder 17, Hunt Papers.

⁵³ Lenore Diem, "The Research Station's Place in History, Historical Chronology of the establishment and Development of the Jackson Hole Biological Research Station," NPS, www.nps.gov/history/history/online_books/npsgr/research_station/chronology.htm (accessed February 1, 2013); Simon Report, February, 1947, Box 1, Folder 17, Hunt Papers.

Miller emphasized the animal display, not the research facility, which in their minds provided a supplemental service not a primary activity. Additionally, the Game and Fish Department also conducted research which created a conflict of interest. Therefore, the commissioners dictated that all of the funds they contributed be spent exclusively in support of the animal display. In part because of the position of the Game and Fish Commission and the growing use of the biological field station, that portion of the complex became known as the Jackson Hole Biological Station of the NYZS early in 1950. As a result of the direct affiliation with the Zoological Society, the society began a grant program providing funding for researchers conducting studies at the Biological Station. That summer twelve individuals received grants.⁵⁴

Evolution of the JHWP and the Biological Research Station

Despite some growing pains and a few unanticipated challenges, success seemed a certainty for the JHWP. Thriving animals, escalating visitorship, and steady use of the research field station created a perfect mix. Yet the political landscape started changing and the Wildlife Park found itself caught in the middle. In fact, the tide started turning back in the closing months of 1949. By 1952, Jackson Hole Wildlife Park, Inc. would no longer exist.

The process began when, on October 31, 1949, the NPS extended the public land use permit allowing the JHWP use of over six hundred acres in the Jackson Hole National Monument (JHNM) until October 31, 1959. The previous permit, written for a five year term, had been scheduled to expire in 1952. JHP matched the NPS permit, extending its lease of land to the JHWP to the same date thus virtually guaranteeing that the Wildlife Park would continue to operate for another ten years.⁵⁵ Perhaps both parties no longer viewed the JHWP as an experiment but as a viable entity.

What happened next really should not have surprised anyone. Two months later, on December 16th, JHP transferred to the federal government the deeds to the 33,562 acres of land in Grand Teton National Park and the JHNM purchased almost twenty years earlier. The dream of John D. Rockefeller, Jr. and his son for the United States to own and manage

the land on behalf of all Americans became a reality. But though the land would be managed by the NPS, it was not yet included in GTNP which was the senior Rockefeller's ultimate goal.⁵⁶

On September 14, 1950 the future of the JHWP unknowingly stepped onto a decidedly different path. On that day the years' long battle to abolish Jackson Hole National Monument (JHNM), which housed the grounds of the JHWP, and to contain Grand Teton National Park (GTNP) ended. President Truman signed into law legislation that did in fact abolish JHNM, but it simultaneously incorporated the former Monument into an enlarged GTNP. John D. Rockefeller, Jr. and Albright celebrated the victory of their long fought crusade.⁵⁷ Laurance celebrated too, but he also had reason to be concerned about the wildlife park that he and others had worked so diligently to create.

With the JHWP now wholly within a national park, the views and policies of the NPS could not be ignored. From the beginning everyone involved with the Park knew that the NPS opposed its development. Ever since Albright's "zoo" in Yellowstone closed in the late 1920s the agency had progressively turned away from such animal displays. NPS Director Newton Drury quietly expressed his opinion that the "experiment" of the JHWP would fail and thus validate the agency's policy against confinement of wild animals.⁵⁸ Now, in late 1950, Rockefeller felt that the time had come for him to concentrate on other projects but he worried about who would assume responsibility for running the JHWP if he and the NYZS backed away.

1951 experienced a quiet, relatively uneventful beginning. A technical change transpired in May that dealt exclusively with the research station. The organization changed its name from the Jackson Hole Biological Station of the NYZS to the Jackson Hole Research Station of the NYZS (JHRS). On the surface it seemed a mere formality but the simultaneous drafting of a policy statement enhanced the professionalism of the Research Station. Perhaps because of its affiliation with the JHWP, the Research Station declared its main purpose "to promote research in the broad field of ecology with special emphasis on animal behavior." Reflecting the influence of Simon, the policies also stressed the importance of cooperative relationships with colleges and

⁵⁴ Simon Reports, February 15, 1950 and June 15, 1950, Box 18, Folder 16, Blair Papers.

⁵⁵ Fabian to Simon, December 19, 1949, Box 4, Series 10, Folder 5, RG5 GTNP.

⁵⁶ Press Release, Box 2, Folder 1949, Winger Papers.

⁵⁷ Righter, *Crucible*, 140-141.

⁵⁸ *Ibid.*, 130-131.

universities, museums and other institutions, and especially State and Federal government agencies whose responsibilities were tied to the local area.⁵⁹ The formalization of the JHRS and a mid-summer visit to the JHWP by former Gov. Miller caused concern about the future of the wildlife park.

The possibility of the Game and Fish Commission (GFC) taking over the operation of the wildlife exhibit developed over a few short weeks in July. It began with correspondence between former Governor Leslie Miller and Lester Hunt, by then no longer Wyoming's governor but a U. S. Senator. Both men expressed their serious disappointment with the condition of the animal display. Miller reported that when he visited the JHWP just a few weeks earlier the exhibit area did not contain any moose, deer, or antelope, just elk and bison. They shared the opinion that the original purpose of the JHWP, the exhibition of Wyoming's game animals had been supplanted by the research activities. Still convinced that it could "be made one of the greatest attractions for tourists in the whole of the United States..., especially for children," Hunt proposed that the GFC assume control and operation of the wildlife exhibit while leaving the research functions to someone else.⁶⁰

Almost simultaneously, Kenneth Chorley, an officer of Jackson Hole Preserve, Inc. and Rockefeller shared similar thoughts. They discussed the possibility of separating the animal exhibition and research functions, anticipating that Osborn and Simon would assume the management of the Research Station. However, they overlooked any possible interest that the GFC might have in taking over the animal display and instead had planned to approach the NPS. That changed on July 16th when Senator Hunt contacted Chorley and suggested that the GFC, not the NPS, assume control of the exhibit. Almost immediately, Chorley contacted Rockefeller to share the idea presented by the Senator. It seemed the perfect solution, for Rockefeller not only questioned the interest of the NPS but also feared that if the NPS did take over the wildlife display "they would go about it in a half-hearted way, and it would finally just peter out."⁶¹

The proposal was discussed several weeks later during the August meeting of the JHWP Board of Directors. The idea received wide approval. Rockefeller requested the drafting of a letter to the GFC making a formal inquiry regarding its interest level and what conditions might apply.⁶² Miller committed himself to convincing the Commission members of the benefits of the plan, but both he and Hunt anticipated a challenge from Bagley. Known to be fiscally conservative, getting Bagley to approve the allocation of the necessary funds for the undertaking could have been Hunt's biggest hurdle.⁶³

An indirect answer to the question of the acquisition of the animal display of the JHWP by the GFC came on January 3, 1952. On that day the Commission voted to discontinue its financial support, minimal as it had been compared to that of Rockefeller and the NYZS, of the JHWP. John Sherrin, president of the Commission, gave no explanation in his notification of the decision to Rockefeller. But there had been a series of minor conflicts between the GFC and management of the Park that had begun in 1948. When their concerns fell on deaf ears and improvements were not made, the commissioners lost interest in the project. Certainly politics also played a role. Everyone knew of Senator Hunt's support of the Park and of his desire for the GFC to assume responsibility for it. But the commissioners, appointees of the State's current governor and a political foe of Hunt, Frank Barrett, refused to support anything endorsed by Hunt. As long as Gov. Barrett remained in office, and their suggestions and concerns continued to be ignored, the GFC would not approve additional funding for or acquisition of the wildlife exhibit.⁶⁴

A review of Simon's reports to the Board during 1951 and 1952 indicates that the Wildlife Park and the Research Station continued normal operations during this period of uncertainty. The reports contained information about the animals—their condition, the winter feeding program, the number of calves born each spring, the number of animals transferred to other facilities. They explained construction projects, provided Information Center sales figures, reported annual visitation numbers, and

⁵⁹ JHRS Policy Statement, Box 18, Folder 15, Blair Papers.

⁶⁰ Miller to Hunt, July 12, 1951 and Hunt to Miller, July 16, 1951, Box 22, Folder 32, Hunt Papers.

⁶¹ Chorley to Fabian, July 17, 1951, Box 4, Series 4, Folder 1, RG5 GTNP.

⁶² Bagley to All Commissioners, August 28, 1951, Box 18, Folder 16, Blair Papers.

⁶³ Hunt to Miller, July 19, 1951 and Miller to Hunt, July 25, 1951, Box 22, Folder 32, Hunt Papers.

⁶⁴ Minutes: Wyoming GFC, January 3, 1952, p. 448, MA124, Roll 56-33-62, rr 10, dn 1.3, Game and Fish Department, Wyoming State Archive; Simon to Osborn, February 18, 1952 and Osborn to Simon, July 1, 1952, Box 4, Series, 4, Folder 3, RG5 GTNP; Fabian to Chorley, August 28, 1952, Box 5, Series, 14, Folder 2, RG5 GTNP.

described any unusual events. The late spring and early summer reports often told of how severe the preceding winter weather and snowfall had been and gave information regarding the studies to be conducted at the Research Station during the upcoming summer and the awarding of grants. Simon also proudly reported on the publication of any reports that resulted from studies conducted at the Research Station. Either Simon and his staff did not know about the discussions to separate the Wildlife Park from the Research Station or they felt that the situation was out of their hands and went about their work, business as usual.

If Simon really was uninformed, that situation changed in early July, 1952 when he received a confidential letter from Osborn. As president of the NYZS, Osborn worked closely with Simon regarding the activities of the Research Station. Following the decision of the GFC at the beginning of the year to discontinue its financial support and refusal to take control of the game display, Rockefeller began negotiating in earnest with the NPS. By the end of June they had agreed upon a plan whereby the NPS would fund and continue to operate the Wildlife Park and the NYZS would retain control of the Research Station with Simon continuing as its director. Some of the details still had to be negotiated but Osborn anticipated the transfer to occur before the end of the year.⁶⁵

Osborn's timetable proved accurate. In preparation for the transfer, the Jackson Hole Research Station administratively separated from the JHWP in August. Negotiations then concentrated on the division of non-real property. Certain buildings, fixtures, equipment and other assets were assigned to the Research Station. The federal government took possession of the balance of the property needed for the continued operation of the wildlife exhibit through an Instrument of Transfer. At the same time, the JHP formally gave control of the Research Station to the NYZS. The filing of the Notice of Dissolution, stating that "Jackson Hole Wildlife Park, a Wyoming corporation will be dissolved forever," occurred on October 30, 1952.⁶⁶

The legal entity of the JHWP dissolved but the wildlife exhibit continued, at least for a while. Even though the State retained ownership of the

animals, the GFC allowed them to remain on the property under the care of the NPS. In addition, Commissioner Bagley generously offered the Commission's support and assistance to GTNP Superintendent Freeland in operation of the exhibit and any expansion to it that the NPS might undertake in the future. Expansion never happened. And it was not long before Rockefeller's concern about the commitment of the NPS to the exhibit became a reality.

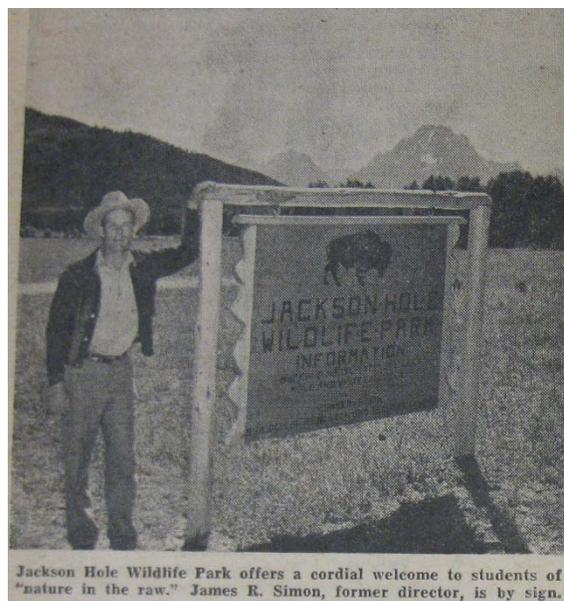


Figure 9. Jim Simon, director of the JHWP, 1946-52.⁶⁷

Arthur Demaray succeeded Director Drury the previous year but he had no intention of reversing the policy against artificial confinement of wild animals. Wildlife management practices in the national parks now fell in line with the beliefs of Olaus Murie and other like minded conservationists. A park ranger, Karl Allan, oversaw the exhibit and cared for the animals for a number of years but over time interest in maintaining the exhibit waned. By the late 1950s the NPS turned its attention to the Mission 66 project, an effort to expand facilities in preparation for the 50th anniversary of the founding of the NPS. Construction of a new visitor center near Park Headquarters in Moose became the major priority for GTNP. In comparison, the wildlife exhibit of the former JHWP was an afterthought.⁶⁸

⁶⁵ Osborn to Simon, July 1, 1952, Box 4, Series 4, Folder 3, RG5 GTNP.

⁶⁶ Historical Chronology, NPS, www.nps.gov/history/history/online_books/npsg/research_station/chronology.htm; Instrument of Transfer, October 15, 1952, Box 4, Series 10, Folder 5, RG5 GTNP; Notice of

Dissolution, October 30, 1952, Box 5, Series 14, Folder 1 RG5 GTNP..

⁶⁷ Photo taken from an article by Carl E. Hayden printed in the Salt Lake Times Home Magazine, November 14, 1954, Series 1, Box 9, Allan Papers.

⁶⁸ Biography, Series 1, Box 3, Allan Papers, AHC.

In 1968, some of the remaining bison broke through a portion of deteriorating fencing, escaping their artificial confines. The descendants of those renegade bison now thrive on their own as the living legacy of the experiment to bridge tourism and conservation. Today's tourists are equally enthralled by the bison, elk, moose, and other animals found in GTNP. They pull off the road to look in wonder and take photographs just as tourists did at the JHWP decades ago.

The controversial wildlife exhibit officially closed in 1972. Conservation research continues at the University of Wyoming–National Park Service Research Center located at the AMK Ranch on Jackson Lake. The NYZS is no longer involved.

◆ ACKNOWLEDGEMENTS

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Figure 6. Park Ranger Karl Allan feeding JHWP bison, c. 1951-55.⁶⁹

⁶⁹ Photograph, Series 2, Box 7, Karl Allan Papers (hereafter referred to as the Allan Papers), AHC.

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MASS-MOVEMENT DISTURBANCE REGIME LANDSCAPES, HAZARDS, AND WATER IMPLICATIONS: GRAND TETON NATIONAL PARK, WYOMING

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✦ ABSTRACT

The Teton Range is the result of active crustal extension (normal faulting) and is the youngest range in the Rocky Mountains at approximately 2 million years old. This makes it a particularly attractive landscape to study, especially in terms of landform development and morphology because of its youth, state of seismic activity, and its recent deglaciation. These factors have combined to produce a unique fluvial landscape in that the fault-shattered metamorphic/igneous rocks of the range have been/are being eroded from their source cliffs at high rates which has covered the glacially scoured valley floors with colluvium such as talus slopes, rock slide, avalanche, and debris flow deposits. This project was focused on the characterization of all forms of mass movement, especially rock slides, multiple talus types (rockfall, alluvial, avalanche), protalus lobes, protalus ramparts, lobate and tongue-shaped rock glaciers, and their collective effects on water retention and its late-season delivery in the Grand Teton National Park, WY. A major goal of this project was to reclassify many of the mass movements in the park in an effort to streamline and simplify previous efforts by other scientists. Methods used during this study included field reconnaissance and measurements acquired during the summers of 2010 and 2013 and measurements taken from various datasets (NAIP imagery, shape files used within a GIS [ArcMap 10.0], and Google Earth™). Mass movement deposits, as well as ice glaciers and long-term snowbanks, were mapped and interpreted. Overall conclusions are that the major sources of mass movements from the Archean crystalline core of the range are the result of extensive jointing, fault-shattering, increased frost-wedging at higher altitudes, slopes steepened by prior glacial erosion, and extensive snow avalanches. Areas

of Paleozoic sedimentary rocks marginal to the crystalline core produce rockslides as a result of steep dips and unstable shales beneath massive overlying carbonates. The presence of internal ground ice enables development of protalus lobes, thicker rock-fragment flows, and thinner boulder streams. Such ground ice is likely to enhance late-season water delivery downstream unless climate warming and recurrent droughts become too extreme.

✦ INTRODUCTION

The role of rockslides-rock avalanches in mountain landscapes has been well documented in Himalayan, Alpine, and some Rocky Mountain regions (Hewitt 2006, Shroder 1998a,b, Shroder and Bishop 1998, Shroder et al. 1999, 2010, 2011). Although the abrupt slope failures themselves are extremely short-lived events, the persistence of rock-wall detachment scars and the various deposits themselves can persist for long periods as influences on water diversion and impoundment, fluvial and lacustrine sediment retention, sediment H₂O storage as fluid (water) and solid (ice), and the release of occasional landslide lake outburst floods (LLOF). In addition the more incremental or slower accumulation of collateral mass-movement deposits, such as talus, alpine debris flow cones, snow avalanches, and some rock glaciers and boulder streams with internal ice permafrost also can have both similar and different effects.

The Teton Range is an area of high relief, containing high-gradient drainage and amplified rates of, often catastrophic, colluvial activity. High altitude snowfall (~2 km) is generated as moist Pacific air masses are uplifted over the mountain barrier (Foster

et al. 2010). These streams are essentially derived from melt-waters of fresh annual snowpack, firn fields, and remnant glaciers of the late Pleistocene. Because the area is nearly deglaciated, excepting small vestiges of past sizable glaciers (the Teton glacier, etc.), Teton Range trunk-streams are “misfits” or “underfit”, in that they are presently too small to have created the valleys they occupy (Huggett 2007). Mass movement processes such as debris flows, avalanches, and rockfalls / rockslides occur at extremely high rates in Teton Range. This high-frequency of mass movement is largely due to tectonic and climatic forcing, coupled with the effects of variable rock types and weathering, and post-glacial debuttressing of valley walls. These colluvial processes further complicate / perturb the “misfit” fluvial regime with high and frequent debris / rock inputs which overload or even dam streams, causing epicyclical responses (Hewitt, 2006) to the constant / chaotic inputs of mass movement.

This situation of continual or extended disruption of a fluvial regime has been discussed by Hewitt (2006) as a “disturbance regime”, which refers to “the long-term or permanent consequences of relatively brief, but reoccurring episodes, usually of high magnitude or at critical sites”, which produce landforms “whose location and history and are dependent on the disturbances” (Hewitt 2006, p367). According to Hewitt (2006, quoting Benda et al. 2003), the landforms of a disturbance regime “tend to be polygenetic and exhibit morphological heterogeneity”, also called “patchy heterogeneous morphologies” (Burchstead et al. 2010). Though Hewitt was mostly concerned with mega-scale rock avalanches, or sturzstrom (Shroder and Weihs 2010), the same phases of the landslide interruption epicycle are observable in Teton canyons.

Teton Range canyons / streams fit under the classification of “a disturbance regime landscape”, in that there is an abundance of frequently occurring mass movements that are clearly affecting the centerlines of trunk-streams. It is the primary goal of this paper to describe and explain selected examples of trunk-stream positions in terms of their incongruence / congruence with glacial trough centerlines, and the disturbances which have affected their locations in the Teton Range.

Problem statement

Studies concerning the role of various mass movements and their effects on water delivery are well documented in other ranges such as the Himalaya or

other Rocky Mountain ranges; however, colluvial stream disturbances have not been explained or described for the Teton Range.

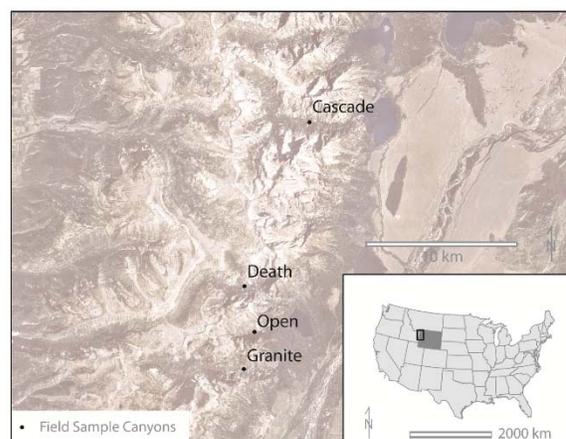


Figure 1. Study area canyons of Grand Teton National Park.

Purpose and objectives

The purposes and objectives of this study were to:

1. Begin with Marston et al.’s (2010) prior funded seminal work for UW-NPS Research Center on cross-valley profiles and mass-movement hazards in deglaciated canyons of Grand Teton National Park as a fundamental basis for further geomorphological mapping.
2. Apply Hewitt’s (2006) methodology for recognizing landslide interruption epicycles in mountain valleys in the Grand Teton National Park, specifically Cascade, Death, Open and Granite canyons (Figure 1).
3. Adapt the landslide interruption epicycles of Hewitt (2006) to small discharge canyon streams in Grand Teton National Park as paradigmatic examples of mass-movement control of small-basin alpine drainages (Shroder et al. 1999).
4. Develop an overview of ground-water and ground-ice retention in Teton alpine valleys relative to mass-movement deposits as porous and permeable aquifers, as well as partial aquitards to surface flow.

Significance

Mass movements, glaciers, and rock glaciers in GTNP affect water delivery throughout the park, can pose hazards to park users, and are known to create

long and short term changes in the park landscape. Because mass movements, glaciers, and rock glaciers largely dictate water releases downstream, it is imperative that data be created about their character and the manner in which they affect the fluvial regime. Additionally, because these features are often hazardous to humans, studies that investigate their genesis and continued evolution are warranted in the interest of park safety.

✦ BACKGROUND

The Teton Range is the result of active crustal extension or normal faulting, and is one of the youngest ranges of the Rocky Mountains. Although movement on the Teton Fault began ~9 mya, the Teton Range itself is essentially largely Quaternary-aged (i.e. perhaps only ~2 million years old) (Smith et al. 1993, Byrd et al. 1994). Fault scarps and associated stratigraphy reveal Holocene slip rates of 0.45 – 1.6 mm/yr for the Teton Fault that are consistent with a range of recurrence intervals for large, scarp-forming earthquakes of 1600 to 6000 yr. Hampel et al. (2007) have even hypothesized that the post-glacial slip rates on the Teton Fault increased as a result of melting of the Yellowstone ice cap and deglaciation of the Teton range. The influence of high ground accelerations associated with large earthquakes was judged as particularly important in the Teton region by Smith et al. (1993).

Mass movements in the Teton Range are profuse, and much of the valley floors of the range are blanketed by the deposits of various forms of mass movements that occur above (rockfalls, rockslides, debris flows, avalanche, etc.). Case (1989), in his original aerial photographic mapping of landslides of Wyoming, was able to delineate the greater proportion of the state's slope failures, but given the massive size of the undertaking without enough (or any) field checking for accuracy in mapping, inevitable omissions or errors accumulated. Mass movements come in a great many variable types, which over time, weathering, soil formation, and revegetation, can become obscured as to genesis. The prior work of Marston et al. (2010), which used Case (1989) as an initial base map in five canyons (Paintbrush, Cascade, Garnet, Death, Granite), provides a foundation for mapping of the existing deposits which were omitted/not recognized, misclassified, and/or delineated inaccurately. According to Marston et al (2010), because a propensity of mass movement deposits in GTNP are found below Pinedale glacier trimline positions, glacial debuitressing has played a large role in mass movement deposition since the most

recent glaciation. Already in the European Alps, the western Himalaya and elsewhere, degradation of rockwall permafrost is thought to have caused some rock failure such that formerly frozen surficial fracture systems no longer retain bearing strength, thus spontaneously failing (Arsenault and Meigs 2005, Cossart et al. 2008, Stoffel and Huggel 2012).

The Pleistocene glacial history of the Teton region has been worked out in fair detail by Pierce and Good (1992), Licciardi and Pierce (2008) and a number of others. Old glaciations, perhaps from the early and middle Pleistocene, are known to have occurred in the Jackson Hole region but their record is poor and whether or not they occurred in the rising but lower altitude Tetons of the time is unknown. The oldest, fairly well understood Munger (Bull Lake?) filled all of the Jackson Hole valley with ice from about 157 to 151 ka, until about 136 ka (Pierce and Good 1992, Licciardi and Pierce 2008); Precambrian crystalline rocks from the Tetons in the tills and moraines in Jackson Hole show it is likely that cirques and valleys from the Tetons were also filled with ice at this time. During the succeeding Pinedale glacial, ice advanced from highlands into Jackson Hole from the east, northeast, and north, perhaps because of storms moving up through the Snake River Plain in the Idaho region and building up the Yellowstone ice cap. Glaciers of the Teton were smaller, although they did join the south-flowing Snake River Lobe of that ice north of Jenny Lake. To the south of there, however, end moraines of valley glaciers from the Tetons extended no more than 2.5 km beyond the mountain front. The precise timing of the Pinedale glaciers from the Tetons has recently been constructed with cosmogenic dating of boulders and glacially striated bedrock at about 14 ka (Licciardi and Pierce 2008), but some radiocarbon dates indicate Pinedale ice as late as 9000 yr, perhaps persisting to warm altithermal time around 6000 years ago (Love et al. 2003) when it would have all melted away in most of the lower Teton Valleys. This 14,000 to 9000 year estimation of the melting away of Pinedale ice in Late Pleistocene to Early Holocene time is important because it would be the approximate beginning time for emplacement of the post-glacial, mass-movement debris in the valleys of the Teton landscape. Prior to that time, of course, all mass-movement debris from the valley sides would have fallen on the glacier ice of the time and been transported to the mountain front where it would have contributed to the end moraines encircling the lakes of Jenny, Bradley, Taggart, and Phelps, as well as the mouths of Glacier Gulch and Open Canyon (Love et al. 2003).

The relative youth of the Tetons makes them a particularly useful place to study in terms of landform development and morphology, recent deglaciation, and state of seismic activity, which can be expected to produce significant mass movement through valley wall deglacial debuttressing as the last of the Pinedale ice melted away, as well as horizontal seismic accelerations to the glacially oversteepened valley walls. Foster et al. (2010) noted that the tall, steep hillslopes of the Teton canyons provided shading, as well as plentiful snow influx from avalanching, and insulating debris cover from rockfalls to the valley floor glaciers. Tranel et al. (2011) found that the large talus and mass-movement aprons in some places indicate that the interglacial alpine fluvial system is locally transport-limited and unable to keep pace with the mass movement. The thick mass-movement fans may also enhance chemical weathering of the bedrock beneath them by trapped ground water which would have thereby facilitated periodic glacial incision or fluvial transport during peak flow conditions.

These factors have combined to produce a unique post-glacial, fluvial landscape in that the fault-shattered, metamorphic and igneous, crystalline rocks of the range have been/are being eroded from their source cliffs at high rates that have covered the glacially scoured valley floors with colluvium such as talus slopes, rockslides, avalanche debris, and debris flow deposits. These colluvial deposits have apparently caused the centers of “trunk” stream channels to be variably incongruent with the glacially eroded valley centers.

✦ STUDY AREA

Location

The Teton Range is located in northwestern Wyoming at about latitude 43° 46' 46" N longitude 110° 50' 10" W. The range is approximately 72 km long and 20 km wide and is flanked by the south-flowing Snake River ~10 km to the east and by the Wyoming / Idaho state border ~5km to the west (Figure 1). The Tetons are the first topographic barrier to moist Pacific air masses moving through the western Snake River Plain (Foster et al. 2010). These conditions favor orographic uplift of moist air masses that in turn drop large (modeled at >200) amounts of precipitation high in the range (Foster et al. 2010). This situation has created “elevated peaks high above the surrounding topography” (Foster et al. 2010), or “topographic lightning rods” (Brozović et al. 1997, Foster et al. 2010).

Quaternary chronology

The chronology of glacial and other landforming events in the Tetons and Jackson Hole area has been evaluated by a succession of scientists who were impressed with the abundance of glacial, fluvial, mass-movement, and faulted landforms that occur in the area. Plentiful cirques high in the Tetons, glacierized and glaciated valleys with striking parabolic cross sections, prominent terminal and recessional moraines, strong river terraces, extensive and pervasive, polygenetic talus slopes and rockslides, and fresh fault scarps at the front of the Teton Range that truncate lateral moraines; all of these landforms have generated the impressive and iconic landscape of the Grand Teton National Park in western Wyoming. When the first government-sponsored surveys first came to the region from the 1870s to 1900, early researchers noted that glaciers had produced piedmont lakes impounded by morainal material (Bradley, 1973), and the fluvial terraces along the Snake River were related to glacial outwash (St. John 1877). Blackwelder’s classic work in 1915 established the Buffalo, Bull Lake and Pinedale glacial stages from recognition of moraines near Togwotee Pass into Jackson Hole and glaciated valleys on the north and south sides of the nearby Wind River Range. Fryxell (1930, 1935) then successfully applied Blackwelder’s glacier-stage nomenclature to the Tetons and Jackson Hole area and his application of the terminology has stood the test of time.

Most recently Pierce and Good (1992) and Licciardi and Pierce (2008) carried the Quaternary chronologies forward and updated them with fairly precise cosmogenic exposure-ages of the Bull Lake and Pinedale glaciations in the Teton Range and Jackson Hole areas. One of the primary changes between the older work and the newer is the attribution of a lesser role to glaciers from the Teton Range and an enhanced role to the southern part of the Yellowstone ice mass. Boulders that occur along the southern limit of the penultimate ice advance in Jackson Hole give erosion corrected ages of 136±13 ka, with oldest ages of 151-157 ka that correlate with Marine Isotope Stage (MIS 6), as well as with Bull Lake glacial deposits of the Wind River range and West Yellowstone. The timing of the next major glacial advance in the region is the Pinedale (MIS 2) with maxima varying from ~18.8 to ~16.5 ka, to possibly 14.6ka around the southern margins at Jenny Lake. Late Pinedale events in the Teton – Jackson Hole region suggest that major advances or stillstands of a large valley glacier from the east flank of the Teton Range occurred > 6kyr after the global Last Glacial Maximum (LGM) just prior to the younger

Dryas, followed by full and rapid deglaciation of the whole Yellowstone Plateau.

An important observation is the strong climatic gradients observed between the floor of Jackson Hole to the east and deeper into the mountains to the west as a reflection of the westerlies and the resulting rain-shadow gradients. For example (Pierce and Good 1992), the mean annual precipitation at Jackson is only about 4.3 cm, whereas only 10 km west at Wilson it is about 10 cm.

◆ METHODS

Field reconnaissance

Each mass movement deposit visited in the field was visually observed and photo documented. For some deposits, such as the Rendezvous rockslide, observing both the headscarp and toe was possible (because it was accessible), providing more comprehensive field data for those deposits. Slope angles of deposits were measured using an Abney hand level where vegetation was permitting. Dipping strata were measured with a Brunton pocket transit. Water output from mass movements was measured qualitatively where possible, such as return flow from a landslide's toe.

Geomorphological mapping

Combined with data collected in the field, geomorphological mapping was concluded in the laboratory using ArMap 10.0. Several data were used to map/delineate and describe landforms under study. These data included (but were not limited to):

- National Aerial Imagery Program (NAIP) imagery (2012, 2009) ~1m resolution
- National Elevation Dataset (NED) ~10m resolution
- Geologic Map by Love et al. (1992)
- Landslides of Wyoming shapefile by Case (1989)
- Google Earth™ imagery

In general, field and lab-discovered mass movements, protalus lobes, glaciers, rock glaciers, and slow rock fragment flow deposits were digitized using NAIP imagery and aided by Google Earth™. The digitized outputs (a shapefile) were then accoutremented with attribute data such as mean elevation and mean deposit aspect. This attribute data was subsequently used in Excel 2010 to produce summary statistics of the various deposits.

Landslide interruption cycle identification

The Hewitt (2006) landslide interruption cycle of five phases, each with variable sediment assemblages, constitutes the *landslide-interrupted valley landsystem*, which will be utilized as the theoretical background for the primary mapping tool. As Hewitt (2006) has noted, this type of landsystem creates naturally fragmented fluvial systems in which a *disturbance regime geomorphology* can be identified. The five phases to be identified are: (1) *Landslide complex*, with associated mass movement emplacement forms (rock slide, rock fall, debris flow, etc.) (Shroder et al. 2005); (2) *Impoundment complex*, with associated aggradation and constructional landforms upstream of the barrier, and possible downstream erosion and/or sedimentation; (3) *Degrading interruption complex*, with trenching and removal of the impoundment complex and downstream sedimentation; (4) *Superimposed interruption complex*, with exhumation of buried valley fill and incision into pre-landslide valley floor; and (5) *"Shadow" interruption complex*, with minor but persistent legacies of interruption, mainly bedrock forms.

The application of Hewitt's (2006) landslide interruption cycles to landforms in the Teton Range involved:

- Modifying of the landslide interrupted valley landsystem to reflect the different nature of the Teton mountain valleys from those in the western Himalaya with large-discharge rivers in them where the landsystem categorization was first developed.
- Differentiating landslide impoundments from paleo-beaver dam impoundments, or even paleo-beaver dam modification, or augmentation of a prior mass-movement impoundment.
- Mapping the locations of streams running

over bedrock, as opposed to other kinds of sediment covering bedrock where possible in the field.

- Differentiating between the kinds and sources of the sediment covering the bedrock.
- Insofar as possible, estimate grain size, thickness, and porosity/permeability by visual inspection as well as to enable a first approximation of hydraulic retention and conductivity for ground water estimations.
- Estimate ground ice on the basis of surface morphology (rock-glacier and boulder lobe characters and profiles).

✦ PRELIMINARY RESULTS AND DISCUSSION

Geomorphological mapping

Efforts to expand and correct/reclassify previous mapping done by Case (1989) and Marston et al. (2010) resulted in many new, or corrected, delineated deposits. This study identified 57 features (glaciers [10], rock glaciers [20], protalus lobes [22], slow rock fragment flows [3], rockfall talus [1], and a single slump block). Some of these features were not previously mapped by Case (1989) or Marston et al. (2010) (2 protalus lobes and 1 rock glacier). There were also some features from Case (1989) that required reclassification based on field and laboratory findings. These reclassifications were performed for protalus lobes, rock glaciers, and slow rock fragment flows that were purported by Case (1989) to be something different. In total, there were 12 deposits in which there were discrepancies between Case's (1989) and this study's findings. Because of the use of DEMs, high resolution imagery of various dates and digital globes such as Google Earth™, our findings are more resolute than Case's (1989) work, which was limited by the use of aerial photography and sporadic fieldwork, if any.

Landslide interruption epicycles

Our preliminary assessments of the canyons selected for this study indicate a number of examples of phenomena which will be useful in applying the Hewitt (2006) designations. For example, Phase One (emplacement) and Phase Two (impoundment) can be observed in Cascade Canyon where a debris flow has

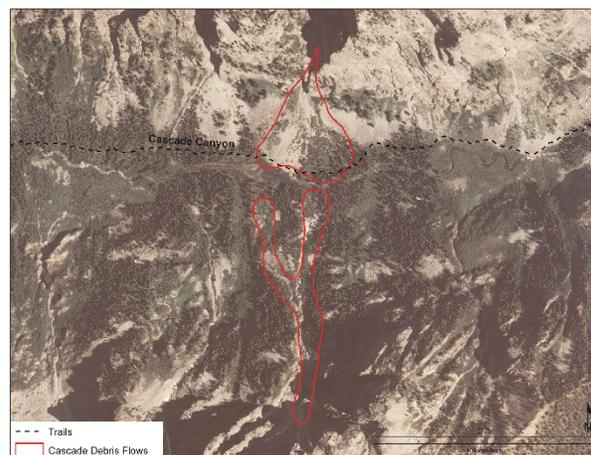


Figure 2. Planimetric view of opposing debris flow deposits and subsequent impoundment in Cascade Canyon using NAIP aerial photo (2009).



Figure 3. Planimetric view of a rockslide deposit and subsequent impoundment in Leigh Canyon using NAIP aerial photo (2009).

emplacement of the landslide, or limited discharges may have precluded significant downcutting and lateral erosion to take parts of the valleys into the more advanced stages of Hewitt's classification scheme. The Rendezvous Rockslide in Granite Canyon (Figure 4) may fit some of the criteria for Phase Four in that the impoundment area has been drained and slightly incised; however, the incision is limited to the lake sediments and not the bedrock beneath. No evidence of Phase Five (epigenetic gorges) were observed during this study. It is likely that the scales of Teton processes (such as mass movements and water discharge) and time since the most recent deglaciation have not been of sufficient magnitude to produce the landforms that Hewitt (2006) found in the much older and larger-scale Himalayas.

Rendezvous rockslide

The Rendezvous Rockslide is a large slope failure on the northwest-facing side of Rendezvous Mountain above Teton Village near Jackson Hole, WY. It can be accessed from the top by an arduous and dangerous descent from the tramway ride stop at the top of the ski area, or from the trail up Granite Canyon to the toe of the failure in Granite Creek. The slope failure descends from an altitude of about 9600 feet (2925 m) on a generally northwestern trajectory, down to an altitude of about 7880 feet (2400 m) in Granite Canyon, which is a descent of about 1720 feet (525 m) vertically downward in about 1.2 mi (2 km) downslope (Figures 4 and 5).



Figure 4. Planimetric view of Rendezvous Rockslide using NAIP aerial photo (2009). Adjacent photos are located on map with red X's. Several lobes (1, 2, 3) are thought to represent at least three separate failure events contributing to this deposit.

The bedrock geology map of the region (Love et al. 1992) shows that the direct or proximate cause of the landslide was the presence of the massive carbonates of the Gallatin Limestone, Bighorn Dolomite, and the Darby Formation that occur above and overload the unstable Park Shale Member of the Gros Ventre formation (Love et al. 2007). The combination of the weight of these overlying formations totaling some 980 feet (300 m) of thickness, as well as the $\sim 20^\circ$ angle of dip to the northwest down into the Granite Canyon valley, and the abundant precipitation and high freeze and thaw of the mountain environment have combined to produce the slope failure.

The uppermost main scarp of the slope failure at the top of the Rendezvous Mountain ridge has been eroded down to a low rounded ridge at about 9560 feet (2914 m) that is only about 160 feet (48 m) high, but on the nearby left (west) flank of the landslide the huge

cliffs of Gallatin Limestone, and Bighorn Dolomite rise some 600 feet (180 m) above the surface of the landslide, where major rock blocks have been provided to the failure. Furthermore, about halfway down the lateral west margin of the landslide, a second major lateral scarp cliff of dominantly carbonate rocks of the Darby Formation also rises a similar amount in huge cliffs.

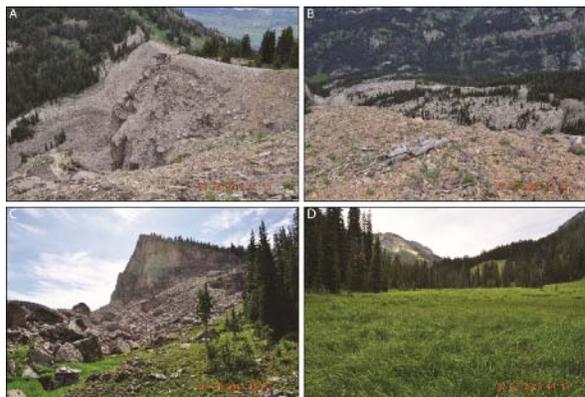


Figure 5. Photos taken at Rendezvous Rockslide. Photos A and B taken at head scarp. Photo C was taken at midslope and margin of landslide. Photo D was taken at the landslide toe, which caused impoundment of Granite Creek and the deposition of sediments in this now-drained lake.

The overall surface of the landslide mass is a hummocky rolling terrain, with several undrained depressions, one of which holds an intermittent small lake and grassy area in the upper third of the mass, about 580 m down from the top of the slide. The depression appears to hold water for at least part of the year as a result of the presence of impermeable shale remnant masses that outcrop around the depression. The landslide measures about 2 km in length and is about half a km wide in the middle and lower sections, although it is only about 0.2 km wide at the narrower top. The uppermost part has a considerable amount of remnant shale exposed in heaps and mounds where it has been forced by the presumably repetitive slope movements. The lower two thirds of the landslide mass has plentiful large boulders, ten of which were measured on Google Earth™ and found to average ~ 21 m in diagonal long axis. Midway down the slope failure on the left (southwest) flank where a change in movement direction occurs from WNW to NW, two offsetting shear planes daylight at the margins to form two stepped terraces, each about 10 m high, the risers of which are the surface manifestation of the shear planes. It is apparent that the main mass of the slope failure has subsided here to show the shear planes.

The lowermost toe of the Rendezvous Rockslide is estimated to be at least 60-80 m thick (perhaps thicker), and appeared to be comprised of at

least two main episodes of movement, one above and overriding the other. The lowermost part of the toe was composed of large boulders, the interstices of which appeared filled with weathered debris and soil, whereas the uppermost part of the toe appeared to have a dominance of open matrices, with far less weathering degradation. This lowermost and apparently older toe is conspicuous in having a plentiful forest cover of large, old-growth conifers that are well-rooted in the weathered soils that have developed throughout the lower portion of the mass. Although no date estimates could be obtained from soil thickness measurements in the limited time available for investigation, it is possible that these two movement lobes may represent dominant movement during times of greater precipitation and/or permafrost degradation at the end of the Pleistocene or early Holocene. Presumably, the slope failure would not have been active because it was frozen during Pinedale glaciation and any prior mass movement would have been removed by glacier ice in Granite Canyon, but in the subsequent melting away of Pinedale ice, and the unstable climate associated with the Little Ice Age in late Holocene, other movement could have occurred.

The Rendezvous Rockslide was low velocity as it moved slowly and most probably intermittently down into Granite Canyon but did not climb the north side of the canyon at all. In all probability the mass was comprised of many small and independent motions that collectively brought successive masses of rock fragments of the Paleozoic rock fragments to lower positions in the valley over multiple years of rock motion, more in wetter years, and less in drier. The hydraulic associations of the Rendezvous Rockslide are unknown, although it is likely that almost all of the precipitation that falls upon the feature infiltrates downward through the profuse open porosity between the plentiful boulders and becomes groundwater. Much of this water would have been absorbed by the shales lower down and contributed to their plasticity. The basal slip surface(s?) of the landslide appear to be largely on the uppermost Death Canyon Limestone Member of the Gros Ventre Formation.

The overall slope of the outer landslide surface is about 13° , which compares with the generalized dip of the bedrock at this location of $\sim 20^\circ$. The $\sim 7^\circ$ difference in amounts can be explained by the landslide accumulating mass in the valley below, which would reduce the overall surficial gradient. It is thus apparent that the cause of the slope failure was the incompetence of the Park Shale, which permitted the motion of the landslide to run largely along the bedding planes at the top of the Death Canyon

Limestone. This latter rock unit forms a prominent planar shelf of resistant bedrock that is characteristic of much of the high topography elsewhere on Rendezvous Mountain (shown in Figure 30 of Love et al. 2007), as well as the head of Death Canyon, where it forms a prominent landform of conspicuous size that is known as the Death Canyon Shelf. This feature extends southwest-northeast laterally within the Grand Teton National Park for over 5 km, averaging some 300-400 m in width with conspicuous rockfall talus and protalus lobes along it with conspicuous rockfall talus cones and protalus lobes and ramparts that have developed from the rock fragments emanating from extensive freeze and thaw of the rock cliffs of Big Horn Dolomite and Darby Formation rocks outcropping along it.

The toe of the Rendezvous Rockslide partially blocked the course of Granite Creek that runs in the bottom of Granite Canyon, which caused upstream aggradation and the deposition of a flat plain of finer clastics (gravels, sands, silts, and clays). The aggradational plain extends upstream for ~ 450 m and ~ 200 m in width and is covered with sedges, grasses, and willows in between the multiple channels of Granite Creek that have developed over the aggradational plain. In the bottom of Granite Creek stream channel, swirls of ascending sand-grain plumes attest to water under pressure from below that is rising into the channel from shallow groundwater base flow that comes in from uphill water sources, probably from both sides of the canyon; landslide source on the southwest side, as well as the opposite northwest side where water can also infiltrate into the low gradient slopes there.

The Rendezvous Rockslide is a reasonably typical type of slope failure that is fairly characteristic all over various parts of Wyoming in other uplifted mountain terrains where the carbonates and shales of the Lower Paleozoic produce similar mass-movement landform features. For example, at the head of Shell Canyon in the western Bighorn Range, a similar suite of rocks has produced even larger and more pronounced failures of the bedrock, with extensive glide blocks, rockslides, and slow-flow features under similar structural conditions of dipping carbonates and shales at moderate to higher altitudes.

Alpine debris cones and fans

The alpine debris cones and debris fans emplaced in the many canyons of the Grand Teton National Park have been formed by a variety of processes that require considerable elucidation to

delineate process and form in such a fashion as to serve as explanatory templates for similar assessments in other mountain ranges. Certainly such work has been undertaken in many other environments such as in the European Alps, the Canadian Rockies, the Colorado Rockies, the Himalaya, and elsewhere, but still a refresher look at the features can be instructive, particularly where common polygenetic overprinting of process and form can cause misinterpretation. All of the alpine mass movement forms can constitute a variety of talus accumulations that originate solely, or by some combination of falling rock fragments, running water from rainstorms or snow melt on mountain slopes, or by snow avalanches (White 1981). These accumulations of alpine debris form in cones or fans at various angles of repose, from the steep ones at $>35^{\circ}$ - 45° for **rockfall talus**, to 35° - 38° for the upper slopes $<28^{\circ}$ for the talus toes of **alluvial talus**, and $<25^{\circ}$ for **avalanche talus**, which also has gently concave-up toes where the snow avalanches sweep out. In addition, talus subtypes occur of the more strongly developed **avalanche boulder tongues** or avalanche roadbank tongues, and the **protalus ramparts** with rock fragments that move out over snow banks to pile up as ridges at the base of talus slopes (White 1981). All of these constitute what can be quite polygenetic forms of alpine talus that is emplaced in what has been considered a reasonably non-catastrophic fashion, wherein most of the rock clasts come down as isolated unit rockfalls and slides, or are emplaced by snow avalanches, or by isolated rivulets in rainstorms (Figures 6 and 7).

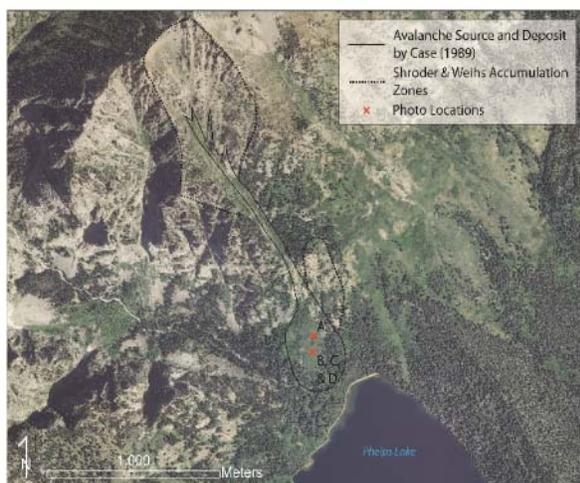


Figure 6. Planimetric view of Death Canyon avalanche source and deposit using NAIP aerial photo (2009). Avalanche polygon delineated by Case (1989) (solid line) was modified in this study (dashed line). Adjacent photos are located on map with red X's.



Figure 7. Photos taken in and near Death Canyon of an avalanche source and deposit. Figure A shows source area. Figure B shows large boulder transported during 2010-2011 avalanche season. Figures C and D show still growing downed trees beneath boulder and on deposit area.

This reasonably non-catastrophic emplacement is contrasted with the truly catastrophic, very rapid, and large forms such as the larger rockfall debris streams, rock avalanches, or sturzstroms, rock slides, debris slides, or the large slump-earthflows and large slow debris flows that are so characteristic of areas with extensive and weak sedimentary rocks. The Teton Range has a sedimentary rock cover of Lower Paleozoic shales and carbonates to the west and south that lap onto the Precambrian crystalline rocks at the core of the upfaulted block that constitutes the highest portions of the range (Figure 8). These sedimentary rocks, with their unstable shales beneath massive carbonates, are the main source of rock rubble that makes up the widest variety of mass movement in the outer fringes of Grant Teton National Park. In the high core of the range, however, the crystalline rocks of gneisses, granites, amphibolites, metagabbros and the like are not as conducive to the formation of large mass movements as are the less stable sedimentary rocks, but still the extensive jointing, fault shattering, steep slopes, and higher altitudes that promote considerable freeze and thaw can also contribute large quantities of rock rubble that are commonly remobilized into extensive talus cones and fans, as well as the glacier moraines, rock glaciers, protalus lobes, and the like that characterize much of the range. Unlike the Himalaya and Hindu Kush where the relief and steep slopes are so much greater and high seismicity and massive rock avalanches from crystalline rocks abound (Shroder and Weihs 2010, Shroder et al. 2011), large rock avalanches have not been mapped in the Tetons, although a variety of large failures of sedimentary rocks are known. The nearest known seismically induced rock avalanche or rapid rockslide was the one across the Madison River in 1959 125 km NNW of the Teton Range that was

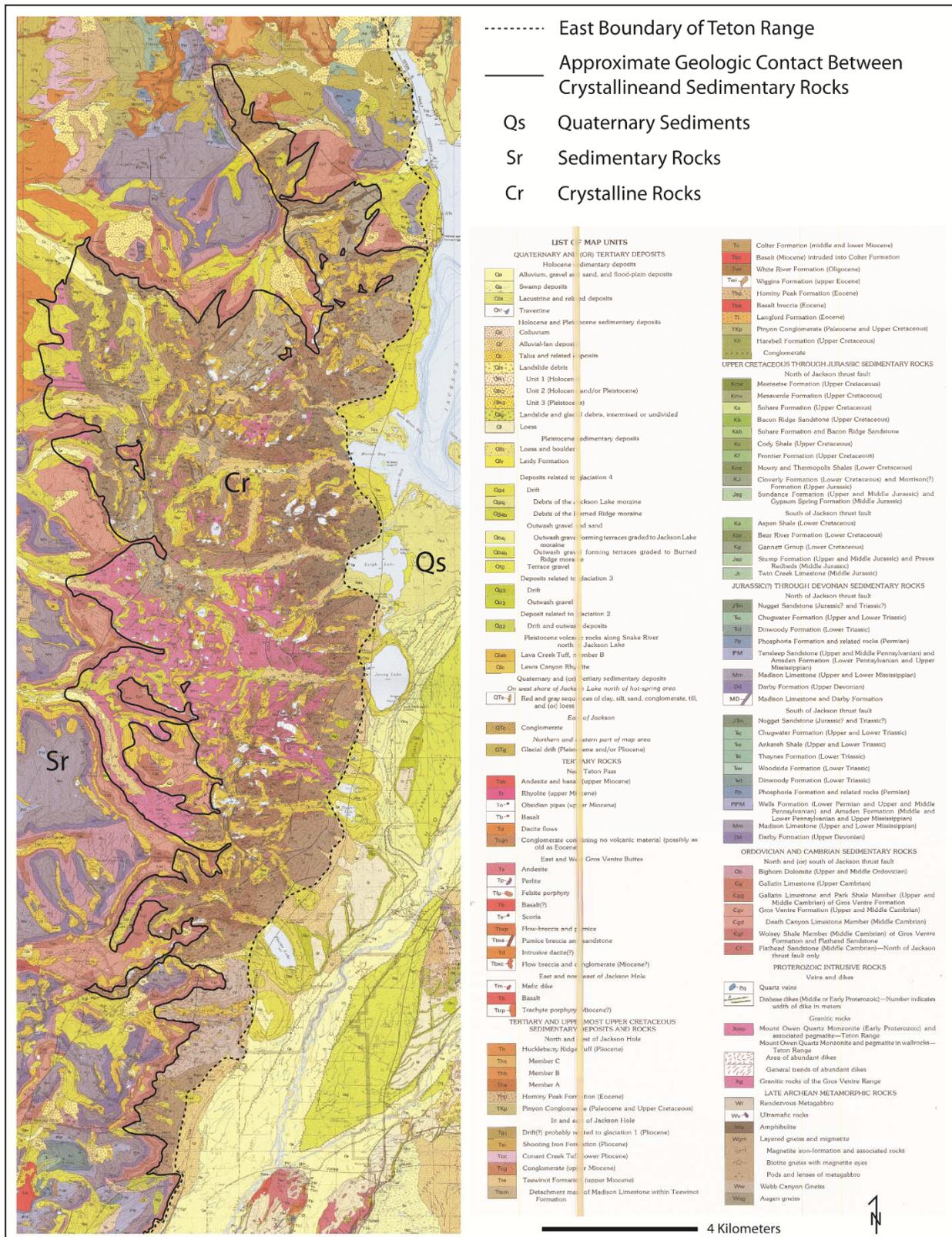


Figure 8. Geologic map of the Teton Range. Modified from Love et al. (1992).

produced by a magnitude 7.5 earthquake. The well-known Gros Ventre Rockslide of 1925 that occurred just 20 km east of the Teton Range was caused mainly by increased shear stress exerted from excess snowmelt and rainwater loading, coupled with the Tensleep Sandstone overlying Amsden shale dipping into the Gros Ventre River valley where the river had previously undercut the slope and thereby reduced shear resistance. Numerous other slump, slow debris flows and earthflows are known in the general region as well, mainly from combinations of weak and dipping sedimentary rocks and plentiful precipitation that loads slopes with heavy surcharge weights, dissolves cements, causes extensive freeze and thaw, brings in seepage pressures, and causes friable shale to lose strength, which collectively results in many slope failures.

Glaciers and rock glaciers

Glaciers are masses of permanent snow and ice that move slowly downhill under the influence of gravity, and rock glaciers are similar masses of ice that are completely or largely covered with rock fragments, which obscure the ice cores or interstitial ice cements beneath. Rock glaciers are distinguished from other forms of alpine debris by having steep fronts at the angle of repose that are caused by the top moving faster than the base, with the result that the rock fragments pile up steeply at the front (Giardino et al. 1987). The formation of glaciers occurs as winter snows accumulate to such an extent that all of the winter's accumulation does not melt entirely away each summer, and instead some snow converts to crystalline firm or pellets of ice that last through the melt season into the next winter. After the passage of some 3 – 5 years, the mass of stored ice can become sufficiently large so as to begin flow downhill as an ice glacier. Rock glaciers can begin formation as either masses of rock fragments into which meltwaters drain and refreeze to reconstitute as interstitial ice cements. They can also begin as masses of snow and ice in snow banks, or even ice glaciers that become covered with so much rock debris that the original snowbank or glacial origin can be lost and the masses come to move downslope through various causes of freeze and thaw or permafrost creep, but always with steep fronts of rock fragments at the angle of repose. Talus slopes can fill with such expanding interstitial ice to bulge out at the bottom as protalus lobes, which if developed to an extent that the projection of the talus slope down to the horizontal is greater than the projection of the lobate front down to that same plane, then the feature is considered to be a protalus lobe, but if the lobate

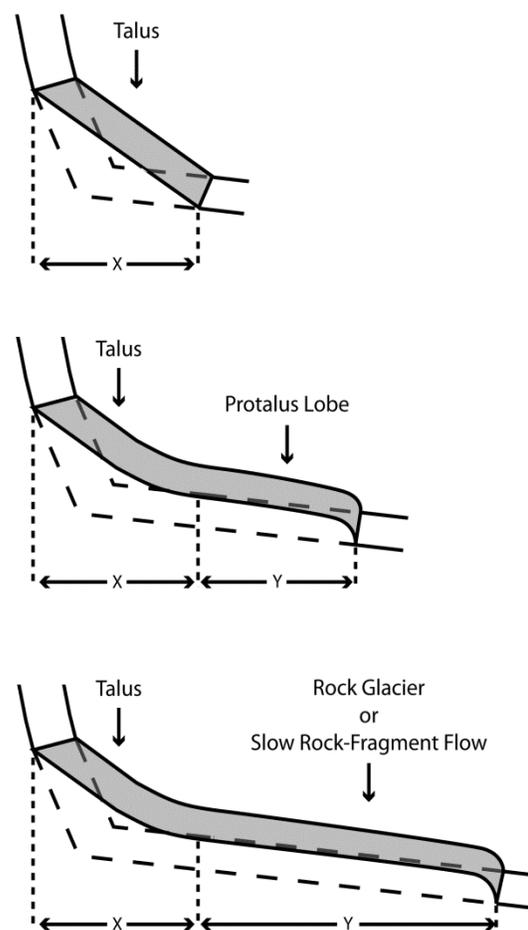


Figure 9. Generalized graphic of talus slopes, protalus lobes, and rock glaciers or slow rock-fragment flows.

front bulges out and travels further than the projected talus extent, then the feature is a lobate rock glacier (Figure 9). On the other hand, the ice-cored rock glaciers can commonly form from the overall downwasting of the ice glaciers until all, or almost all, of the original ice is covered up and the true glacial nature of the feature is lost. A renewal of cold temperatures or development of greater refreezing of the down-trickling meltwaters from snow melt or the like can then cause the ice core to push the terminus of the feature forward again so that a steep front of rock fragments at the angle of repose develops, at which point a tongue-shaped rock glacier with an ice core has formed.

Because both glaciers and rock glaciers represent ice resources stored away for different amounts of time until finally melted, they constitute important sources of meltwater when finally converted from solid into liquid at some point in their history.

Thus in Grand Teton National Park, it is important to better understand the hydrologic cycle as it is constituted in the region, especially if this hydrologic cycle changes greatly in coming years due to climate warming and drying.

Most of the glaciers recognized in the Teton Range have a north or east aspect, with the exception of Falling Ice Glacier on Mount Moran, which faces to the southeast. All these recognized ice glaciers occur on the east side of the range (Fryxell 1935), which is no doubt due primarily to the westerly winds that blow snow over the range to form east-facing cornices that avalanche down to form the glaciers on that side, as well as to decreased solar radiation on the east sides of the range as the sun is more intensive late in the day in the west. Many of the tongue-shaped rock glaciers on the high peaks of the Teton Range, on the other hand, occur on the west and north sides where snow does not accumulate as much as to the east, although the rock fragments from high freeze and thaw are still abundant, and the altitude is great enough and the topographic and rock-fragment shielding is enough so that the ice does not melt away (Figure 10). These tongue-shaped rock glaciers show by their occurrence in deep cirques that they were indeed once ice glaciers, and their lobate nature, with many longitudinal ridges and furrows and steep fronts at the angle of repose show that they remain active.

Glaciers in the Teton Range were first missed by the early explorers in the Hayden surveys of the 19th century, but later in the 20th were noted and described by a variety of people (Fryxell 1930, 1935, Reed 1964, 1967, Edmunds et al. 2011), but because most are small and not the lengthy and impressive ice masses of the polar regions or the high alpine ranges of the Himalaya and other famous ranges, the Teton glaciers have been considerably discounted by many. Devisser (2008) has noted that in the Tetons, roughly 276 permanent snow and ice bodies occur with a minimum elevation of 2694 m, a maximum of 4096 m and an average of 3127 m, and a total combined area of 6.9 km². Many of these are immobile snowfields, not true, moving glaciers. The Teton Range does contain 10 of Wyoming's named glaciers, the largest of which is Teton Glacier, which Devisser (2008) calculated at 0.30 km², but Edmunds et al. (2011) noted its diminution successively from 1967 at 0.258 km² to 2006 at 0.215 km². Edmunds et al. (2011) also assessed Middle Teton Glacier and Tepee Glacier for the same time period and noted collectively that the greatest loss of glacier mass occurred from 1983 to 1994, which coincided with a rise in temperatures and a reduction in snowpack.

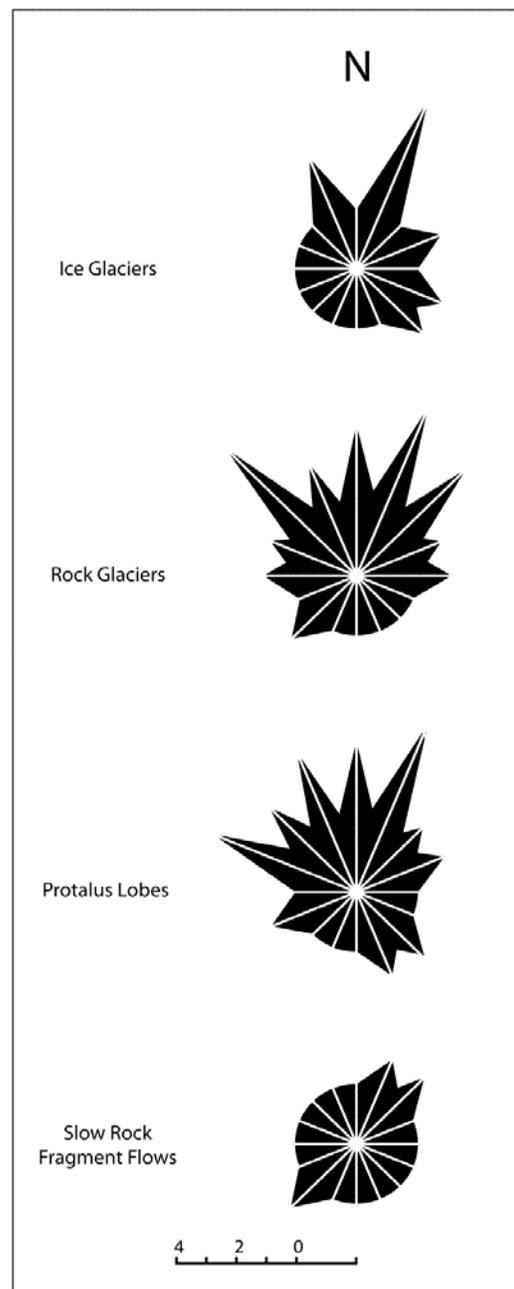


Figure 10. Radar diagrams of aspect directions of various deposits in GTNP. Note that these data represent features mapped for this project, and not for the entirety of the range.

The rock glaciers of the Teton Range are largely unnamed and unstudied, which is unfortunate because they do represent a fair amount of unaccounted for permafrost ice that most likely provides considerable late summer – early fall meltwater overland flow and groundwater base flow into the mountain streams.

◆ MANAGEMENT IMPLICATIONS

Mass movements, rock glaciers, and glaciers as water retention features

Results of this study confirm and reiterate that mass movements, rock glaciers, and glaciers in GTNP attenuate water at up-elevation locations, and arguably for years to centuries depending on the feature. These landforms, then, affect the local hydrologic cycle, and perhaps dramatically, through the lag and pulse effects of stored or mobilized water downstream, respectively. This situation has the potential to exacerbate the ever-present, cascading, trophic effect on most biota in the absence or abundance of water. Monitoring of precipitation and stream discharge at plentiful locations throughout the park would help future scientists better untangle the influences of landform classes or individual features on water distribution in GTNP.

Lack of gauges in GTNP streams

At present, there are no water discharge recording stations in GTNP streams. This situation impedes long term monitoring of the quantity and timing of up-canyon water attenuation/release. Adding these gauges would benefit further investigations of the water resources in that having baseline data of water availability would help insure correct management treatments be used to secure floral and faunal assemblages, as well as any ecosystem services supported by water. Additionally, streams in Grand Teton National Park are undisturbed (anthropogenically) and so these “pristine” waterways could serve as benchmark streams for unmodified/modified water delivery system studies, a practice of the U.S. Geological Survey.

Future hazards to park visitors

While it is fairly impossible to “predict” individual mass movements with any certainty, (sans the precursors to an imminent failure like ground cracks) the ability to recognize areas more prone to failure is likely a more fruitful pursuit. Because the geologic contact (unconformity) between the Archean crystalline rocks and Paleozoic sedimentary rocks of the range creates a situation of comparatively more labile, or “weaker” rocks, at the margins of, and inside the canyons of GTNP, prudence should be exercised in not placing campgrounds and hiking trails on or near such areas where, for example, daylighting sedimentary rocks are overlying crystalline basement rocks.

Nomenclature of Teton landforms

While a vast majority of the landforms in GTNP are properly classified, this study has uncovered several instances in past studies where a feature has been incorrectly classified. In doing so, we have reclassified any landforms whose character does not match the textbook description of the feature. This may have implications to park managers in terms of signage, or park information provided to the general public.

◆ ACKNOWLEDGEMENTS

We thank the UW-NPS Research Station and the Association of American Geographers Mountain Geography Specialty Group Chimborazo Fund for partial funding of this project. We are very grateful for everyone’s logistical assistance and hospitality at the research station, notably Dr. Hank Harlow and Celeste Havener. We also thank the National Park Service, especially Kathy Mellander, for technical support.

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IDENTIFYING RARE MONTANE MEADOW PARNASSIAN BUTTERFLY POPULATIONS ACROSS GRAND TETON NATIONAL PARK, WYOMING

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✦ ABSTRACT

The pristine, protected ecosystem of Grand Teton National Park (GRTE) is the ideal location to study the relationships between butterfly populations and the habitats on which these insects depend. Two montane meadow butterfly species, *Parnassius clodius* and *Parnassius smintheus*, were investigated in this study to identify patterns of habitat occupancy relating to variables across GRTE and into the surrounding territory of Bridger-Teton National Forest (BTNF). Population dynamics of *P. clodius* have been intensively studied by our research group over several consecutive years in one isolated population in Grand Teton National Park. However, little has been investigated regarding the Parnassian butterflies' population range across the GRTE ecosystem. For this study, presence-absence butterfly surveys were conducted across 45 meadow sites in preferred habitat during the *Parnassius* flight season (June – July 2013). We found that *P. clodius* occupied 80% of the meadows surveyed, which was far greater than was originally predicted. *P. smintheus*, the more rare Parnassian butterfly in the GRTE ecosystem, was only found at 9% of the meadows surveyed. Understanding population ranges and habitat limits of these butterfly populations will be useful for managers and scientists within GRTE, and will assist conservation efforts for other related Parnassian species that are threatened or endangered worldwide due to habitat loss and climate change.

✦ INTRODUCTION

The Clodius Parnassian (*Parnassius clodius*) and Rocky Mountain Parnassian (*Parnassius smintheus*) are two range-restricted high-elevation montane meadow butterfly species whose survival is highly dependent upon their surrounding environment. Montane meadow butterflies are sensitive to synchrony in plant-insect interactions relating to spring emergence timing, constrained to potentially shrinking habitats caused by tree encroachment (Roland et al. 2002, Roland and Matter 2007), and vulnerable to genetic isolation due to their small, isolated populations (Dirnbock et al. 2011). These two Parnassian species currently exist in several locations across Grand Teton National Park (GRTE) and the surrounding ecosystem. However, the related European Apollo Butterfly (*Parnassius apollo*) has been declining since the turn of the century due to long-term climatic changes, habitat succession, anthropogenic factors, and intrapopulation factors that include genetic erosion and behavioral changes in small demes (Nakonieczny et al. 2007).

Although *P. clodius* and *P. smintheus* are not currently threatened species, recent population fluctuations determined by mark-recapture studies performed by the Debinski lab from 1998 – 2000 (Auckland et al. 2004) and from 2009 – 2012 (Sherwood and Debinski, unpublished data) on one population of *P. clodius* in GRTE indicate the need for additional monitoring. Mark-recapture studies were conducted on what is considered to be one of the largest populations of *P. clodius* in GRTE along Pilgrim Creek Road (Auckland et al. 2004) to assess population parameters including sex ratio, population

size, percentage of mated females, and emergence dates for males and females. However, there is limited information about the general population range of this butterfly genus across GRTE and it would be valuable to know how the Pilgrim Creek population compares to other populations within the ecosystem.

To determine where current populations of Parnassian exist in the park and surrounding ecosystem, presence-absence butterfly surveys were conducted for this study in potentially suitable habitat for *P. clodius* and *P. smintheus* in meadows across GRTE and into Bridger-Teton National Forest (BTNF) territory. In addition, potentially suitable habitats of *P. clodius* and *P. smintheus* were analyzed in the GRTE and BTNF study sites by collecting vegetation and nectar data to identify habitat requirements for these rare species. The results of this research will allow us to 1) estimate the current distribution patterns for each of the two species, 2) determine the fine-scale differences in habitat requirements between the species, and 3) develop a more rigorous model of habitat suitability for each species.

◆ METHODS

Study area

The butterfly and plant communities of GRTE, located within the large-scale protected ecosystem of the Greater Yellowstone Ecosystem (GYE), have been studied intensely by our lab over the last two decades. From 1997 to 2007, Debinski and colleagues collected long-term data on plant and butterfly distributions across 55 montane meadows in GYE along a hydrological gradient ranging from hydric to xeric meadows (Debinski et al. 2006, Debinski et al. 2010, Debinski et al. 2013). Parnassian butterflies' habitat preferences as determined by the long-term plant and butterfly surveys (Debinski et al. 2006, Debinski et al. 2010, Debinski et al. 2013), along with GIS vegetation data layers provided by the 2002-2005 Grand Teton National Park Vegetation Mapping Project (Cogan et al. 2005) were used to locate potentially suitable Parnassian habitat in the GYE ecosystem. GRTE includes a wide variety of habitat types encompassing both hydrological and elevation gradients. Based on the butterflies' known habitat preferences, meadow sites for this study were restricted to montane mesic forb herbaceous vegetation, montane xeric forb herbaceous vegetation, and meadows with low sagebrush (*Artemisia arbuscula*) or tall sagebrush (*Artemisia tridentata*) vegetation cover.

Field surveys

Presence-absence butterfly surveys were performed for *P. clodius* and *P. smintheus* across 45 meadow sites of the butterflies' preferred habitat requirements in GRTE and BTNF in the summer of 2013. To account for imperfect detection, presence-absence surveys were conducted twice at each site throughout the butterflies' flight season (MacKenzie et al. 2002) with two independent observers searching for the butterflies for 30 minutes (MacKenzie et al. 2006) for a total of four surveys per site. If the butterfly species occupied the meadow in at least one out of the four butterfly surveys, then the butterfly was considered present at that meadow site. Butterfly surveys were only performed during optimal butterfly survey conditions (mid-June to mid-July at times between 10:00 and 17:00 hours when the temperature was above 21°C and wind was <16km/h).

◆ RESULTS

As seen in Appendix 1, *P. clodius* was present at 36 out of the 45 meadow sites surveyed and *P. smintheus* was located at three out of the 45 meadow sites surveyed. The two Parnassian species only occupied the same meadow site once throughout the study and six of the study sites were unoccupied by both species. Of the sites surveyed for this study, *P. clodius* was found across a wide range of elevations from 2,006 meters to 2,503 meters and *P. smintheus* occurred at a more restricted range of 2,043 meters to 2,099 meters. Figure 1 shows a map of the study area of GRTE and BTNF displaying the population range of the more common Parnassian butterfly across the GYE ecosystem, *P. clodius*.

◆ DISCUSSION

This research indicates that *P. smintheus* is considered to be the more rare Parnassian species in GRTE, however this trend does not hold true across their habitat range in the entire GYE ecosystem. Based on previous butterfly and bird surveys conducted by the Debinski Lab, *P. smintheus* was more abundant in the northern region of the GYE ecosystem in Gallatin National Forest (Debinski et al. 1999, Debinski et al. 2006, Debinski et al. 2010). Of the meadow sites with preferred Parnassian habitat requirements, *P. clodius* occupied a surprisingly high percentage of the meadows, far exceeding our prior predictions of their population range in GRTE. While it is encouraging in the context of long-term viability that *P. clodius* was found at more sites than was

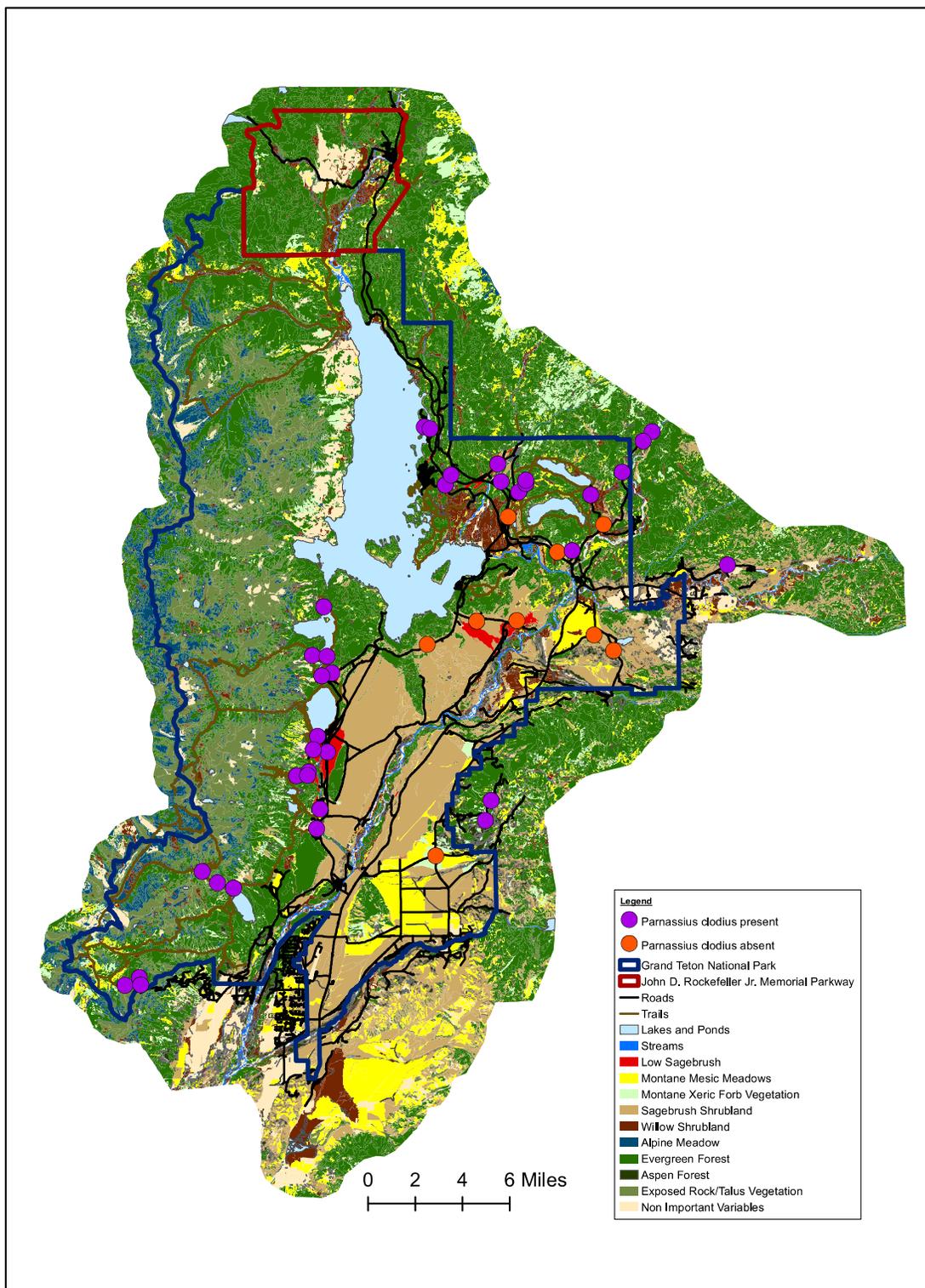


Figure 1. Vegetation map of Grand Teton National Park displaying occupancy of *Parnassius clodius* butterfly in meadow study sites surveyed from mid June – mid July 2013.

originally predicted, it is important to also consider the total number of butterflies recorded at each study site summed across the four surveys. The majority of meadows occupied by *P. clodius* had an overall low abundance: 22 out of the 36 meadows contained less than 8 individuals. The remaining 13 sites had higher abundance, ranging from 14 to 35 total individuals recorded throughout the study. Additional mark-recaptured studies would need to be performed at these sites to obtain a better estimate of the population sizes before any conclusions could be made on the status of these populations.

Occupancy modeling analysis in program PRESENCE (Hines and MacKenzie 2006) is currently being conducted using these butterfly presence-absence data to estimate detection probabilities (p) and the probability of a site being occupied (ψ) for both species across all of the meadow sites. Additionally, vegetation data for each meadow site were collected and vegetation analysis is underway to determine what habitat variables influence the occupancy of these montane butterflies.

◆ ACKNOWLEDGEMENTS

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Appendix 1: UTM (Universal Transverse Mercator) coordinates of the Grand Teton National Park and Bridger–Teton National Forest study sites (UTM NAD 1983 Zone 12N) with presence-absence data of butterflies *Parnassius clodius* and *Parnassius smintheus* for each meadow site collected from mid June – mid July 2013.

Meadow Site	UTM Northing	UTM Easting	Parnassian Presence-Absence
Aimee's Meadow	533942	4861337	<i>P. clodius</i> present
AMK Ranch	528713	4865045	<i>P. clodius</i> present
AMK Road	529077	4864934	<i>P. clodius</i> present
Antelope Flats	529470	4835784	Both species absent
Bearpaw Lake Intersection	521838	4852775	<i>P. clodius</i> present
Bearpaw Lake Trail	522079	4849388	<i>P. clodius</i> present
Buffalo Fork	549358	4855639	<i>P. clodius</i> present
Christian Pond	534432	4858912	Both species absent
Climbers Ranch	521577	4838973	Both species present
Cow Lake 1	535004	4851840	<i>P. smintheus</i> present
Cow Lake 2	532269	4851812	<i>P. smintheus</i> present
Cygnets Pond	530146	4861081	<i>P. clodius</i> present
Death Canyon Phelps Lake Junction	515719	4833590	<i>P. clodius</i> present
Death Canyon Ranger Cabin	513571	4834713	<i>P. clodius</i> present
Death Canyon Trail	514608	4833957	<i>P. clodius</i> present
Dump Road	530523	4861790	<i>P. clodius</i> present
Elk Ranch 1	540261	4850850	Both species absent
Elk Ranch 2	541592	4849795	<i>P. smintheus</i> present
Grand View 1	535627	4861193	<i>P. clodius</i> present
Grand View 2	535609	4861415	<i>P. clodius</i> present
Grand View Parking	535142	4860599	<i>P. clodius</i> present
Hidden Falls Trail	521439	4843954	<i>P. clodius</i> present
Lozier Hill Meadow	538775	4856609	<i>P. clodius</i> present
Lozier Hill Road	537747	4856522	Both species absent
Lupine Meadow	521129	4843032	<i>P. clodius</i> present
Mt. Moran Turnout	528887	4850207	Both species absent
North Jenny Lake	522388	4848251	<i>P. clodius</i> present
Paintbrush Canyon Trail	521072	4849468	<i>P. clodius</i> present
Pilgrim Creek	533718	4862533	<i>P. clodius</i> present
Rendezvous Mountain 1	508298	4826970	<i>P. clodius</i> present
Rendezvous Mountain 2	509291	4827468	<i>P. clodius</i> present
Rendezvous Mountain 3	509376	4827000	<i>P. clodius</i> present
Shadow Mountain Hairpin	532852	4838189	<i>P. clodius</i> present

Sound of Music	533257	4839554	<i>P. clodius</i> present
String Lake Parking	521728	4848059	<i>P. clodius</i> present
Surprise Lake Meadow	520001	4841263	<i>P. clodius</i> present
Surprise Lake Trail 1	520818	4841498	<i>P. clodius</i> present
Surprise Lake Trail 2	520745	4841270	<i>P. clodius</i> present
Taggart Lake Trailhead	521361	4837657	<i>P. clodius</i> present
Timbered Island	522115	4842890	<i>P. clodius</i> present
Two Ocean Lake Road 1	540926	4858405	Both species absent
Two Ocean Lake Road 2	540030	4860396	<i>P. clodius</i> present
Wilderness Road 1	544237	4864715	<i>P. clodius</i> present
Wilderness Road 2	543598	4864076	<i>P. clodius</i> present
Wilderness Road 3	542182	4861987	<i>P. clodius</i> present

DESCRIBING THE MOUNTAINSNAILS (*OREOHELIX* SP.) OF GRAND TETON NATIONAL PARK, WYOMING

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✦ ABSTRACT

Invertebrates are receiving an increasing amount of conservation attention across North America. Currently, about 40% of the animals listed under the U.S. Endangered Species Act (ESA) are invertebrates (www.NatureServe.org). The National Park Service and other agencies require better information on invertebrate faunas in order to effectively conserve this important group of animals. One way to prioritize invertebrate groups for study is to assess the number of rare taxa within a given genus. In this context, *Oreohelix* (mountainsnails) are a top priority because the genus is assumed to support a very high percentage of rare and endemic taxa. Additionally, *Oreohelix* species in Wyoming and surrounding states have been petitioned for ESA listing in the recent past. The diversity of *Oreohelix* forms in Wyoming is not well-understood, and the current taxonomy may not reflect the true pattern of diversity within the state. Therefore, we are studying both the morphology and genetic structure of *Oreohelix* in Grand Teton National Park to begin to understand the diversity of mountainsnails in the state. We collected *Oreohelix* from 4 locations in Grand Teton National Park. Based on shell and internal characteristics, all individuals were identified as *O. subrudis*. We are currently preparing specimens for DNA sequencing.

✦ INTRODUCTION

Invertebrates compose 99% of the animals on earth (Ponder and Lunney 1999). Despite the fact that most animals lack a backbone, far less is known about invertebrates than their vertebrate counterparts.

Non-marine mollusks are a diverse group of invertebrates composed of terrestrial and freshwater snails and bivalves, and these animals are one of the most critically impaired groups on earth (Lydeard et al. 2004). Unfortunately, the highest number of recorded extinctions has occurred within the mollusk group. About 24,000 terrestrial mollusks are described, and an estimated 11,000 to 40,000 terrestrial mollusks are currently undescribed (Lydeard et al. 2004). Of the described species, 1,222 (5%) were on the 2002 International Union for Conservation of Nature Red List of Threatened Species (www.redlist.org, Lydeard et al. 2004).

Land snails are particularly threatened because of several life history traits. First, snails move small distances each year, making dispersal extremely limited (Overton et al. 2009). Because few individuals immigrate to new colonies, gene flow among neighboring populations is probably limited. These reasons likely promote the formation of locally-endemic forms. Second, climate change may have the greatest effect on high elevation species, such as snails in the genus *Oreohelix* (mountainsnails). Species may shift their ranges as climate warms; however, species that live at high elevations may be in jeopardy as they will have less area at higher elevations to move (Muller et al. 2009).

Oreohelix are charismatic land snails that are understudied, despite being easily observed (10-20 mm diameter). The lifespan of these snails is unknown. They carry their young internally (ovoviviparous) and juvenile snails are born at ~2.5 whorls, which is unique among snails (Anderson et al. 2007). In the food web, *Oreohelix* play a fundamental

role by consuming organic matter (Speiser 2001). These snails are also food for many animals, such as birds, small mammals, and reptiles.

Snails in the genus *Oreohelix* are generally considered rare, and their taxonomy is in desperate need of revision. NatureServe lists 80 species or subspecies of *Oreohelix* in North America, of which 47 (60%) are considered imperiled or critically imperiled (www.NatureServe.org). Furthermore, several *Oreohelix* snails have been proposed for listing under the ESA, including *Oreohelix strigosa cooperi* endemic to the Black Hills, *Oreohelix carinifera* known from Montana and possibly Wyoming, and *Oreohelix pygmaea* in the Bighorn Mountains of Wyoming and Montana. If these snails are to be protected, we must first understand their diversity and distribution. Many land snails were initially identified using shell characteristics, but shells can vary widely and are not a reliable means of identifying *Oreohelix* (Pilsbry 1916). The last revision of the genus was done in 1939 and many of the species were based on shell morphology (Pilsbry 1939). A revision of the *Oreohelix* genus is needed to understand what taxa are unique and which are widespread. In order to revise the genus, dissections and DNA sequencing should be done together. The objective of the project was to collect *Oreohelix* within Grand Teton National Park, measure morphological characteristics, and sequence their DNA to understand what species live in the park. Additionally, the project will help resolve taxonomic issues within Wyoming and the western United States where these snails are found. This project is part of a larger effort by the Wyoming Natural Diversity Database to understand the diversity of *Oreohelix* in Wyoming.

◆ METHODS

We hiked to areas with known *Oreohelix* populations in Grand Teton National Park (L. Tronstad, personal observation) and surveyed other areas with suitable habitat. We collected ~10 individuals from each observed population segment. Snails were drowned in water for 24-36 hours so that the foot protruded from the shell for dissection. After that time, we increased ethanol concentration over 3 days to a final concentration of 80% to preserve the snails and their DNA. In the laboratory, we identified *Oreohelix* using the available key (Pilsbry 1939) and recent studies (e.g., Weaver et al. 2006, Chak 2007). We measured morphology that is pertinent to *Oreohelix* identification, including both shell (diameter, height, umbilicus diameter, whorls, number of bands, height to width ratio, umbilicus ratio) and

internal characteristics (penis length, ribbed penis length, number of penis ribs, ribbed penis ratio, and noted any swollen areas). Shell characteristics were measured with digital calipers and internal characteristics were measured with a calibrated ocular micrometer in a dissecting microscope. The ribbed penis ratio was calculated as the length of the penis that was ribbed divided by the total penis length. The umbilicus ratio is the diameter of the umbilicus divided by the diameter of the shell. We are currently preparing specimens for DNA sequencing.

◆ PRELIMINARY RESULTS

We collected 36 *Oreohelix* specimens from 4 areas in Grand Teton National Park (Granite Creek, Ditch Creek, Moose Creek, and Owl Creek; Figure 1). These areas had calcium in the bedrock (e.g., limestone), which is needed to build their shells.



Figure 1. Locations where we collected *Oreohelix* in Grand Teton National Park. We collected snails at 2 locations in both Owl and Moose Creeks. The inset map shows the location of the map in Wyoming.

All the individuals we collected best matched the description of *Oreohelix subrudis* (subalpine mountainsnail). Pilsbry (1939) described *O. subrudis* as having shells 14-21 mm in diameter, ~11 mm in height, and the diameter of the umbilicus is ~1/3 of the shell's width (Table 1). Pilsbry (1939) reported that

most individuals had 2 bands on their shell. We observed that most individuals from the park had 2 brown bands and some individuals had additional small bands on their shells. Characteristics of some individuals from Granite Creek were smaller because several of the individuals we collected were juveniles (<5 shell whorls). Pilsbry (1939) described the internal characteristics of *O. subrudis* as having a mean ribbed penis ratio of ~0.50 and having 4 or 6 ribs on the penis (Table 2). Additionally, the median portion of the penis was swollen on most of the individuals we dissected which is a unique characteristic of *O. subrudis* (Pilsbry 1939).

Table 1. Mean shell characteristics of *Oreohelix* from 4 areas of Grand Teton National Park.

Site	Ditch	Granite	Moose	Owl
Diameter (mm)	19.5	16.6	18.9	20.4
Height (mm)	12.0	8.8	10.7	11.7
Height/Diameter ratio	0.61	0.53	0.57	0.58
Umbilicus (mm)	3.5	3.3	3.5	4.1
Umbilicus ratio	0.18	0.20	0.19	0.20
Whorls	5.1	4.6	5.0	5.1
Bands	4.3	2.2	4.8	2.0

Table 2. Mean internal characteristics of *Oreohelix* from 4 areas of Grand Teton National Park.

Site	Ditch	Granite	Moose	Owl
Penis length (mm)	10.4	6.0	9.4	10.4
Ribbed penis length (mm)	5.7	6.3	5.1	5.5
Ribbed penis ratio	0.54	0.63	0.54	0.52
Number of penis ribs	6	4	6	5

◆ MANAGEMENT IMPLICATIONS

According to current taxonomy, *Oreohelix subrudis* is one of the most widespread species within the genus. *O. subrudis* ranges from British Columbia to New Mexico and from Washington to Wyoming. *O. subrudis* is considered vulnerable in British Columbia, Utah, and New Mexico, and secure in Montana (not ranked in other states and provinces; www.NatureServe.org). In Wyoming, we have collected *O. subrudis* from the Bighorn Mountains near Ten Sleep, Heart Mountain north of Cody (Tronstad 2011), and the Gardner Mountain Wilderness Study Area west of Kaycee (Estes-Zumpf et al. 2014). Pilsbry (1939) reported *O. subrudis* from Mammoth in Yellowstone National Park. DNA sequencing from individuals collected from Grand Teton National Park will help resolve taxonomic issues within the mountainsnails.

Of the 80 *Oreohelix* taxa currently recognized, many are assumed to be endemic to a single locale (www.NatureServe.org). These assumptions have led to 27 taxa (34%) being recently petitioned for ESA listing, including 3 *Oreohelix* taxa in Wyoming. Such listing petitions will likely increase in frequency. Currently, about 40% of ESA-listed animals in the U.S. are invertebrates. In Wyoming, 13 invertebrates have been petitioned for listing, all within the past 8 years. Twenty invertebrates are listed under the ESA in adjacent states, with 7 of those taxa being listed in the past 10 years and 16 of those taxa listed in the past 22 years. The trend is clearly towards more invertebrate animals being petitioned for, and granted, ESA protection in the western U.S., and *Oreohelix* taxa are prime targets. The paucity of basic information regarding actual species and subspecies diversity substantially complicates management and policy decisions such as ESA listing, recovery, and delisting. This is a debate that needs to be informed by objective science. The regulatory implications of ESA listing are alone severe enough to justify targeted research to delimit species and distributions within *Oreohelix*.

◆ ACKNOWLEDGEMENTS

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YELLOWSTONE NATIONAL PARK



PATHS OF RECOVERY: LANDSCAPE VARIABILITY IN FOREST STRUCTURE AND FUNCTION 25 YEARS AFTER THE 1988 YELLOWSTONE FIRES

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✦ ABSTRACT

Understanding succession following severe wildfire is increasingly important for forest managers in western North America and critical for anticipating the resilience of forested landscapes to changing environmental conditions. Successional trajectories set the stage for future carbon storage, abundance and distribution of fuels, and habitat for many species. Early successional forests are increasing throughout the West in response to greater fire activity, but few long-term studies have considered succession following stand-replacing wildfires over large areas. The size and heterogeneity of the 1988 Yellowstone fires created novel opportunities to study succession at an unprecedented scale following severe fire, and we have studied the consequences of these fires for >20 years. In 2012, we began a re-sampling effort in long-term vegetation plots within the area burned by the 1988 fires to answer three overarching questions: **(1) Are stand structure and function beginning to converge twenty-five years after the Yellowstone Fires, and what mechanisms may contribute to convergence or divergence?** Heterogeneity in forest structure was the rule after the 1988 fires, and postfire lodgepole pine (*Pinus contorta* var. *latifolia*) densities ranged from zero to >500,000 trees/ha. The post-1988 cohort of lodgepole pine is reaching a time of critical

transitions in structure and function. **(2) Are plant community composition and species richness converging or diverging across gradients in local fire severity, post-fire lodgepole pine density, elevation and soil type a quarter-century after the 1988 fires?** A central objective in our research has been to understand the relative influence of contingent factors (e.g., local fire severity) vs. deterministic factors (e.g., elevation, soils) on postfire ecosystem development, and how these influences may change through time. **(3) How do canopy and surface fuels vary across the postfire landscape, and how will the variation in fuels influence potential fire behavior a quarter century post-fire?** Field sampling was conducted for this third question during summer 2012, and data analyses and interpretation are in progress. Overall, results from the proposed study will enhance understanding of succession after one of the most notorious fires of the 20th century. Yellowstone's postfire forests may serve as benchmarks for forests throughout the region and effective sentinels of change for the Rockies.

✦ INTRODUCTION

The 1988 Yellowstone fires ushered in the new era of wildfire in the West. The size and heterogeneity of the fires created novel opportunities

to study succession and ecosystem processes at an unprecedented scale following severe fire in a wilderness-like setting. We have studied the causes and consequences of these fires for >20 years, with a primary focus on understanding postfire succession. To date, we have published >70 peer-reviewed articles related to fire in Yellowstone, and our findings have made important contributions to forest management as well as to terrestrial ecology (Turner 2010). The wealth of our early postfire data and potential for having the original researchers resample the long-term study plots offers a unique opportunity to understand succession following one of the most notorious fires of the 20th Century. Yellowstone's postfire forests may be effective sentinels of change for the Rocky Mountains, and our results will provide benchmarks relevant for forests throughout the region.

◆ STUDY AREA

Our study is being conducted within forests burned by the 1988 fires in Yellowstone National Park (YNP), which encompasses ca. 9,000 km² in northwestern Wyoming. Stand-replacing fires occur in YNP at 100-300 yr intervals (Schoennagel et al. 2003), but the 1988 fires were remarkable for their severity and size, affecting ~36% of YNP. About 80% of YNP is dominated by lodgepole pine forest, although subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and whitebark pine (*Pinus albicaulis*) can be locally abundant. In these forests, severe fire kills all trees and consumes the shallow litter layer present in unburned forests. Postfire forests in YNP initially had nearly complete cover of bare mineral soil and essentially no duff.

◆ METHODS

During summer 2013, plant community composition was re-sampled in 42 plots in three crown-fire patches that we have studied since 1990 (Turner et al. 1997, 2003). Briefly, we revisited 42 permanently marked sampling plots (10 m x 1 m) in three crown-fire patches (Cougar Moderate, Fern Large, and Lake Moderate; see Turner et al. 1997). As in our previous sampling campaigns, we identified and tallied all vascular plant species present within each plot.

We re-visited fourteen 0.25-ha plots to measure inorganic N availability and litterfall rates (see Turner et al. 2009). Litter traps and resin bags were deployed in 2012 and collected in 2013. Litter was returned to the lab, sorted, dried to constant mass,

the mass was recorded, and the litter was subsampled for carbon and nitrogen analysis. We also collected lodgepole pine foliage samples for analysis of foliar chemistry.

We re-sampled aspen in 22 permanent plots in which the height, basal diameter, and density of postfire aspen seedlings have been measured since 1996 (see Romme et al. 2005).

◆ PRELIMINARY RESULTS

Data from the summer 2013 field season have been entered and data analyses are in progress. Preliminary results are summarized briefly here.

Plant community composition. Plant species richness has increased substantially. The total number of species recorded in the subset of 42 plots re-sampled in 2013 has steadily increased, from 49 species in 1991 to 95 species in 2013. Alpha diversity has increased in all geographic locations, but beta diversity (which reflects plot-to-plot variation) has changed relatively little, suggesting that species have been gaining relatively evenly within the crown-fire patches. Multivariate analyses are in progress.

Postfire ecosystem function. Resin-adsorbed nitrogen (N) averaged 4.1 µg nitrate-N/g resin/day (range 0.44 to 12.97) and 1.92 µg ammonium-N/g resin/day (range 0.54 to 6.43) among the fourteen 25-yr old postfire lodgepole pine stands. Total resin-adsorbed N was positively related to total soil N ($r = 0.73$, $p = 0.003$) and negatively related to soil pH ($r = -0.61$, $p = 0.02$). Current year lodgepole pine foliage averaged 1.33% N, ranged from 1.04% to 1.52%, and declined with increasing lodgepole pine density. Data analyses are in progress.

Postfire aspen size. Aspen seedling height nearly doubled between 1996 and 2013 (from 29.0 ± 1.5 to 58.0 ± 5.0 cm), and basal diameter increased (from 7.0 ± 0.4 to 9.7 ± 0.7 mm.). Aspen height and diameter were positively related to soil pH and unrelated to lodgepole pine density. Ungulate browsing was high (> 80% of seedlings) in 1996 and very low (< 3% of seedlings) in 2013. Aspen results will be presented by W. D. Hansen at the 2014 meeting of the Ecological Society of America.

In addition, one paper based on the 2012 summer field season for this project has been published. Copenhaver and Tinker (2014) reported new allometric equations that predict aboveground

biomass and aboveground net primary production for 25-yr old lodgepole pine. These equations will be combined with non-destructive field measurements to calculate stand-level productivity and fuels estimates (as in Turner et al. 2004).

◆ ACKNOWLEDGEMENTS

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OLD FAITHFUL VISITORS CENTER EXHIBIT OBSERVATION STUDY

◆

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◆ OBJECTIVES

This report was a result of volunteer research orchestrated by Katy Duffy, Interpretive Planner, Yellowstone National Park. The data collection was a direct need for grant compliance for the National Science Foundation associated with exhibits for the new Old Faithful Visitor Education Center, which opened to the public in August, 2006. The objective of this research was to understand visitor interaction with these exhibits using an unobtrusive form of data collection.

◆ METHODS

Volunteer researchers from Stephen F. Austin State University met with Ms. Duffy, Ms. Linda Young, Ms. Tami Blackford, and Ms. Rebecca Garoville at a conference room at the Park Headquarters in Mammoth Hot Springs on Monday, July 22, 2013. Discussions had already taken place between Ms. Duffy and Ms. Linda Young and Dr. Pat Stephens Williams prior to the trip to Yellowstone.

The data collection site was the Old Faithful Visitor Education Center (OFVEC) opened in August, 2006. The Visitor Education Center, located nearby to Old Faithful itself contains an information desk, exhibit hall, Yellowstone Association Store, an auditorium for Yellowstone videos, restrooms, and offices. Each day park staff count the number of visitors to the OFVEC using an electronic counter

mounted at each of the Center's three entrances. During July 26th the official count was 9,125 visitors while 8,035 were counted during the 8 a.m. to 8 p.m. time period in which the Center is open to the public. For Friday, July 26th, 3.3% (302/9125) of visitors were studied in the Exhibit area while on Saturday, July 27th, 2.6% (202/8035) of visitors were studied.

Ms. Duffy had established a research protocol and had already collected data at the Old Faithful Visitor Education Center. The volunteers followed Ms. Duffy's protocol. Eight students from Stephen F. Austin State University were selected and used as data collectors. They were trained by Ms. Duffy in the data collection protocol and supervised by the professors with a graduate student, Ms. Sarah Fuller, selected as the lead volunteer assistant. The following is the protocol for data collection.

Form

Ms. Duffy created a data collection form used for the process. On the data collection form were three demographic questions: visitor's sex, age, and type of group. Once these data were recorded, next the volunteers recorded data pertaining to the total time at an exhibit, and ten questions related to activities at the exhibit:

- whether the person skipped the exhibit,
- whether the person skipped the exhibit with the exhibit occupied by one or more individuals,
- whether the person looked at the exhibit,
- whether the person read all or part of the information on the exhibit,

- whether the person read aloud information on the exhibit,
- whether the person interacted with the exhibit,
- whether the person engaged in shared interaction at the exhibit,
- whether there was unintended interaction at the exhibit,
- whether one or more photos was taken of the exhibit,
- and whether there was any other behavior at the exhibit not previously identified.

If an individual was observed engaging in any of these activities, data collectors were to indicate the activity on the form. As the visitor left the exhibit, the time at the exhibit was noted and recorded on the form.

Protocol

Two days were selected for data collection: Friday, July 26th and Saturday, July 27th. On Friday, students collected data from 9:30 a.m. to 4:00 p.m. for a total of 6.5 hours and on Saturday, July 27th from 10:30 a.m. to 3:30 p.m. for a total of 5 hours. A total of 11.5 hours of data collection was used.

Students were dressed in normal, visitor attire and stationed at specifically selected points inside the Exhibit Hall where they could clearly observe the visitors without intruding upon, or influencing, the visitor experience. These locations were selected based on Ms. Duffy's recommendations and an on-site review of the exhibit area. Students were to maintain an unobtrusive appearance throughout the data collection time.

Following the data collection period, data were entered into an Excel spreadsheet and then copied into an SPSS data file for analysis. The data files were cleaned and some checks of data input accuracy were made. Data analysis was performed using standard statistical techniques in SPSS Version 21.

◆ RESULTS

Observation results

Observations were conducted during two consecutive days, Friday, July 26th and Saturday, July 27th, 2013 by the researchers and research assistants. During July 26th, observations were made from 9:30 a.m. to 4:00 p.m. (total of 6.5 hours) and during July 27th observations were made from 10:30 a.m. to 3:30

p.m. (total of 5 hours); total number of hours was 11.5. During this time, the OFVC was open for a total of 24 hours.

Every fifth person entering into the Exhibit Hall was observed. A total of 514 visitors were observed following the research protocol. Of those, 58.8% (n=302) were observed on July 26th and 41.2% (n= 212) were observed on July 27th (Table 1).

Table 1. Date of observation.

	Date	Frequency	Percent	Valid Percent	Cumulative Percent
Valid	07/26/13	302	58.8	58.8	58.8
	07/27/13	212	41.2	41.2	100.0
	Total	514	100.0	100.0	

More visitors were observed in the afternoon (59.9%) compared to the morning (40.1%) (Table 2).

Table 2. Time of day of observation.

	Time of Day	Frequency	Percent	Valid Percent	Cumulative Percent
Valid	morning	203	39.5	40.1	40.1
	afternoon	303	58.9	59.9	100.0
	Total	506	98.4	100.0	
Missing	System	8	1.6		
Total		514	100.0		

Demographics of visitors

The sex distribution was almost even with males representing 51.1% of visitors and females comprising 48.9% of visitors (Table 3).

Table 3. Sex of visitors.

	Sex of Visitor	Frequency	Percent	Valid Percent	Cumulative Percent
Valid	female	250	48.6	48.9	48.9
	male	261	50.8	51.1	100.0
	Total	511	99.4	100.0	
Missing	not known	3	.6		
Total		514	100.0		

Age of visitor was estimated by each observer using eight age categories: 10-14, 15-19, 20s, 30s, 40s, 50s, 60s, and 70 or older. Some one-quarter of visitors were 10 to 19 years old. The modal (typical) age of visitors was in the forties (19.3%) while 9.2% of visitors were in their 60s or older (Table 4).

Table 4. Age of visitor.

Age of Visitor	Frequency	Percent	Valid Percent	Cumulative Percent
Valid 10-14	66	12.8	12.9	12.9
15-19	60	11.7	11.7	24.6
20s	62	12.1	12.1	36.6
30s	97	18.9	18.9	55.6
40s	99	19.3	19.3	74.9
50s	82	16.0	16.0	90.8
60s	38	7.4	7.4	98.2
70 or older	9	1.8	1.8	100.0
Total	513	99.8	100.0	
Missing not known	1	.2		
Total	514	100.0		

Individuals were observed in the context of their group make-up as they were moving through the exhibit hall. Groups were designed as one of the following: alone, multi, couple, family, or other. The distribution of groups is below. The most prevalent group type was family (53.2%) while couples represented the next most common group type (21.9%) (Table 5).

Age was cross-tabulated by sex to look at age distribution more closely. Despite the protocol of every fifth visitor being selected as they entered the hall, males were more likely to be observed than females among those 10-14, 20s, and 60s while females were more likely than males to be observed among those 15-19, 30s, 40s, 50s, and 70 or older. However, the percent differences were relatively small and less than 5% for all age groups (Table 6).

In looking at whether time of day was related to group type, the cross tabulation revealed families

and singles were more likely to be observed in the afternoon while the multi group and couples were more likely observed in the morning (Table 7).

Table 5. Type of group for visitors.

Group Type	Frequency	Percent	Valid Percent	Cumulative Percent
Valid alone	96	18.7	18.8	18.8
multi	29	5.6	5.7	24.5
couple	112	21.8	21.9	46.4
family	272	52.9	53.2	99.6
other	2	.4	.4	100.0
Total	511	99.4	100.0	
Missing not known	3	.6		
Total	514	100.0		

Table 6. Age of visitor of sex of visitor.

Age of Visitor		Sex		Total
		female	male	
10-14	Count	28	38	66
	% within Sex	11.2%	14.6%	12.9%
15-19	Count	34	26	60
	% within Sex	13.6%	10.0%	11.7%
20s	Count	29	33	62
	% within Sex	11.6%	12.6%	12.1%
30s	Count	51	45	96
	% within Sex	20.4%	17.2%	18.8%
40s	Count	50	49	99
	% within Sex	20.0%	18.8%	19.4%
50s	Count	40	41	81
	% within Sex	16.0%	15.7%	15.9%
60s	Count	13	25	38
	% within Sex	5.2%	9.6%	7.4%
70 or older	Count	5	4	9
	% within Sex	2.0%	1.5%	1.8%
Total	Count	250	261	511
	% within Sex	100.0%	100.0%	100.0%

Table 7. Group type by time of day of observation.

Group Type	Time of Day		Total
	morning	afternoon	
alone			
Count	38	58	96
% within Time of Day	18.8%	19.3%	19.1%
multi			
Count	12	16	28
% within Time of Day	5.9%	5.3%	5.6%
couple			
Count	50	59	109
% within Time of Day	24.8%	19.6%	21.7%
family			
Count	101	167	268
% within Time of Day	50.0%	55.5%	53.3%
other			
Count	1	1	2
% within Time of Day	0.5%	0.3%	0.4%
Total			
Count	202	301	503
% within Time of Day	100.0%	100.0%	100.0%

Time spent at exhibits

Researchers used stop-watches to observe the total time spent at each of the exhibits. For all visitors, the mean time was 1.4129 minutes (standard deviation = 1.59 minutes), or about 85 seconds (standard deviation = 95 seconds). Because of skewness, the median (Md = .88 minutes) may be the better measure of central tendency. The minimum recorded time was .02 minutes (1 second) while the maximum recorded time was 10.03 minutes, or 602 seconds. Some 75% of visitors were at the exhibits two minutes or less while 90% were at the exhibits 3.3 minutes or less (Table 8).

Visitor activities at exhibits

Below is a summary table that displays results from each of the exhibits (Table 9). The table shows the number of individuals observed who

engaged in at least one activity for a particular exhibit, the mean number of activities observed (eight possible activities per exhibit) as well as the minimum number and the maximum number. In addition, the table displays the mean and standard deviation of times at each exhibit.

Table 8. Total time at exhibits.

		Statistic	Std. Error
Total Time (minutes)	Mean	1.4129	.06999
	95% Lower Confidence Interval for Mean	1.2754	
	5% Upper Bound	1.5504	
	5% Trimmed Mean	1.2091	
	Median	.8800	
	Variance	2.518	
	Std. Deviation	1.58689	
	Minimum	.02	
	Maximum	10.03	
	Range	10.01	
	Interquartile Range	1.70	
	Skewness	2.093	.108
	Kurtosis	5.388	.215

The number of visitors observed was 514. Among these, there were 831 individual observations recorded, indicating that the average visitor stopped at about 1.5 exhibits while in the exhibit area. The number of observations varied by exhibit. More individuals were recorded at the diorama (n = 130) than any other exhibit while the rock exhibit had the fewest number of individuals (n = 48).

Results show that 831 total observations were made during the data collection phase. The grand mean number of activities per exhibit was 1.56. Mean number of activities was the lowest at the rock exhibit while the above/below ground exhibit resulted in the highest mean number of activities (M = 2.29).

Total time in minutes at each exhibit was recorded for each visitor. The grand mean was 2.44 minutes for all exhibits. Times at exhibit varied from a low of 0.92 minutes at the diorama to 3.07 minutes at the rock exhibit.

Table 9. Descriptive statistics for exhibits.

Exhibit	Number of Observations	Number of Activities at Exhibit			Time at Exhibit	
		Mean	Min	Max	Mean	Standard Deviation
HT	65	1.68	1	5	2.70	1.97
Gush	56	1.29	1	3	2.79	1.90
Steam	63	1.38	1	3	2.60	1.78
Hiss	50	1.22	1	5	2.61	1.80
Bubble	52	1.40	1	5	2.74	1.97
Diorama	130	2.12	1	5	0.92	0.91
Volc	65	1.55	1	3	2.79	2.27
Heat	61	1.39	1	3	3.07	2.31
H2O	52	1.46	1	5	3.01	2.26
Frac	54	1.22	1	2	3.00	2.21
Rock	48	1.19	1	3	3.07	2.21
Above/ Below Ground	68	2.29	1	5	1.12	1.17
pH	67	2.09	1	4	1.33	1.22
Totals	831	1.56	1	3.92	2.44	1.84

The three demographic factors (sex, approximate age, group structure) were analyzed to determine if they significantly impacted total time at each of the exhibits. Thirty-nine One-Way ANOVA tests were conducted to examine the data for mean differences by sex, age, and group. Of the 39 tests, only one produced a significant outcome-total time at the Diorama Exhibit by group. Those having the longest time at the Diorama exhibit were those in multi-groups (M = 1.78 minutes) and couples (M = 1.03) while those spending the least time there were those who appeared to be alone (M = 0.75) (Table 10).

◆ DISCUSSION

It is obvious that use of the visitor center is not uniform throughout the day. Larger numbers of visitors do not arrive until 9 a.m. or so and by 4 p.m. the number of visitors in the visitor center has decreased dramatically from levels earlier in the day. Highest visitation appears to be during the mid-day hours of 10 a.m. to 3 p.m.

Table 10. ANOVA results of total time (in minutes) at the Diorama Exhibit by group.

	N	Mean	Std. Deviation	Std. Error	95% Confidence Interval for Mean		Minimum	Maximum
					Lower Bound	Upper Bound		
alone	26	.7515	1.06383	.20863	.3218	1.1812	.05	4.70
multi	10	1.7770	1.34790	.42624	.8128	2.7412	.42	4.00
couple	30	1.0333	.90807	.16579	.6943	1.3724	.08	3.93
family	63	.7778	.66223	.08343	.6110	.9446	.03	3.05
Total	129	.9094	.90776	.07992	.7512	1.0675	.03	4.70

It is also obvious that use of the visitor center is a function of eruption times of Old Faithful. Immediately prior to and following an eruption, visitation of the exhibit area increased.

From the observations here there is some baseline information from which to build. There is now documented use by specific age groups and dynamics, times, and exhibits. A deeper look into the data here may give specific indications of what particular types of exhibits seem to draw specific audiences and engage them for what might be perceived as an accurate amount of time for them to clearly internalize the message of the exhibit. This information will help in the future design of exhibits and exhibit halls with specific audiences and intents in mind.

YOUNG SCIENTIST! CHILDREN'S AREA

◆ RESULTS

Demographics

Observers recorded data on 54 children while they were in the children's area. Of those 54 children, 31 (57.4%) were boys and 23 (42.6%) were girls (Table 11).

Table 11. Sex of Child.

	Frequency	Percent	Valid Percent	Cumulative Percent
Valid Girl	23	42.6	42.6	42.6
Boy	31	57.4	57.4	100.0
Total	54	100.0	100.0	

Age, using four age groups, of the child was estimated and recorded as well. About 9% were younger than kindergarten age. The modal category was kindergarten through 3rd grade with 44.4% in this category. Those in the fourth through 8th grade were the second most common (29.6%) and about one-of-six children (16.7%) were in high school (Table 12).

Table 12. Age of Child.

	Frequency	Percent	Valid Percent	Cumulative Percent
Valid Pre-K	5	9.3	9.3	9.3
K-3rd	24	44.4	44.4	53.7
4th-8th	16	29.6	29.6	83.3
9th-12th	9	16.7	16.7	100.0
Total	54	100.0	100.0	

Researchers also recorded the type of group with which the children entered the children's area. Three group types were identified and recorded: alone, with single adult, or with family. Over 50% of children came to the area with their family. Another third came to the area with a single adult while 13% entered alone (Table 13).

Table 13. Group Type.

	Frequency	Percent	Valid Percent	Cumulative Percent
Valid alone	7	13.0	13.0	13.0
with single adult	18	33.3	33.3	46.3
with family	29	53.7	53.7	100.0
Total	54	100.0	100.0	

Lastly, the number of children in the group was noted; this included the child being observed. Two was the modal category (40.7%) while another 35.2% entered alone (Table 14).

Table 14. Number of Children in Group.

	Frequency	Percent	Valid Percent	Cumulative Percent
Valid 1	19	35.2	35.2	35.2
2	22	40.7	40.7	75.9
3	9	16.7	16.7	92.6
4	3	5.6	5.6	98.1
5	1	1.9	1.9	100.0
Total	54	100.0	100.0	

Time in area

Once the child entered the children's area, time was recorded using a stopwatch until the child exited the area. Total time was recorded in seconds and in minutes. The results for the number of minutes the observed children were in the children's area are in the table below (Table 15). The mean time in the children's area was 3.63 minutes (SD = 3.12 minutes). The median was 2.83 minutes, which means that about half the children were there less than 2.83 minutes and about half were there more than 2.83 minutes. The minimum time was .13 minutes (or about 8 seconds) while the maximum time was 16.15 minutes. Ninety percent were in the area less than 7 minutes.

Total time in the children's area was examined using the demographic variables to determine if any of the variables explained variability in the time spent in the area. Sex of the child did exhibit some variability in average time: boys (M = 2.97) were in the area for a shorter time period than girls (M = 4.52). However, the mean difference of 1.55 was not statistically significant at the 0.05 level ($p = .07$). Of note, the standard deviation for girls (SD = 3.80) was well over one minute more than for boys (SD = 2.33); this suggests that time in the area for boys was more consistent and less varied than for girls (Table 16).

Table 15. Total Time in Young Scientist! Children's Area.

	Statistic	Std. Error
Mean	3.6287	.42392
95% Lower Confidence Interval for Mean	2.7784	
95% Upper Bound	4.4790	
5% Trimmed Mean	3.3221	
Median	2.8333	
Variance	9.704	
Std. Deviation	3.11516	
Minimum	.13	
Maximum	16.15	
Range	16.02	
Interquartile Range	3.58	
Skewness	1.630	.325
Kurtosis	3.980	.639

Age also could influence the amount of time in the children's area. Pre-Kindergarten children had the longest average time in the area (M = 3.93) while high schoolers had the shortest mean time (M = 2.43). However, while there were mean differences by age group, the test for statistical significance was not significant at the .05 level (p = .673) (Table 17).

Next, total time in the children's area was examined with group type. Children entering in a family group spent the longest total time (M = 3.13 minutes) while those alone had the shortest mean time in the children's area (M = 1.14 minutes). The One-Way ANOVA test for significance of mean differences was not significant at the .05 level (p = 0.069) (Table 18).

Table 16. Total time in children's area by sex.

Sex	N	Mean	Std. Deviation	Std. Error	95% Confidence Interval for Mean		Minimum	Maximum
					Lower Bound	Upper Bound		
girl	23	4.52	3.80	.792	2.88	6.16	.38	16.15
boy	31	2.97	2.35	.421	2.11	3.83	.13	9.97
Total	54	3.63	3.12	.424	2.78	4.48	.13	16.15

Table 17. Total time in children's area by age group.

Age Group	N	Mean	Std. Deviation	Std. Error	95% Confidence Interval for Mean		Minimum	Maximum
					Lower Bound	Upper Bound		
Pre-K	5	3.93	1.40	.554	2.391	5.469	1.90	4.90
K-3rd	24	3.85	3.83	.782	2.237	5.472	.22	16.15
4th-8th	16	3.87	2.93	.732	2.308	5.430	.13	9.97
9th-12th	9	2.43	1.82	.608	1.032	3.835	.37	5.50
Total	54	3.63	3.12	.424	2.778	4.479	.13	16.15

Table 18. Total Time (in minutes) in children's area by group type.

Group Type	N	Mean	Std. Deviation	Std. Error	95% Confidence Interval for Mean		Minimum	Maximum
					Lower Bound	Upper Bound		
alone	7	1.138	1.040	.393	.177	2.10	.13	2.88
with single adult	18	3.795	2.955	.696	2.33	5.27	.38	9.97
with family	29	4.126	3.318	.616	2.86	5.39	.20	16.15
Total	54	3.629	3.115	.424	2.78	4.48	.13	16.15

Last, total time in the area was analyzed by number of children in the group. Results were statistically significant (p = .024). Those who were in the children's area alone spent significantly less time, on average, in the area (M = 2.00 minutes) compared to those who were in a group of three children (5.33 minutes) (Table 19).

Table 19. Total time in children's area by number of children.

Number of Children	N	Mean	Std. Deviation	Std. Error	95% Confidence Interval for Mean		Minimum	Maximum
					Lower Bound	Upper Bound		
1	19	2.00	1.71	.392	1.18	2.83	.13	5.53
2	22	4.35	3.59	.766	2.75	5.94	.20	16.15
3	9	5.33	3.25	1.08	2.83	7.83	1.38	10.88
4 or 5	4	3.59	2.52	1.26	-.421	7.60	1.00	6.53
Total	54	3.63	3.12	.424	2.78	4.48	.13	16.15

Individual exhibits

The table below shows the percentage (rounded to the nearest whole percentage) of children who entered the Young Scientist! area and their participation in the nine behaviors for each of the eleven exhibits (which includes the junior ranger station located in the near right corner of the room) (Table 20).

Only the observing and geysers model exhibit drew participation by over half of all children. Some 80% of children went to the observing exhibit and 76% of children went to the geysers model exhibit. The exhibits most likely skipped were the "Is It True?" exhibit with 82% skipping it and the ID Wildlife exhibit with 80% skipping it. The mean for all exhibits was 61% skipped.

Very few children skipped exhibits while exhibits were occupied; this occurred for only two exhibits (ID Wildlife and Predicting Geysers).

The most read exhibits were the Geysers Model (15%), Predicting Geysers (13%), and the Is it True? (11%). All other exhibits had fewer than 10% of children doing any reading. Reading aloud was less prevalent than reading to one's self (as might be expected). Reading aloud was observed for only three exhibits (Observing, Is It True?, and Geysers Model), each of which had 2%.

Interaction was observed for all eleven exhibits with an average of 19% across all exhibits. Interaction varied by exhibit, ranging from a high of 56% for the Observing exhibit to a low of 6% for the Young Scientist Trivia and Geysers Model exhibits. On average, shared interaction occurred 6% of the time. Observing had the highest amount of shared interaction (26%). Animal Tracks (9%), Geysers Model (7%), and Jr. Ranger (7%) had some shared interaction, too.

Behaviors were cross-tabulated with the demographic variables to determine if any statistical significant patterns existed. Results of all tests are shown below in the table (Table 21). Significant relationships are identified and the characteristic of the demographic variable with the highest frequency of that particular behavior is identified. For example, the relationship between skipped and sex was significant and furthermore, results indicate that boys were more likely to skip the junior ranger station than girls.

Table 20. Percentages of children at each exhibit engaging in selected behaviors.

Exhibit Name	Skipped	Skipped, Occupied	Read	Looked	Read Aloud	Interact	Shared Interaction	Unintended Interaction	Photo Taken
Observing	20%	0%	9%	43%	2%	56%	26%	0%	0%
Layers of Life	69%	0%	4%	24%	0%	7%	4%	0%	0%
Young Scientist Trivia	78%	0%	9%	19%	0%	6%	4%	0%	0%
Is it True?	82%	0%	11%	6%	2%	15%	2%	0%	0%
Stage	65%	0%	0%	17%	0%	28%	2%	0%	0%
Eating Silica	56%	0%	7%	32%	0%	22%	6%	0%	0%
Animal Tracks	67%	0%	9%	22%	0%	19%	9%	0%	0%
ID Wildlife	80%	2%	0%	13%	0%	7%	0%	0%	0%
Predicting Geysers	67%	4%	13%	20%	0%	19%	1%	0%	0%
Geysers Model	24%	0%	15%	70%	2%	6%	7%	0%	0%
Jr. Ranger	63%	0%	2%	19%	0%	22%	7%	0%	0%
Mean	61%	1%	7%	26%	1%	19%	6%	0%	0%

Table 21. Relationships between demographic variables and behaviors in children's area.

Behavior	Sex	Age	Group Type	Number of Children
Skipped	Junior Ranger (boys more likely to skip than girls)	Junior Ranger (most likely to skip were high schoolers and least likely to skip were pre-schoolers)	No significant relationships	No significant relationships
Skipped, Occupied	No significant relationships	No significant relationships	No significant relationships	No significant relationships
Read	Animal Tracks (boys more likely than girls)	Is it true? (Children in 4 th – 8 th grade more likely); Eating Silica (Children in 4 th – 8 th grade more likely) Geyser Model (Children in 4 th – 8 th grade most likely)	Is it true? (Children with single adults more likely)	No significant relationships
Looked	No significant relationships	No significant relationships	No significant relationships	No significant relationships
Read Aloud	No significant relationships	No significant relationships	No significant relationships	
Interact	No significant relationships	Observing (Pre-K children more likely) ; Animal Tracks (Pre-K children more likely)	ID Wildlife (Children with single adult more likely)	No significant relationships
Shared Interaction	No significant relationships	No significant relationships	No significant relationships	Junior Ranger (Children in groups of three children more likely)
Unintended Interaction	None observed	None observed	None observed	None observed
Photo Taken	None observed	None observed	None observed	None observed
Other	None observed	None observed	None observed	None observed

GREATER YELLOWSTONE ECOSYSTEM



DEVELOPING NON-DESTRUCTIVE METHODS TO DETERMINE NATAL ORIGINS OF SNAKE RIVER CUTTHROAT TROUT IN THE JACKSON LAKE WATERSHED

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Photo Scott A. Carleton

✦ INTRODUCTION

Across their native ranges, cutthroat trout populations are imperiled due to habitat loss, habitat alteration, and introduction of non-native species (Liknes and Graham 1988, Behnke 1992, Hitt et al. 2003). These changes have not gone undetected and a great deal of time and money have been invested in conservation and restoration of cutthroat trout populations (Kershner 1995, USDA 1996, Young and

Harig 2002, Baker et al. 2008). The success of these projects is tightly linked to the ability of resource managers to prioritize management efforts. Specifically, where should the investments of time and money be focused to yield the greatest impact on conservation and restoration. This study proposes to use a relatively new, proven analytical tool, stable isotope analysis, to identify differences in the stable isotope signatures of tributary streams entering Jackson Lake. These differences are translated into the tissues, specifically otolith bones, of cutthroat trout

that use these tributaries during early life stages or upon return for spawning (Kennedy et al. 2002, Muhlfeld et al. 2005, Coghlan et al. 2007, Barnett-Johnson et al. 2008, Walther et al. 2008, Ziegler and Whitley 2010). The ability to link adult trout back to their natal origins and identify where these adults are returning to spawn will provide the data resource managers need to prioritize conservation and restoration efforts in the upper Snake River watershed, with special emphasis on tributary streams entering Jackson Lake.

Why are stable isotopes so useful in exploring this conservation need?

Within a watershed, bedrock geomorphology can exhibit a high degree of heterogeneity. This is especially evident in the Rocky Mountains of the western United States, specifically in and around the Grand Teton and Yellowstone National Parks (Figure 1). Geologic heterogeneity of watersheds is the key to understanding the power of isotopic analysis in reconstructing the life histories of fish. Different geologic substrates (granite, sandstones, limestones, etc.) often contain different proportions of elements. Most elements have different forms, called isotopes, and the ratio of these isotope forms changes between rock types and with the age of the rock (Barnett-Johnson 2008). Different rock types have variable, yet predictable, abundances of the isotopes of different elements. For example, the element strontium has two stable isotope forms; strontium 86 and strontium 87. As rocks form, they incorporate different amounts of the strontium isotopes. Additionally, as rocks age, radioactive rubidium (Rb) decays to strontium 87 thus altering the abundance of this isotope in the rock. Using new analytical techniques, we can measure these differences and quantify the ratio of the heavier (87) to the lighter (86) isotope of strontium. This is important, because when streams and rivers arise from different geologic substrates within a watershed, they often yield significantly different strontium isotope signatures.

We can indirectly measure the strontium isotope signature of the geologic substrates in a watershed. As water passes over rock or percolates through the ground it slowly erodes the rock and becomes a direct, elemental and isotopic, reflection of the rock type(s) it has passed over and through. Fish

absorb the strontium isotope signature of the water directly into their tissues. Fish then become a direct reflection of the water they live in, which is a direct reflection of the geology the water has passed over and through.

One particular tissue in fish that records this environmental signature is an ear bone called an otolith. Fish lay down daily layers in their otoliths that are made up of elements from the water where a fish is currently living. These daily bands accrete into monthly and annual bands that fisheries biologists routinely use to age fish (Huber et al. 1987). Because these bands accumulate daily over the lifetime of a fish, when it moves between isotopically different waters this signature is permanently recorded in the layers of the otolith (Muhlfeld et al. 2005, Barnett-Johnson et al. 2008).

Using this approach, we successfully characterized the strontium isotope signatures of tributaries and fish living in these tributaries within the Jackson Lake watershed in 2011 (Carleton 2012). Our success has been directly linked to the heterogeneity of the geology surrounding Jackson Lake and the upper Snake River (Figure 1). This heterogeneity is highly predictive of differences in the strontium isotope signature of tributaries that arise within them and fish that inhabit or use them seasonally.

Now that we have successfully used these differences to differentiate tributaries and the fish living in them, we proposed the current study to: 1) investigate the use of non-destructive sampling methods to characterize strontium isotope values in fish tissues by comparing and contrasting otolith isotope values with scales from the same Snake River cutthroat trout, 2) compare and contrast values from the 2011 study to differentiate tributaries in the Jackson Lake watershed with values obtained from the proposed study to determine repeatability of this work, and 3) use the results of the strontium isotope analysis from water and fish otoliths to describe differences across tributaries that we can then use to link adult and juvenile cutthroat trout in Jackson Lake back to their natal origins and describe fidelity of spawning adults to tributary streams non-destructively.

Geology Surrounding Jackson Lake, WY



Figure 1. Geomorphological heterogeneity surrounding Jackson Lake, indicated by differences in color and pattern, also indicate possible differences in strontium isotope signatures of waters originating from these geologic substrates.

✦ METHODS

Fish sampling and otolith analysis

In cooperation with the Wyoming Game and Fish Department in Jackson, Wyoming, we collected native and non-native trout during annual Jackson Lake sampling work at the end of June, 2013 to obtain otoliths and scales for isotope analysis and we also collected five native or five non-native trout from tributary streams of Jackson Lake using standard hook and line techniques and backpack electrofishing during July - August, 2013. Sagittal otoliths were removed, placed into vials with ultrapure (milli-Q) water and cleaned using an ultrasonic water-bath for 5 minutes to remove tissue. Otoliths were mounted sulcus side up on a microscope slide with Crystalbond

(Crystalbond™ 509, Ted Pella Inc. Redding, CA) and sanded using a MTI Corporation UNIPOL-1210 grinding/polishing machine (1200 grit sand paper wetted with milli-Q water) to reveal the core to the edge.

Laser ablation multi-collector inductively coupled mass spectrometry was used to assess $^{87}\text{Sr}:^{86}\text{Sr}$ in otoliths throughout the life of each fish. Otolith analysis was conducted at the University of California - Davis Interdisciplinary Center for Plasma Mass Spectrometry using a New Wave Research UP213 laser ablation system coupled with a Nu Plasma HR (Nu032) multiple-collection high-resolution double-focusing plasma mass spectrometer system. Line scans across the face of the otolith from the core to the edge generated $^{87}\text{Sr}:^{86}\text{Sr}$ profiles throughout the life of the fish. A scanning speed of 10

$\mu\text{m/s}$, laser pulse frequency of 10 Hz, beam width of 40 microns, and 65% laser power were used. A carrier gas (Helium) was used to carry ablated material into the mass spectrometer where it was mixed with Argon gas before entering the plasma. $^{87}\text{Sr}:^{86}\text{Sr}$ values were normalized in relation to $^{87}\text{Sr}:^{88}\text{Sr}$ (0.1135) to correct for instrumental mass fractionation. ^{87}Rb interference of ^{87}Sr (a possible contaminant found in industrial argon gas) was monitored by measuring ^{85}Rb minimizing interference. Instrumental accuracy was ensured using a modern marine coral (an in-house calcium carbonate standard). By ablating this standard, a comparison was made for each standard run to values known for modern day sea water to account for any instrumental drift throughout runs ($^{87}\text{Sr}:^{86}\text{Sr} = 0.70918$) (Hobbs et al. 2010). Ablations of the standard yielded $^{87}\text{Sr}:^{86}\text{Sr} = 0.70920 (\pm 0.000098; n = 49)$. Samples were adjusted throughout sessions to known values of the coral standard.

Statistical analysis

Data from scales and otoliths were analyzed using a paired T-test. Repeatability of strontium in different years was analyzed using a student's T-test. Discriminant function analysis was used to classify tributaries and Jackson lake otolith isotope values.

◆ RESULTS

Field collections

We collected 23 adult Snake River cutthroat trout and 13 adult lake trout from Jackson Lake and 46 juvenile trout from 10 different tributaries in the Jackson Lake watershed.

Scales

We had mixed success ablating scales collected from both adult and juvenile trout. Laser power sufficient enough to extract enough material for isotope analysis resulted in the laser ablating through the material and not generating any data. For trout collected from Jackson Lake, we were able to generate data from only 17 of 36 fish due to similar reasons. Strontium isotope values of scales were higher than paired otolith values (0.7127 ± 0.0047 and 0.7100 ± 0.0005 , respectively; Paired T= 2.41, $p = 0.03$, $N=17$).

Repeatability and differentiation

In 2013, we collected juvenile Snake River cutthroat trout, brown trout, and brook trout from 7 of 8 streams sampled in 2011 (Appendix 1). We did, however, obtain samples from three additional

tributaries not sampled in 2011 (Appendix 1). Strontium otolith isotope values did not differ between years in 4 of the 7 streams, but did differ in Glade, Arizona, and Lizard Creeks. Differences in the creeks between years was 0.0002, 0.0005, and 0.0001, respectively.

Discriminant function analysis on all 10 tributaries independently was only 63%. Only North Moran Creek, Upper Polecat Creek, and Bailey Creek had 100% classification rates. Misclassified creeks were grouped based on misclassification assignments into AGLU (Arizona, Glade, Lizard, and Upper Sheffield Creeks) and PDQ (Pilgrim, Dime, and Quarter Creeks). Discriminant function analysis on the reorganized creeks improved to 85%. When the reorganized creeks were run with Jackson Lake, classification success decreased to 83% with one fish from Jackson lake classifying to the PDQ grouping and 3 of 20 AGLU fish classifying to Jackson Lake.

Natal origins

Thirteen of the 23 Snake River cutthroat had primordia isotope values that differed from Jackson Lake (Figure 2A). Eighteen of the 23 cutthroat trout had isotope values throughout their life history indicating they had been residents in the system for most of their lives or had edge values that did not differ from Jackson Lake indicating they moved into the lake from somewhere else and had been in the lake long enough for the isotope values to be recorded in the otolith (Figure 2B). Five of the 23 cutthroat had strontium isotope values from the primordia to the edge that never matched Jackson Lake isotope values (Figure 3). One of the 13 lake trout had natal strontium isotope signatures that matched Jackson Lake values, changed dramatically toward the edge, and then shifted back to the value of Jackson Lake at the edge (Figure 4A). A second lake trout had primordia isotope values indicating its natal origins were not in Jackson Lake and then moved into Jackson Lake where it spent the remainder of its post natal life (Figure 4B). The remainder of the lake trout caught in Jackson Lake, 15 of 17, had strontium isotope signatures that did not differ between the primordia and the edge of the otolith (Figure 4C). Visual assignment of Snake River cutthroat trout with natal origins outside of Jackson Lake found that 8 appear to have originated as juveniles from the AGLU group, 2 from the PDQ group, one from Polecat Creek, and 2 have natal primordia signatures that do not match any measured tributaries (Figure 5A and B).

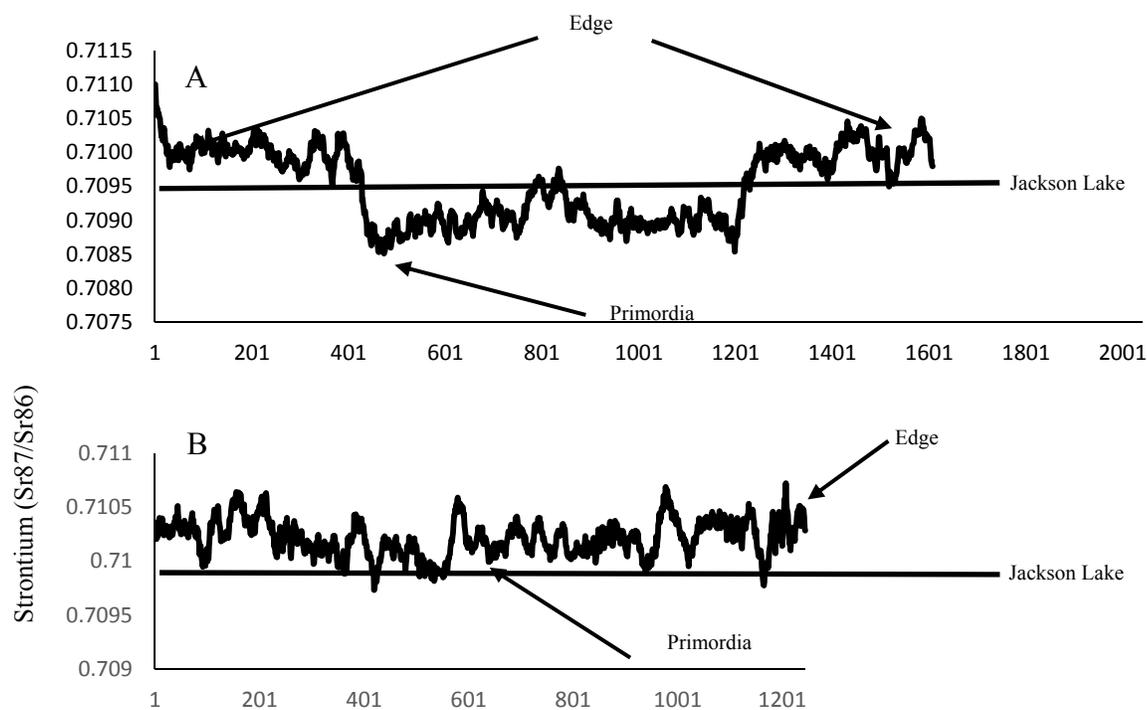


Figure 2. Ablation plots of two representative Snake River cutthroat trout show a shift from a different location of natal origins to the Jackson Lake values (A) and no shift throughout their lifetime (B).

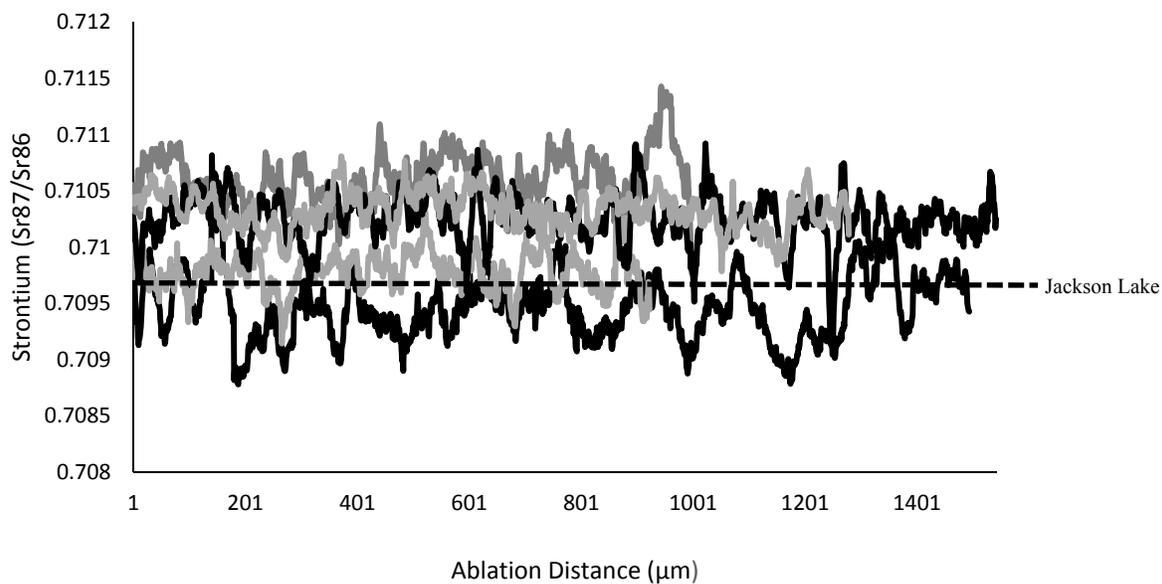


Figure 3. Five of the Snake River cutthroat trout captured have no isotope values that match Jackson Lake indicating they are recent arrivals and have not been in the system long enough to incorporate the lake isotope values into their otoliths.

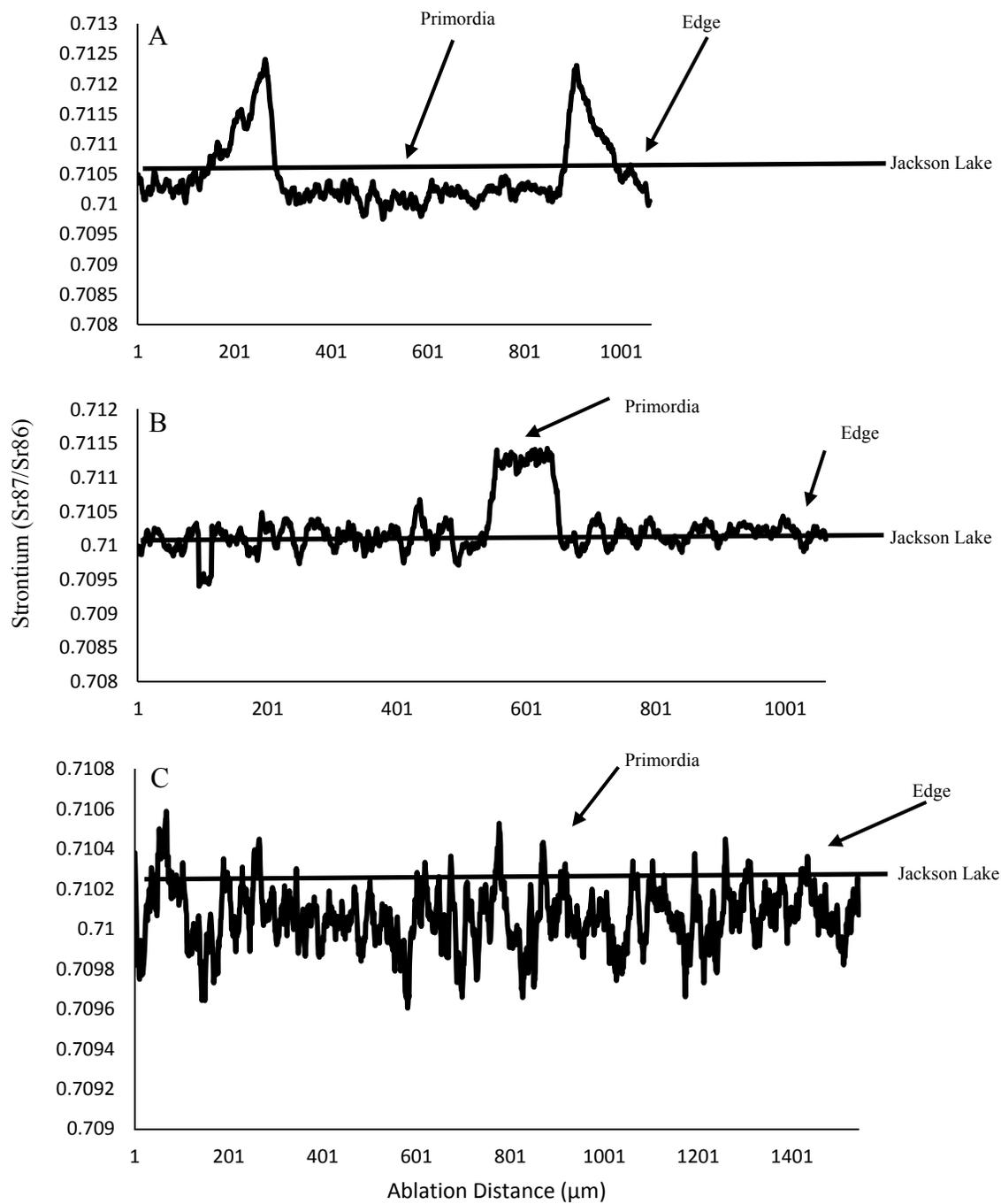


Figure 4. Ablation plots of three lake trout show primordia values that indicate natal origins in Jackson Lake, a movement out of the lake at a later age, and then back into Jackson Lake (A), natal origins not in Jackson Lake but movement into the lake at a young age (B), and a lake trout that was born in and has never left Jackson Lake (C).

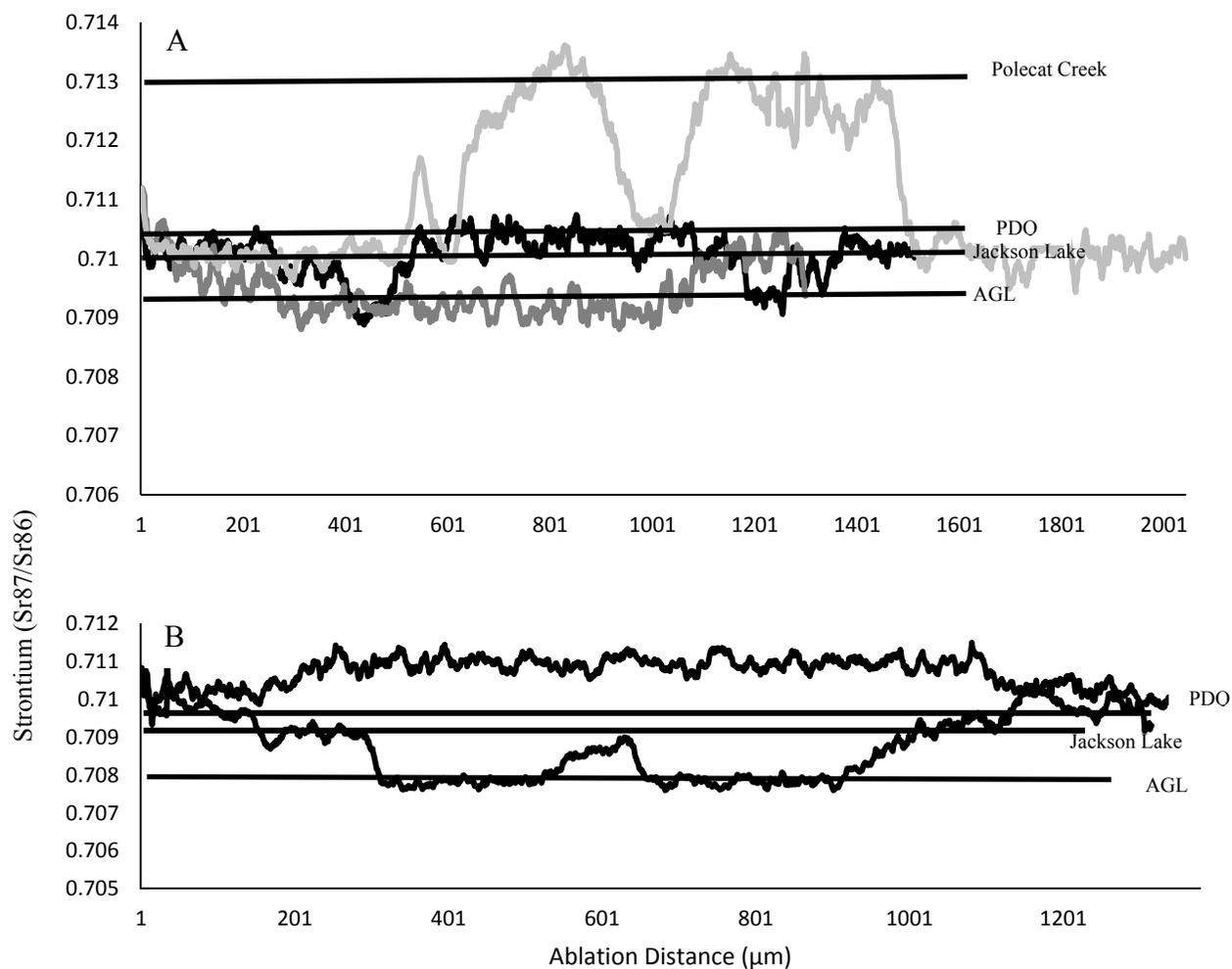


Figure 5. Three Snake River cutthroat trout that have natal values that match streams characterized in the Jackson Lake watershed (A) and two Snake River cutthroat trout that have natal values that don't match streams characterized during this pilot study (B).

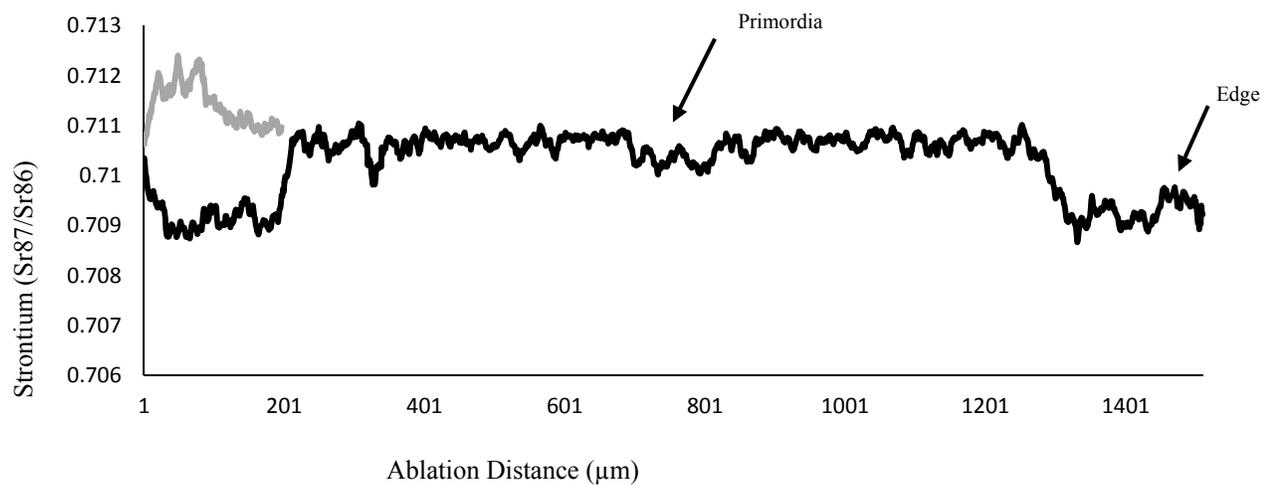


Figure 6. Laser ablation of otolith (black line) and scale (gray line) demonstrate the offset observed between the two tissue types.

◆ DISCUSSION

Non-destructive methods

Scale strontium isotope values differed significantly from otolith isotope values (Figure 6). We know that otolith isotope values very closely resemble the strontium isotope values of the water they live or have lived in throughout their lives (Carleton 2012, Muhlfield 2012). Scale values appear to overestimate the true isotopic value of the water they live in and the variability around these values make it difficult to use scales as a proxy for watershed wide isotopic variation. We are learning from other studies we are currently involved with, that this overestimation is caused by the large amount of phosphates found in scales that are not found in otoliths. When the sample material is introduced into the mass spectrometer, the phosphate groups form aggregations that have similar mass of Sr87. This causes the instrument to overestimate the amount of Sr87 in a sample. We are currently working on a method to minimize this error. At this time, use of scales does not seem to be a viable option to replace otoliths in characterizing watershed isotope values for differentiating fish and assigning adult fish back to their natal origins.

Additionally, even though isotope values are higher in scales, one thing we do not see mirrored in scales that we see in otoliths are the isotopic shifts. Six of the 17 scales were paired with otoliths that showed distinct shifts between the primorida and edge (Figure 6). These scales did not show the same pattern, which leads to further skepticism about their use as substitute for otoliths.

Repeatability of watershed isotope values

Because watershed values are influenced primarily by the rock substrates water flows over and through, values in these systems should change on geologic time scales. To test this we collected fish from the same locations in 2011 and 2013. Overall, otolith isotope values did not differ between years. However, a few locations yielded differences, albeit small, that had statistically different values (Appendix 1). Because much of our inference is at the 3rd and 4th decimal places and because we are dealing with such small sample sizes, we argue that these statistical differences do not translate into biologically significant values. We believe that this method, within the Jackson Lake watershed, has high reproducibility and reliability for future larger scale studies that are needed to better characterize a larger portion of the watershed northward into Yellowstone National Park.

Natal origins

One of the more interesting inferences we hope to make about the fish in Jackson Lake, especially the Snake River cutthroat trout, is their natal origins. Out of the 23 Snake River cutthroat trout collected in 2013, 13 had natal origins that differed from Jackson Lake isotope values (Figure 3). This is not surprising as we know that cutthroat trout migrate up tributary streams to spawn. Of the 13 cutthroat trout with obvious isotope shifts between the primordia and the edge of the otolith, the largest proportion, 62%, were from the AGLU grouping, 15% from the PDQ grouping, one from Polecat Creek, and two from creeks we have not characterized in this system (Figure 5). Our isotope results agree with Stephens (2008) who found most of the creeks on the eastern side of Jackson Lake had the highest numbers of young of year cutthroat trout. What otolith microchemistry allows us to do additionally is put these fish into specific stream groupings, sometimes within specific streams.

What we do find disconcerting in this study is that the groupings do not necessarily follow geographic groupings as predicted. Pilgrim, Dime, and Quarter Creek are at northern and southern ends of Jackson Lake and occupy substrates dominated by different geological rock types (Figure 1). On the other hand, Arizona and Lizard are next to each other and in closer proximity to Sheffield and Glade Creeks which lies more with our predictions. It is interesting that Dime and Quarter and Glade and Sheffield are in such close proximity to one another but have significantly different isotope values. Additionally, Bailey Creek which lies between Arizona and Pilgrim also has a unique isotope value, although one could argue that it is fairly similar to the AGLU groupings (Appendix 1). Our only explanation for the disparity in groupings along the eastern portion of Jackson Lake is that the limestone deposits that extend from Glade Creek down to Pilgrim Creek exert a larger influence on water chemistry than initially hypothesized (Figure 1; white and red dotted geologic types). Furthermore, creeks coming out of the west side of Jackson Lake have predictably high strontium isotope values as can be seen in values from North Moran Creek (0.7567 ± 0.0001) and from water values reported by Carleton (2012) that is characteristic of granites.

While there is some disagreement between a couple of groupings in the watershed, one interesting result from this study is that 5 of the 18 cutthroats captured in the lake did not originate in the lake. Specifically, ablations of the otolith did not produce any values from the primordia to the edge that ever

match Jackson Lake (Figure 3). What this indicates is two different life histories potentially exist for cutthroat trout in Jackson Lake. Some of the cutthroat trout are residents in Jackson Lake and others are seasonally migratory potentially hanging out in the Lake for a short time following spawning (Figure 2B and Figure 3, respectively). We also cannot discount that they might also be new arrivals from upstream towards Yellowstone National Park where the scope and budget for this pilot study have not allowed us to sample and characterize strontium isotope values.

Ultimately, the results of the 2011 and 2013 pilot studies have revealed that strontium otolith microchemistry is a viable tool for differentiating fish in the Jackson Lake watershed and is useful for determining the natal origins of adult cutthroat trout as well as determining whether or not cutthroat trout are residents in the lake itself. We do caution that the results of these studies have been small in scope and sample size and should be used as a launching point to tackle these same questions across the entire watershed from Jackson Lake into Yellowstone National Park, better spatial sampling from tributaries, and increased sample sizes of adult fish from not only Jackson Lake but from the Snake River upstream of Jackson Lake.

◆ ACKNOWLEDGEMENTS

We thank the Jackson Wyoming Game and Fish Department field crew (Diana Miller, Rob Gipson, Traci Stephens) for their assistance in providing data and field work on this project. We also thank Sue Oney for her assistance during the first pilot study in 2011 and Sue Consolo-Murphy for her assistance and support of this pilot study and this program at the field station. Thank you to the former director Dr. Hank Harlow and current director Dr. Harold Bergman for their support at the research station. Special thanks to Celeste Havener for her work keeping us all in line and on schedule. Finally, we thank the National Park Service for providing the funding for this program.

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Appendix 1. Strontium isotope values of trout otoliths sampled in 2011 and 2013 show repeatability across years.

Sample Site	2011	2013	Sample Site	2011	2013
Dime Creek	0.7103	0.7100	Arizona Creek	0.7099	0.7093
Dime Creek	0.7103	0.7103	Arizona Creek	0.7099	0.7095
Dime Creek	0.7103	0.7101	Arizona Creek	0.7098	0.7094
Dime Creek	0.7103	0.7100	Arizona Creek	0.7098	0.7093
Dime Creek	0.7098	0.7100	Arizona Creek	0.7098	0.7093
Berry Creek	0.7108	.	Quarter Creek	.	0.7108
Berry Creek	0.7105	.	Quarter Creek	.	0.7106
Berry Creek	0.7108	.	Quarter Creek	.	0.7104
Berry Creek	0.7103	.	Quarter Creek	.	0.7106
Berry Creek	0.7107	.	Quarter Creek	.	0.7105
Upper Polecat Creek	0.7114	0.7129	Bailey Creek	.	0.7097
Upper Polecat Creek	0.7134	0.7128	Bailey Creek	.	0.7097
Upper Polecat Creek	0.7127	0.7129	Bailey Creek	.	0.7097
Upper Polecat Creek	0.7104	0.7131	Bailey Creek	.	0.7098
Upper Polecat Creek	0.7102	.	Bailey Creek	.	0.7097
Pilgrim Creek	0.7102	0.7102	North Moran Creek	.	0.7557
Pilgrim Creek	0.7103	0.7105	North Moran Creek	.	0.7567
Pilgrim Creek	0.7102	0.7105	North Moran Creek	.	0.7593
Pilgrim Creek	0.7102	.	North Moran Creek	.	0.755
Pilgrim Creek	0.7102	.			
Upper Sheffield Creek	0.7102	0.7088			
Upper Sheffield Creek	0.7102	0.7100			
Upper Sheffield Creek	0.7103	0.7094			
Upper Sheffield Creek	0.7102	0.7100			
Upper Sheffield Creek	0.7100	0.7100			
Glade Creek	0.7092	0.7096			
Glade Creek	0.7092	0.7093			
Glade Creek	0.7093	0.7095			
Glade Creek	0.7093	0.7095			
Glade Creek	0.7094	0.7095			
Lizard Creek	0.7095	0.7095			
Lizard Creek	0.7095	0.7094			
Lizard Creek	0.7095	0.7093			
Lizard Creek	0.7095	0.7094			
Lizard Creek	0.7094	0.7093			

EXPLORING THE PHYSIOLOGICAL MECHANISMS AND ECOLOGICAL CONSEQUENCES OF ENERGETIC TRADEOFFS: AN INTEGRATIVE STUDY OF THE INFLUENCES OF AVIAN MALARIAL INFECTION ON THERMOGENIC PERFORMANCE

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✦ INTRODUCTION

Survival in variable environments often requires careful allocation of resources to competing physiological and behavioral functions. Because these competing processes often have additive energetic costs (Hawley et al. 2012), a limited resource pool forces individuals to make difficult trade-off decisions regarding energetic investments (Lochmiller and Deerenberg 2000). These trade-offs are a cornerstone of life-history theory that is aimed at determining the optimal allocation strategies in variable environments (Ricklefs and Wikelski 2002), and understanding their physiological and ecological consequences has renewed poignancy in the face of the unprecedented rate of anthropogenic environmental change occurring across the planet.

One such trade-off that is of primary ecological importance is related to immune function. Mounting an immune response is an energetically demanding process that potentially draws resources from other energetically expensive activities, such as thermoregulation in small endotherms (Sheldon and Verhulst 1996, Lochmiller and Deerenberg 2000, Norris and Evans 2000). The consequences of this trade-off between immune function and thermoregulatory ability should be especially acute in high-elevation habitats, because the capacity for aerobic thermogenesis is impaired under hypoxic conditions (Rosenmann and Morrison 1975, Chappell

et al. 2007). Thus, even in the absence of an immune challenge, small endotherms living at high altitude are faced with a double bind because their thermogenic capacity is compromised under conditions where thermoregulatory demands are especially severe. Consistent with these expected effects on fitness, survivorship studies of high-altitude endotherms have established strong empirical links between thermogenic capacity and survival in the wild (Hayes and O'Connor 1999). Infection can exacerbate the effects of hypoxia by further compromising thermogenic performance in an environment where any impairment of thermoregulatory capabilities is likely to have profound effects on individual survival, and potentially the persistence of entire populations.

In light of the potential tradeoffs between immune function and thermoregulatory ability, one alarming trend is the upslope movement of pathogens as their vectors track changing global temperatures and other anthropogenic disturbances. One well-known example of altitudinal movement of an important wildlife disease is avian malaria. Malarial parasites are transmitted by mosquito vectors, and several lines of evidence suggest that global climate change is influencing their distributions, exposing naïve avian populations to parasites with devastating consequences (Freed et al. 2005, Garamszegi 2011, Loiseau et al. 2012). For example, populations of Hawaiian honeycreepers, having evolved for approximately 5 million years in the absence of avian

malaria (Fleischer et al. 1998), were decimated when the parasite and their vectors were introduced (Dobson and May 1991, McCallum and Dobson 1995). Historically, honeycreeper populations at higher elevations have been spared because they resided in habitats that were too cool to sustain populations of mosquitos. Recently, however, increasing temperatures on the island of Hawaii have resulted in a general upward movement of parasites and vectors, resulting in a doubling in prevalence, over a decade, of avian malaria in birds found at 1900 m in elevation (Freed et al. 2005). While the general trend is toward warmer temperatures, climate change has also resulted in an increased frequency of severe weather events (e.g., Petoukhov et al. 2013). These extreme weather events may place a premium on thermoregulatory ability, particularly for non-migratory animal species that cannot escape to locations with more benign winter conditions.

Despite the intuitive connections among immunity/thermoregulatory energetic trade-offs, the severity of thermoregulatory challenges in high-elevation habitats, and the growing threat of the invasion by novel pathogens, no previous study has systematically explored the extent, mechanisms and consequences of these interactions within an integrated framework. Grand Teton National Park (GTNP) and the surrounding areas provide an ideal natural laboratory to explore these interconnections. Our focal species (see below) occur in relatively high densities across a broad altitudinal gradient, as well as in both disturbed and undisturbed habitats. Taken together, these factors suggest strong spatial patterns in disease prevalence (e.g., Jones et al. in press) and a high likelihood that individual birds will face decisions about where to allocate their limited energetic resources. Here we describe an integrative study that will take advantage of this natural laboratory to examine both physiological underpinnings and ecological consequences of energetic trade-offs between immune function and thermoregulatory performance in passerine birds. We will focus on common species of resident birds, Red-breasted Nuthatch (*Sitta canadensis*), Mountain Chickadee (*Poecile gambeli*) and Dark-eyed Junco (*Junco hyemalis*). These species are terrific study organisms for numerous reasons: 1) they are common (*P. gambeli* and *S. canadensis*) or abundant (*J. hyemalis*) in GTNP according to the GTNP Bird Checklist; 2) they are all year-round residents and therefore need to cope with changing weather patterns in each season; and 3) previous work has shown populations of each can be infected with avian hematozoa, which cause avian malaria, at relatively high rates (e.g., ~20% in *S. canadensis*, 35% in *P.*

gambeli, [Grenier et al. 1975] ~67% in *J. hyemalis* [Deviche et al. 2001]).

This work will not only have important implications for our understanding of nature and extent of energetic trade-offs, but it also has important long-term conservation implications. From this perspective, our studies of the spatial distributions of avian malaria parasites will provide a crucial first step toward developing an understanding of how disease prevalence is distributed in the region, providing a baseline against which to measure future patterns of prevalence. Our physiological studies of energetic tradeoffs and the effects of disease state on thermogenic performance will in turn illuminate the potential ecological consequences of spatial variation in malaria infection rates.



Figure 1. Dark-eyed Junco in metabolic chamber.

The primary goal of our proposal is to investigate the energetic trade-offs between thermoregulation and immune function in several species of Passerine birds. Conducting this research in wild populations allows us the ability to address how birds deal with chronic pathogenic infection, as opposed to LPS injection that primarily simulates an acute response (e.g., Owen-Ashley and Wingfield 2007).

◆ METHODS

We measured a number of metabolic parameters to assess thermogenic performance and baseline energetic costs associated with infection status. Specifically, we used open-flow respirometry to measure: 1) thermogenic capacity [cold-induced summit metabolic rate (SMR) in heliox (21% O₂, 79% He)]; 2) resting metabolic rate (RMR); and 3) metabolic scope [MS = (SMR – RMR)]. These parameters are commonly used to assess thermoregulatory capacities, cold tolerances, and

baseline energetic costs in birds (Swanson 2010). RMR measurements were made over night using ambient air in a temperature-controlled chamber that was held at temperatures within the thermoneutral zone for small passerines (28°C – King and Swanson 2013). We estimated RMR as the minimum O₂ consumption averaged over a 10-min period. Measurements of SMR were made the following day using a heliox atmosphere (21% O₂, 79% He) in temperature-controlled chambers that were maintained from 0°C to -5°C. Rates of heat loss in heliox are several times greater than in ambient air, which makes it possible to elicit VO₂ max without risking cold injury to experimental animals (Rosenmann and Morrison 1974). We estimated SMR as the maximum O₂ averaged over a 5-min period. Similar protocols have been used to elicit SMR in previous studies (Swanson 2001, Liknes et al. 2002, Swanson 2007, Cheviron et al. 2012, 2013, King and Swanson 2013). To control for the effects of body mass on metabolic parameters, all analyses of RMR and SMR were conducted using an ANOVA framework with body mass as a covariate (Packard and Boardman 1988).



Figure 2. University of Illinois graduate student, Maria Stager, taking metabolic measurements.

DNA was extracted from blood samples using standard protocols. Following DNA extraction, we determined the infection status of each bird using a nested PCR assay (Jones et al. in press). Briefly, we amplified a portion of the cytochrome-b gene of *Haemoproteus* and *Plasmodium*, parasites causing avian malaria, and ran the PCR products on an agarose gel. The presence of a band signifies infection, the absence of a band means the bird is not infected with these parasites. In addition to this plus/minus assay, for all positive individuals we will sequence the amplified portion of the cyt-b gene (Jones et al. in press) to identify the lineage of parasite present in each

infected bird. The PCR and sequencing assay provide detailed information on the identity of parasites causing avian malaria. It is important to note that at this time we are only proposing to survey infection status, we are not making any assessments of outward disease symptoms. That said, future work may specifically investigate disease manifestation. Similarly, although we have initially focused on avian malaria, it is likely that some birds may be infected with other parasites (i.e., those that do not cause avian malaria) as well.

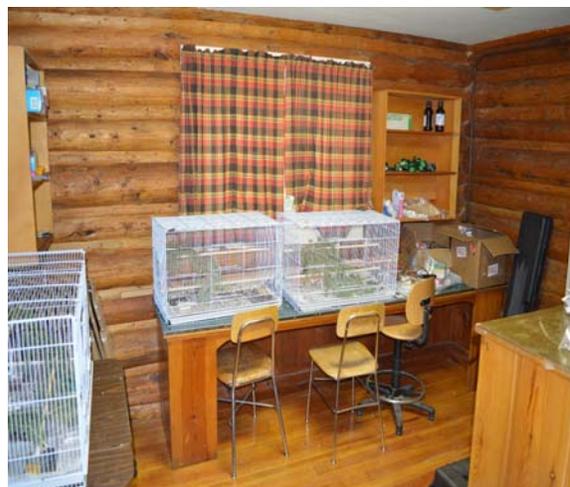


Figure 3. Aviary setup in Berol Lodge.

◆ RESULTS

During the summer of 2013, we measured metabolic parameters (basal metabolic rate and cold-induced summit metabolic rate) in 26 Dark-eyed Juncos, 4 Mountain Chickadees, and 6 Black-capped Chickadees. A majority of these birds have also been screened for the presence of blood-borne malaria parasites (*Haemoproteus* and *Plasmodium*), using protocols developed in the Carling Lab. A total of 6 birds tested positive for one or more malaria strains, all of which were juncos. Interestingly, although we sampled juncos from several localities, all of the detected infections occurred at a single site, just outside the boundaries of Grand Teton National Park (Bridger-Teton Nation Forest, Pacific Creek Rd. 43° 53' 17.23" N, 110° 28' 29.92" W). At this locality, 40% of the sampled birds were infected with malaria, suggesting that it may represent a local hotspot for avian malaria infection. Analysis of the influence of malaria infection on metabolic parameters is ongoing, but early analysis suggests that infection status may only have subtle effects on metabolic performance in juncos.

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ALPINE MOIST MEADOW RESPONSE TO NITROGEN DEPOSITION IN THE GREATER YELLOWSTONE ECOSYSTEM

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✦ ABSTRACT

The deposition of anthropogenic reactive nitrogen (N) in alpine ecosystems can have multiple deleterious effects on plants, soils and hydrology in both the alpine and areas downstream through leaching and export. Thresholds for ecological responses to N deposition have been established for lakes, soils and changes in plant community composition in some areas of the Rocky Mountains. These thresholds offer a target for land and air resource managers to prevent significant changes in ecosystem function, however the underlying feedbacks controlling ecosystem response have not been fully examined. Research originally proposed in association with our UW NPS Small Grant aimed to examine plant to ecosystem interactions within alpine moist meadows between two sites receiving different levels of N deposition. This focus has been modified, in response to site limitations, to examine the mediation of the N cycle by the alpine moist meadow plant community.

✦ INTRODUCTION

Human alteration of the nitrogen (N) cycle has resulted in a drastic change in availability of biologically active N, in both human-dominated and natural landscapes (Vitousek *et al.* 1997). This increased availability has translated into high rates of deposition in regions with expanding populations of people, and widespread changes in land use, such as

areas in the central Rocky Mountains (Baron *et al.* 2000, Matson *et al.* 2002, Benedict *et al.* 2013). Alpine ecosystems are particularly susceptible to increased inputs of N, as higher elevations receive disproportionately more precipitation (Weathers *et al.* 2000, Williams and Tonnessen 2000), making the alpine of the southern Rocky Mountains an ideal location for studying ecosystem responses and processes under elevated N deposition. The Rocky Mountains on the western side of the Continental Divide in Wyoming receive enhanced deposition associated with emissions of nitrogen from agricultural sources, while the eastern side has comparatively low levels of ambient deposition (Figure 1; Van Miegroet 2010, Nanus *et al.* 2003). By comparing the same alpine meadow communities in these mountain regions, our goal was to estimate the existing effects of N deposition in the alpine ecosystem, and compare community level plant-soil feedbacks.

There are many environmental consequences associated with increased N deposition, ranging from ecosystem scale changes in function and services, to local scale changes in diversity of the plant community. The level of N addition necessary to induce environmental consequences, or the ecological threshold, varies between different measures of response and provides a metric of stability for comparing how well that ecosystem is able to stabilize added N. At the community level, numerous studies in the Rocky Mountain alpine have shown that even levels of N deposition at or below 4 kg N ha⁻¹ yr⁻¹

significantly alters species composition in dry meadows (Bowman et al. 2006, 2012). At the ecosystem scale, research in dry meadows has shown that N deposition levels greater than $20 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ was sufficient to induce increases in nitrate leaching (Bowman et al. 2006).

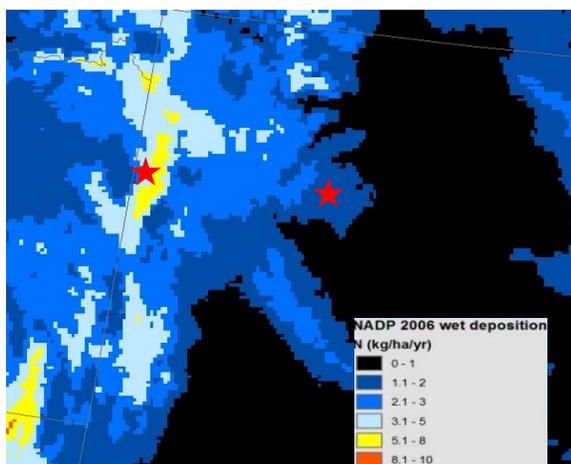


Figure 1. Nitrogen deposition in the Greater Yellowstone Ecosystem of Wyoming, with field sites in this study marked by red stars. The site in Shoshone NF was established in the summer of 2012 and maintained in the summer of 2013. We were unable to establish the GRTE site as planned, due to lack of similarity in plant composition in the alpine between these regions.

Factors contributing to potential differences in ecosystem thresholds, however, include biological changes and feedbacks within an ecosystem. There are three main pathways for plants to influence ecosystem response, including 1) species-level variation in N uptake (Hobbie 1992, Suding et al. 2004, Ashton et al. 2008), 2) storage of nutrients in plant tissue (Bowman et al. 1993, Bowman 1994, Chapin et al. 1997), and 3) loss of N in litter (Hobbie 1992, Steltzer and Bowman 1998, Chapman et al. 2006). While these processes occur at the level of individual plant species, for processes happening at the ecosystem scale it is net plant community contributions that ultimately contribute to subsequent ecosystem responses to N deposition. Understanding the net community response N deposition informs predictions of ecosystem responses to N deposition that take into account internal biological feedbacks. These biotic contributions may provide positive (amplifying) or negative (stabilizing) feedbacks to changes in the environment (Hobbie 1992, Chapin et al. 1997). Stabilizing feedbacks minimize changes in ecosystem while amplifying feedbacks can intensify the effects of environmental change (Chapin et al. 2010).

Under the context of N deposition to alpine ecosystems, characteristics of plants with biotic

stabilizing feedbacks to N deposition may include traits that increase storage of N in plant tissues, and litter with high C:N ratios (Steltzer and Bowman 1998, Bowman 2000). Another mechanism possibly mitigating the impact of N deposition is the immobilization of N in soil or recalcitrant materials, thereby limiting the leaching of nitrate (Janssens et al. 2010). On the other hand, community traits that amplify the effects of N deposition within an ecosystem may include increased rates of N cycling through stimulated productivity rates with a greater input of N rich litter into the soil (low C:N ratios) or increased N turnover in tissues (higher rates of decomposition) and soil (both from deposition and increased herbivory) (Bowman and Steltzer 1998, Throop 2005). These characteristics would facilitate an increase in N availability for plants and microbes, increases in nitrification, and ultimately the loss of 'extra' N from the alpine due to increased nitrate mobility.

Estimation of the thresholds for the amount of nitrogen addition that causes changes to vegetation and soils are a common research goal across the National Park Service, and previous studies have estimated critical load values for N deposition in alpine lakes, and alpine plant communities and soils at ROMO (Baron 2006, Bowman et al. 2006, 2012). Continued research is expanding this concept into GRTE, and the Greater Yellowstone Ecosystem, with implications for management and long-term data comparison (Van Miegroet 2010, Pardo et al. 2011, Hansen 2012). Our research questions for this project were 1) do differences in ambient N deposition gradient translate into differences in ecosystem N availability and coupled changes in plant community indices? And 2) are plant contributions to nitrogen storage and cycling the same between east and west slopes or do they change with levels of N addition?

◆ STUDY AREA

Original study design included two research sites: one in an area of low N deposition (Shoshone National Forest) and the second in an area of high N deposition (Grand Teton National Park; GRTE) (Nanus et al. 2003). Proposed site locations were selected based upon estimated levels of ambient N deposition (low and high) on federally protected land within the Greater Yellowstone Ecosystem (Figure 1). Site positioning at Shoshone National Forest was completed during the summer of 2012, with a goal of establishing a field site in GRTE in the summer of 2013.

The field site at Shoshone National Forest (NF) included three alpine moist meadows, each with a slope <15%. Average elevation at this site is 3200 m, and the site position is 43.930061 N, 109.2930157 W. The area used for research is located NE of the Meadow Creek Trail in the Greybull Ranger District of Shoshone NF.

Despite repeated attempts to locate appropriate alpine meadow communities in GRTE during the summer of 2013 (and 2012); no area was found that met the study site requirements for comparable plant composition, including the main two dominant moist meadow plant species (*Geum rossii* and *Deschampsia caespitosa*). Areas surveyed included Mount Meek Pass, Alaska Glacier Basin, and Rendezvous Peak during visits in July and August 2013. While the exclusion of this site limits the comparison between areas receiving different levels of N deposition in the Greater Yellowstone Ecosystem, we have four other established sites in the Rocky Mountains of Colorado supported through other sources of funding, which will allow the existing site to be of importance in addressing related questions and hypotheses.



Figure 2. Nitrogen deposition samplers installed in the field at Shoshone National Forest

◆ METHODS

Site based measurements

The summer/growing season bulk deposition of nitrogen (N) was measured passively at Shoshone NF using ion-exchange mixed bead resin columns installed for at least 60 days (Bytnerowicz et al. 2001, Fenn et al. 2009, Hansen 2012). Five samplers were installed at the site per summer (Figure 2), and total deposited N was determined using 2M KCl extraction of the sampler resin and analyzing for $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ in the Kiowa Chemistry Laboratory at

INSTAAR, using a Lachat QuikChem 8000 Spectrophotometric Flow Injection Analyzer and a Dionex DX 500 System IonPac AS11 Ion Chromatograph (Sunnyvale, California, USA) (Bowman et al. 2006).

Climate data was extracted from PRISM to examine annual differences in precipitation between years of study (2012-2014), and local weather data will be determined from neighboring climate stations.

Soil measurements

We measured soil N availability using mixed bead resin bags buried in the plant rooting zone during growing season months (five resin bags per meadow). We also measured soil water nitrate concentration, an indication of mobile inorganic N in soil, using lysimeters and vacutainers installed at each of the five plots in each meadow (Figure 3). Soil water samples were attempted during three periods during the growing season, including post snow melt, peak growing season and following plant senescence (Bowman et al. 2012), however no water was successfully sampled using the vacutainers during 2013. Finally, bulk soil samples (10 per meadow) were used to determine relative abundance of N in soil using C:N ratios, soil pH and soil cation exchange capacity.



Figure 3. Soil lysimeter and attached vacutainer collecting soil water for analysis of mobile N (nitrate).

Vegetation measurements

We used the point intercept method to quantify species composition in moist meadows at Shoshone NF (data collected 2012-2013; Jonasson 1988). For this method, we measured 20 plots in each moist meadow (4 meadows) in the summer of 2012, and 10 plots per meadow (3 meadows) in the summer of 2013. Vegetation plots were 1 m by 1 m in area.

For determining total aboveground biomass, we harvested total standing vegetation in 10 cm by 10 cm subplots at peak biomass in the summer of 2012. We plan to specifically target measurement of net primary productivity (annual new growth) collection at peak biomass in the summer of 2014 using the same in-field procedure. This sample harvest will be followed by separation of new and old material in the laboratory.

We also collected plant tissue samples for determining tissue concentrations of C:N for dominant and sub-dominant species at each plot for tissue at peak plant biomass (10 samples per meadow all species 2012, dominants only 2013). Litter collection of dominant species within each meadow will also be performed post senescence to estimate N input to the soil at the end of the growing season (10 samples per meadow; data collected 2014).



Figure 4. Crew measuring vegetation presence and abundance.

◆ PRELIMINARY RESULTS

Site scale data

N deposition at Shoshone NF during the summer of 2012 totaled 0.24 ± 0.08 kg N ha⁻¹ over a 92 day growing season (June 1st- August 31st). Results from the summer of 2013 are still being analyzed at the KIOWA laboratory at the University of Colorado Boulder, and should be completed by April 2014.

We are still in the process of downloading and analyzing associated climate data from years 2012-2014.

Soil data

Soil samples collected at Shoshone NF during the summer of 2012 were found to have an average pH of 5.33 (± 0.08 SE) and a cation exchange capacity (CEC) of 21.47 (± 1.07 SE) cmol_c/kg, indicating well buffered soils. Dominant cations included Ca⁺ and Mg⁺ (77 and 18 percent of total CEC,

respectively), with trace amounts of other cations measured (Al⁺³, Fe⁺², Mn⁺², and Na⁺).

Measurements for concentrations of mobile N (nitrate) in soil water were unsuccessful during the summer of 2013 due to very dry soils throughout the summer. No water was consequently collected despite three attempts and attempts to maintain vacutainers on soil lysimeters for over 24 hours. We plan on making an earlier attempt during the summer of 2014, to include post snowmelt moisture.

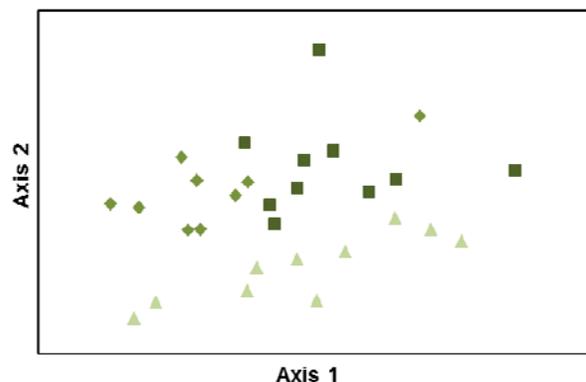


Figure 5. Non-metric dimensional scaling ordination of the plant community composition between three alpine moist meadows at Shoshone NF (each meadow is represented in a different shade of green). Two axes accounted for 85.3% of total variation in composition between plots in each meadow.

Remaining soil data, including measurements of growing season N availability using ion-exchange resin bags, and soil ratios of carbon to N, are on schedule for being completed by May 2014.

Vegetation data

Aboveground biomass of vegetation among the moist meadows at Shoshone NF averaged 2.2 kg/m² (± 0.12 SE). The total species richness was 17.1 species/m² (± 0.41 SE), and the Shannon Diversity Index was 2.02 (± 0.03 SE) across the three moist meadows.

Non-metric dimensional scaling ordination was able to describe the plant community composition in two axes (Axis 1 = 58.5% variation, Axis 2 = 26.8% variation, with a final stress of 15.12, and a final instability of < 0.00000 (Figure 5). Axis 1 was correlated with the presence of *Carex elynodes* ($r^2=0.83$), an as-of-yet-unidentified legume forb ($r^2=0.52$) and *Geum rossii* ($r^2=0.5$). Axis 2 was correlated with an unknown sedge ($r^2=0.76$), and a different unknown forb ($r^2=0.35$). Future analysis will examine environmental correlations with community

composition of individual plots, including soil N availability, C:N, pH, CEC, and soil water nitrate, as well as the relationship of dominant plant types on soil N pools.

Dominant and sub-dominant plant tissue concentrations of carbon and N are still being determined using elemental analysis, and are on target for completion by May 2014.

Future data collection

Supplemental data associated with the Shoshone NF site is planned for collection during the summer of 2014 to address some of the remaining potential feedbacks within the alpine ecosystem components. This will include collections of the net primary productivity of the vegetation at peak biomass (early August) to estimate the annual storage of N in the plant tissue, and plant litter following senescence in the fall. We will also collect soil samples for determining soil texture (percent sand, silt, clay) to differentiate possible soil controls on vegetation that may affect the interpretation of our existing data. Finally, we plan to continue collecting samples in an attempt to measure soil nitrogen mobility using lysimeters and attached vacutainers for collecting soil water samples for nitrate concentration analysis.

◆ **MANAGEMENT IMPLICATIONS**

Although we were unable to implement our full project through the installation of a field site in Grand Teton National Park, we have successfully collected most of our proposed samples from Shosone NF, and plan to visit this site again in the summer of 2014. The grant money awarded our project for the year 2013-2014 was instrumental in the success of collecting those data, and has allowed us to gain additional in-house support to maintain this field site for data collection into the coming year. We will also be able to successfully incorporate the Shoshone site into a larger scale regional study of N deposition in the Rocky Mountains, which will ultimately contribute to two dissertation chapters of A. Churchill.

At this time many of our statistical analyses are preliminary, as soil and vegetation samples are in the process of chemical analysis, and we are waiting on these results before moving forward. These samples are on schedule for completion in the coming months, and we anticipate that our first publication using these data will be written during the fall of 2014. It is our hope that these results will offer regional

conclusions about N deposition in the Rocky Mountains and the GYE, and offer increased information on the internal feedbacks between plants and N processes in alpine moist meadows.

◆ **ACKNOWLEDGEMENTS**

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USING FIELD DATA TO VALIDATE SATELLITE MODELS OF ELK FORAGE IN THE UPPER YELLOWSTONE RIVER BASIN

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✦ ABSTRACT

Spatial and temporal variations in grassland phenology are thought to play a critical role in migration patterns of large herbivores in the Greater Yellowstone Ecosystem. Phenology, referring to the timing of green-up in this study, is directly related to biomass and forage quality. Migratory elk (*Cervus elaphus*), therefore, are believed to follow phenology across an elevation gradient during the growing season to maximize their access to high quality and quantity of forage. Concern that climate change and human land use alterations of phenology may impact the benefits of elk migration highlights the need for landscape-scale vegetation phenology monitoring. Satellite-derived Normalized Difference Vegetation Index (NDVI) shows potential as a remote sensing tool to predict landscape-level shifts in grassland phenology, but is limited by a lack of validation at varying scales, seasons, and in human land use areas. This study is focused on validating the accuracy of satellite-derived NDVI in estimating grassland phenology, biomass, and forage quality throughout the summer growing season within elk migratory ranges in the Upper Yellowstone River Basin. Results from this study will provide managers and researchers with information on the accuracy of NDVI as a tool for monitoring the effects of climate change and human land use on grassland dynamics relevant to migratory elk.

✦ INTRODUCTION

Recent concern that climate change and human land use are altering vegetation phenology, growing season length, and productivity, highlights the importance of understanding the ecological

consequences of altered vegetation dynamics (Inouye 2008). Vegetation phenology was identified by the Intergovernmental Panel on Climate Change report as "...perhaps the simplest process in which to track changes in the ecology of species in response to climate change" (Friedl et al. 1994). Research suggests that altered phenology may result in asynchrony between species, modified competition for resources, altered community interactions, shifts in growing season and productivity of vegetation, and shifts in trophic interactions (Chapin and Shaver 1996, Despain 1990, Inouye 2008).

Understanding the impacts of altered phenology on wildlife population dynamics is becoming especially important in the Greater Yellowstone Ecosystem (GYE), where recent research has suggested that shifts in vegetation phenology may have significant impacts on elk (*Cervus elaphus*) populations (Harris et al. 2009). A recent study by Middleton et. al. (2013) attributes a decline in pregnancy rates of a migratory Yellowstone elk herd, in part, to altered vegetation phenology. In addition to climate change, changes in human land use outside of protected areas have also been shown to alter the phenology of forage in elk migratory ranges north of the park (Piekielek 2012). These studies suggest that the effects of climate change and human land use on vegetation phenology may have significant impacts on migratory elk populations. However, before decision makers can be confident in these findings, more research is needed on the accuracy of the tools used to study vegetation dynamics.

Monitoring vegetation phenology was historically limited by the small-scale of traditional field research (Homer et al. 2004), but has been revitalized by advances in remote sensing. Remote

sensing vegetation indices, such as Normalized Difference Vegetation Index (NDVI), have gained popularity in the study of phenology by offering large spatial and temporal scale information on vegetation dynamics relevant to ecosystem processes (IPCC 2007). Numerous studies have determined the relationship between NDVI, an index that measures red and near-infrared surface reflectance, and vegetation phenology, productivity, and protein content (Homer et al. 2004, IPCC 2007, Maynard et al. 2006). Because of this relationship, NDVI has been used to study wildlife population dynamics and migration patterns (IPCC 2007).

While NDVI is gaining popularity in ecology, little attention has been given to the known limitations of NDVI. Because the scale of satellite-derived NDVI is intended to provide complete spatial coverage over single-pixel accuracy, small-scale NDVI assessments needed for wildlife research are often subject to error (Homer et al. 2004). NDVI is known to be affected by dry biomass, high variability in vegetation within pixel, atmospheric contamination, high soil exposure, and high biomass (Homer et al. 2004). Despite the popularity, no consensus has been made about where and when NDVI measures are accurate or limited in the GYE. For decision makers to be confident in the utility of NDVI in estimating the effects of climate and land use change on vegetation and elk population dynamics, validation of the relationship between NDVI and vegetation biomass, phenology, and forage quality is needed.

Building upon research done by Piekielek (2012) using NDVI to determine biophysical predictors of grassland phenology, this study will use field data to validate the accuracy of NDVI estimates of grassland phenology, biomass, and forage quality in migratory elk summer range in the Upper Yellowstone River Basin of the GYE. Piekielek's (2012) primary findings were that "seasonal variation in solar radiation, water availability, evaporative demand and temperature explain much of the variation in the timing of phenology" (Keatley and Hudson 2010). The goal of this research is to combine Piekielek's (2012) findings and the results from this research to provide comprehensive information on the utility of NDVI in predicting the effects of climate and land use change on vegetation metrics in the Upper Yellowstone River Basin. To achieve this goal, this study will validate the spatial and temporal accuracy of satellite-derived NDVI estimates of grassland phenology, biomass, and forage quality throughout the summer growing season in elk migratory ranges in the Upper Yellowstone River Basin.

◆ STUDY AREA

Study Area The study area consists of grasslands, exurban development, and irrigated agriculture in the southern section of the Yellowstone River Basin and grassland meadows in the northern section of Yellowstone National Park.

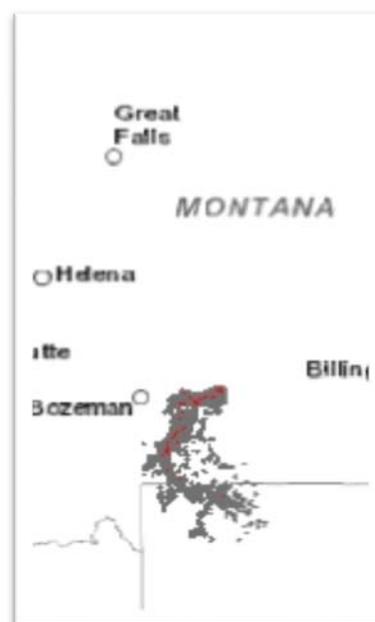
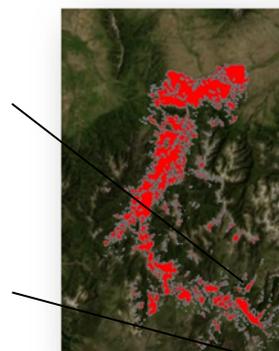


Figure 1: Upper Yellowstone River Basin Study Area Study plot selection.

All 250 m² MODIS satellite grassland pixels were identified by Piekielek (2012) across the study area using vector-delineated habitat types from Despain (1990) and from National Land Cover Datasets. Snow-off date and maximum annual NDVI (time during the growing season when biomass is maximized) analysis from 2001-2009 by Piekielek (2012) were used to categorize each pixel as early, mid, or late max NDVI phenology categories. Using Montana cadastral data, aerial images, and Piekielek's

(2012) NDVI analysis, pixels were categorized as private/non-irrigated, private/irrigated, or public/non-irrigated land uses. Three pixels were selected in each land use and phenology category class.

Field data Within each 250 m² pixel, ten 0.5 m² quadrats were clipped to ground level every 16 days from April to September for the growing seasons. Above-ground dry biomass, chlorophyll concentration, crude protein and in vitro dry matter digestibility were estimated for each quadrat sample. To explore the relevance of the clippings and NDVI to elk, fresh elk fecal samples were collected within each quadrat when available to compare elk fecal sample phenology and forage quality to the grass clippings and NDVI.

Satellite-derived NDVI MOD13Q1 16-day 250m² NDVI images for the ten sample periods were downloaded from the USGS Land Access Distributed Active Archive. Pixels were reprojected, assessed for quality, and rescaled to fit within the -1-1 NDVI range.

◆ PRELIMINARY RESULTS

Field clippings to estimate biomass, phenology, and forage quality were acquired for 144 pixels throughout the summer growing season of 2013. NDVI values for each pixel were acquired for each time period. Crude protein and in vitro dry matter digestibility tests for the quadrat clippings are still in progress. Preliminary results suggest biomass in the private irrigated land use was greater than both private non-irrigated and public non-irrigated land uses (Figure 2). Biomass was shown to increase at a higher rate in late and early plots than it did in mid phenology plots (Figure 3). Preliminary results suggest that the relationship between NDVI and above ground biomass varied by land use and phenology category (Figures 4 and 5).

Research Progress An additional summer of fieldwork will be completed during the 2014 growing season. After the two field seasons, 320 field pixel estimates of biomass, chlorophyll concentration, crude protein, and in vitro dry matter digestibility will be used to determine the accuracy of NDVI estimates of biomass, phenology, and forage quality.

Management implications Results from this study will provide information to managers, researchers, and conservation organizations on the accuracy of remote sensing NDVI in estimates of grassland biomass, phenology, and forage quality in elk migratory ranges in the Upper Yellowstone River

Basin. Results will be useful for understanding and planning for the potential effects of climate change and human land use on elk forage in the GYE.

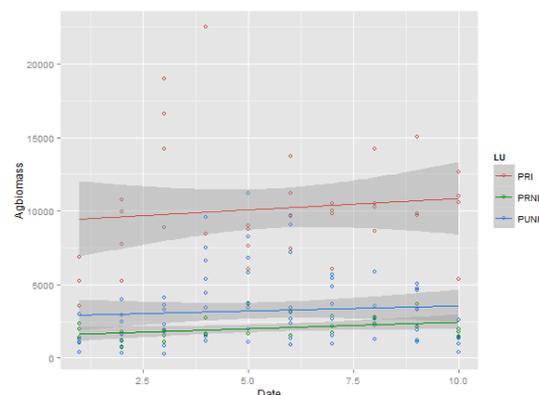


Figure 2. Above ground biomass by date for private irrigated (red), private non-irrigated (green), and public non-irrigated (blue) land use categories.

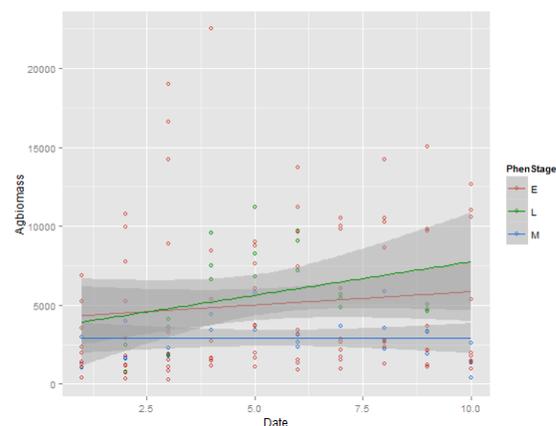


Figure 3. Above ground biomass by date for early (red), mid (blue) and late (green) phenology categories.

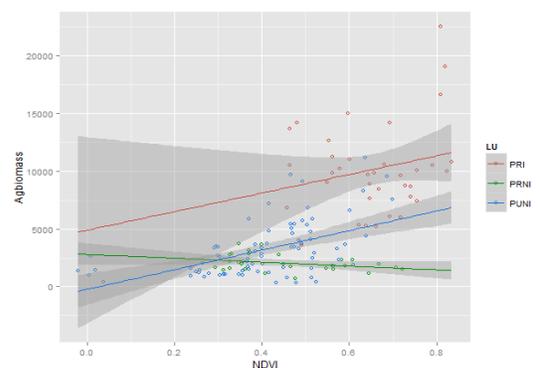


Figure 4. Biomass and NDVI for private irrigated (red), private non-irrigated (green), and public non-irrigated land uses.

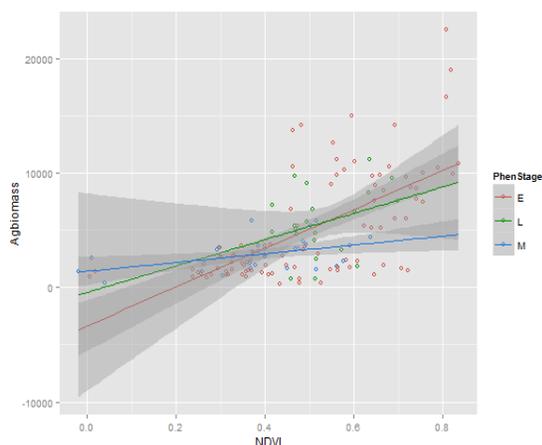


Figure 5. Biomass and NDVI for early (red), mid (blue), and late (green) phenology categories.



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VALIDATION OF FECAL-BASED METHODS FOR MONITORING NUTRITION AND REPRODUCTION OF MOOSE IN THE GREATER YELLOWSTONE ECOSYSTEM

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✦ INTRODUCTION

Understanding the influence of habitat and climate on wildlife nutrition, reproduction and demography is a major goal for natural resource managers and ecologists alike. Although both top-down (i.e., predation and disease) and bottom-up (i.e. habitat and nutrition) forces impact demography, the nutritional condition of an animal is an integration of its environment (Parker et al. 2009) and influences reproduction and survival (Clutton-Brock et al. 1987, Keech et al. 2000, Cook et al. 2004), thus allowing for the identification of limiting factors. Researchers and managers must understand which factors limit population growth before mitigating actions can be taken.

The demography of large herbivores is affected by juvenile survival (i.e., recruitment; Gaillard et al. 2000, Raithel et al. 2007), and natural resource managers often index recruitment by estimating juvenile-adult female ratios via ground or aerial surveys (Czaplewski et al. 1983). Although these ratios may be a robust characterization of recruitment, they are likely not a good measure of reproductive rate in populations where neonates and juveniles are frequently consumed by large carnivores. Additionally, because pregnancy and subsequent survival of juveniles is strongly influenced by maternal condition (Clutton-Brock et al. 1987, Keech et al. 2000, Cook et al. 2004), recruitment rates alone cannot provide inference regarding the mechanism (i.e. relative strengths of top-down vs. bottom-up limitation) driving variation in reproduction and survival of young.

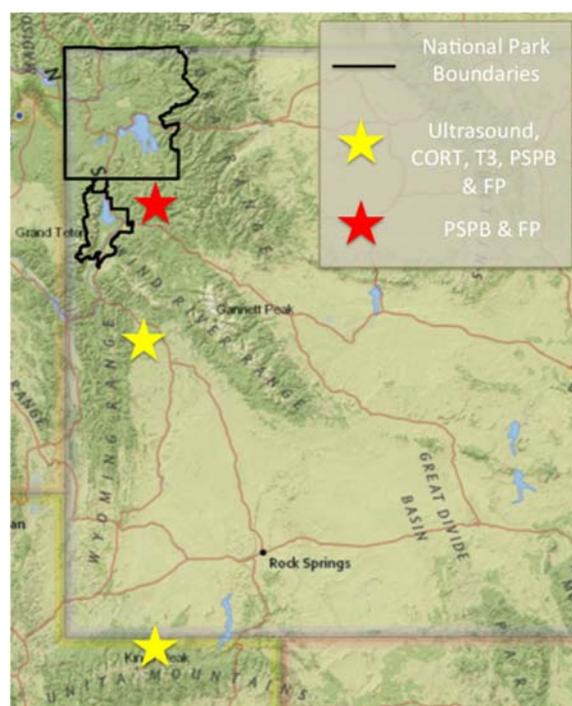


Figure 1. Map of study area within the GYE. Black lines delineate National Park boundaries. Yellow stars indicate sampling areas where ultrasound, GC (CORT), T3, PSPB and fecal progesterone (FP) data were collected. Red stars indicate sampling areas where only PSPB and FP data were collected.

Only recently have non-invasive methods for obtaining *in-vivo* nutritional data been developed and tested in free-ranging animals. Researchers rely on measures of body condition and reproduction through ultrasonography, body condition scoring, and presence of pregnancy specific protein B (PSPB) in serum to inform them about habitat quality, nutritional

condition and reproductive rates (Keech et al. 2000, Cook et al. 2004, Monteith et al. 2014). However, these methods are expensive and require the capture and handling of animals, which may be undesirable in many settings. Alternatively, more affordable, non-invasive, fecal-based methods to estimate nutritional condition and pregnancy may be used. The less-prohibitive nature of fecal-based approaches provides researchers and managers with data on nutritional condition and reproduction, and hence the potential to advance our understanding of habitat-demography relationships.

Increasingly, two popular methods for non-invasive (fecal-based) assessment of nutritional condition are the endocrine markers known as glucocorticoids such as cortisol and corticosterone (GC; Wasser et al. 2000) and triiodothyronine (T3; Wasser et al. 2010). GCs provide nutritional support during stressful events, such as unpredictable food shortages or predator escape, by promoting lipid metabolism and glucose production in support of metabolic needs. This adaptive response helps maintain energy balance during periods of restricted caloric intake (McEwen and Wingfield 2003). When reduced caloric intake is chronic, animals rely more heavily on endogenous reserves of energy (Parker et al. 2005), and a continued GC response mobilizes energy for metabolic needs. Due to this dynamic, GCs are expected to increase as nutritional condition declines (e.g., du Dot et al. 2009, Schultner et al. 2013), but this relationship may vary at similar levels of nutritional condition based on forage quality and availability (McEwen and Wingfield 2003, Wikelski and Cooke 2006). Interestingly, the GC response to negative energy balance is expected to have a cascading effect on thyroid function and metabolism (Eales 1988). T3, a prominent thyroid hormone, plays an important role in regulating metabolism and is positively correlated with metabolic rate (Danforth and Burger 1989). T3 is predicted to decrease with declining caloric intake and reduce energy use through its influence on metabolism (Danforth 1984). Thus, fecal measures of GC and T3 provide a potential lens through which nutritional limitation can be studied.

Because GCs rise dramatically when animals are experiencing a negative energy balance (McEwen and Wingfield 2003) and subsequently promote the mobilization of endogenous energy reserves (Porterfield 1997), this endocrine marker consistently relates to the nutritional condition in free-ranging vertebrates (e.g., Kitaysky et al. 1999, du Dot et al. 2009, Schultner et al. 2013). However, there are few examples of studies that quantify the relationship between T3 and the nutritional condition of free-

ranging animals, including large herbivores (but see Bahnak et al. 1981, Bishop et al. 2009), with the majority of the literature focused on sudden and unpredictable caloric restriction in laboratory settings (see Eales 1988 for review). In contrast, caloric restriction in large herbivores inhabiting temperate latitudes is predictable (i.e., during the winter season) and this taxonomic group is known to carry over energy reserves between seasons to deal with such caloric bottlenecks (Middleton et al. 2013, Monteith et al. 2013). Therefore, the endocrine responses of large herbivores may be considerably different from the responses to starvation and caloric restriction observed in laboratory settings or in free-ranging animals that do not store substantial energy reserves.

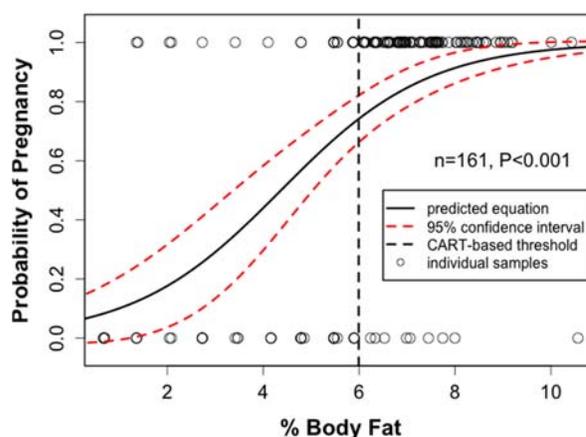


Figure 2. Percent body fat (February) in relation to pregnancy. The vertical, hashed line represents the CART-based percent body fat threshold for pregnancy, meaning body fat must be typically $>6\%$ during mating season. Because of such a nutritional threshold, pregnancy rate can be used as a proxy for indexing individual- and population-level nutritional condition.

The life-history strategies of large herbivores result in energetic trade-offs between reproduction and survival, where survival is highly conserved (Stearns 1992, Eberhardt 2002). Because of this life history, pregnancy status of individuals and pregnancy rates of populations are indicative of their nutritional condition (e.g., see Figure 2). Progesterone has been used to evaluate pregnancy in mammals for decades, and progesterone (progesterone metabolite) levels found in feces are indicative of pregnancy status (Monfort et al. 1993, Garrott et al. 1998, Cain et al. 2012, Murray et al. 2012). Historically, use of the fecal-based method to accurately determine pregnancy status has been hindered by limited statistical evaluation of progesterone thresholds. Several studies of large herbivores with known pregnancy status based on PSPB analysis use simple visual assessments (Monfort et al. 1993, Cook et al. 2002, Murray et al. 2012) or

comparisons of pregnant and non-pregnant groups (Garrott et al. 1998, Berger et al. 1999) to determine fecal progesterone thresholds (but see Cain et al. 2012) for a rigorous assessment of fecal progesterone threshold for large herbivores with uncertain pregnancy status). If fecal progesterone thresholds for species can be determined, researchers will be able to perform single-sample pregnancy tests, and thus quantify nutritional condition and reproduction of individuals and populations.

By understanding the relationship between T3, GC, and nutritional condition, non-invasive techniques for evaluating the linkages between habitat, nutritional condition, pregnancy and recruitment rates can be established. By comprehending the extent to which populations are limited by resources while simultaneously quantifying pregnancy and juvenile survival (i.e., calf-cow ratios or recruitment), researchers and managers can assess the relative influences of top-down and bottom-up forces on a population (Bowyer et al. 2005). Herein, we first validate the relationship between GC, T3 and nutritional condition, as well as develop a fecal-based pregnancy test for moose in the Greater Yellowstone Ecosystem. Secondly, based on the accuracy of our fecal-based approaches for monitoring nutritional condition and reproduction, we provide suggestions for methodological frameworks and future research. To validate the relationship between GC, T3, nutritional condition and pregnancy, we test the following predictions:

1. GC concentrations will be negatively related to nutritional condition. We expect higher levels of stress, indicated by high concentrations of GC, in individuals in poor nutritional condition.
2. T3 concentrations will be positively related to nutritional condition. We expect higher metabolic rates, indicated by high concentrations of T3, in individuals in good nutritional condition.
3. Probability of pregnancy will be positively related to the concentration of progesterones found in feces. We expect there to be a clear threshold in fecal progesterone concentration that is indicative of pregnancy.

◆ METHODS

Sampling

To assess the relationships between GC, T3 and nutritional condition, as well as to develop a fecal

progesterone threshold for determining pregnancy status, we used the gold standards of ultrasonography and PSPB analysis to determine the nutritional condition and pregnancy status, respectively, of moose in the GYE and northern Utah (Figure 1). We captured 55 adult, female moose on winter ranges using a hand-held net gun fired from helicopter. Each moose was hobbled and blindfolded prior to data collection. To determine the nutritional condition of a subset of moose (n=36), ultrasonography was used to determine the maximum depth of subcutaneous rump fat (Stephenson et al. 1998) and a palpation method was used to develop a body condition score (Cook et al. 2007). Ingesta-free body fat (IFBFAT; percent body fat) was calculated using an extension of Cook et al. (2010) predictive equations (Monteith et al. In Prep). A blood sample (20ml) was collected via jugular punch and feces were extracted in all moose (n=55). Blood samples were centrifuged and serum was pipetted into a 5ml cryovials and stored at -20°C until analyzed for PSPB concentration. Fecal samples (n=55) were placed in a plastic bag and stored at -20°C until analyzed for GC, T3 and progesterone concentrations.

Measuring PSPB and fecal hormones

The commercially-available BioPRYN wild assay was used for determination of PSPB concentration of all samples (n=55), and was completed by BioTracking LLC (Moscow, ID). BioPRYN wild is a typical sandwich enzyme-linked immunosorbent assay (ELISA) for determination of PSPB levels in serum samples that utilizes horseradish peroxidase labeled antibodies to cause a color change in the sample wells of a 96-well microplate. The assay includes 4 standards run in duplicate on each plate. The standards are halving dilutions from 1 ng/ml to 0.125 ng/ml. Color development of the assay occurs with the addition of 3,3',5,5'-Tetramethylbenzidine. Sulfuric acid is added to stop the reaction. The presence of color development was used to determine pregnancy status. In a subset of individuals (n=25), the optical density for each well was obtained from a plate reader with a filter wavelength of 450 nm (VersaMax, Molecular Devices, Inc). Simple linear regression was then used to fit an equation to the standards for each plate. The resulting equation was used to calculate a quantitative measure of PSPB concentration in each serum sample.

Pellets from each of 55 moose fecal samples were homogenized, and then freeze-dried. All samples were freeze-dried for 24-48 hours in a Labconco Freeze-Dry system at -50°C, and then thoroughly homogenized into a fine powder. Approximately 0.1g

was weighed from each sample, and a pulse-vortex double extraction with 15mL 70% ethanol was performed. Ethanol extracts were then stored at -20°C until assay. Radioimmunoassays were performed on ethanol extracts at previously validated dilutions for fecal GC and T3 ($n=36$), and progestagens ($n=55$), using MP Biomedicals' 125-I corticosterone kit, 125-I Total T3 kit & an in-house 3-H progesterone assay, respectively. The Center for Conservation Biology at the University of Washington (Seattle, WA) conducted GC, T3, and progestagen assays for 36 fecal samples, with the remaining 19 progestagen assays performed by the Smithsonian Conservation Biology Institute (Front Royal, VI). Levels of fecal hormones were then reported as ng per gram of dried feces. All hormone extracts were run in duplicate in each assay, and only those with intra-assay variation (%CV) below 10% were accepted, and controls were included in each assay to track inter-assay variation.

Validation of nutritional, GC and T3 relationships

For GC and T3 to be a biologically meaningful metric of nutritional state (i.e., malnutrition) we must understand how these hormones relate to the nutritional condition of animals. To determine the relationship between GC, T3 and nutritional condition (IFBFAT; percent body fat) simple linear regression was applied (Kutner and Nachtsheim 2004). In these models we treat nutritional condition, as determined by a gold standard (i.e., ultrasonography and BCS techniques), as the dependent variable and fecal GC and T3 concentrations as the independent measure. Predicted equations, 95% confidence intervals and 95% prediction intervals are presented (Kutner and Nachtsheim 2004).

Fecal progestagen as threshold for pregnancy

To develop a fecal progestagen threshold from which pregnancy can be determined for any given fecal sample, we applied a classification and regression tree (CART; Breiman 1984) analysis. CART is especially appropriate for our purposes because the classification component is designed to produce discriminant values of independent variables in the process of predicting values associated with the dependent variable (Breiman 1984). In this model we treat pregnancy status, as determined by a gold standard (i.e., ELISA measures of PSPB), as the dependent variable and fecal progestagen concentration as the independent measure. We also present the results of a logistic regression, including the predicted equation and associated 95% confidence interval, as a visual representation of the data.

RESULTS

Validation of nutritional, GC and T3 relationships

Fecal GCs were weakly related to nutritional condition (Figure 3, $n=36$, $P=0.16$), but suggest that individuals in poor nutritional condition are characterized by high CG levels. This model possessed little predictive power, as indicated by wide prediction intervals (Figure 3). Conversely, fecal T3 was more strongly related to nutritional condition ($n=36$, $P=0.008$). However, the relationship is negative (Figure 4), indicating that individuals in poor nutritional condition had relatively high metabolic rates, which is in contrast to our prediction. Similar to the relationship between GC and nutritional condition, the T3 model lacked predictive power (Figure 4). Although neither fecal GC nor T3 possessed predictive power, these hormonal markers may still serve as an index to nutritional condition when comparing populations or subpopulations (see Discussion).

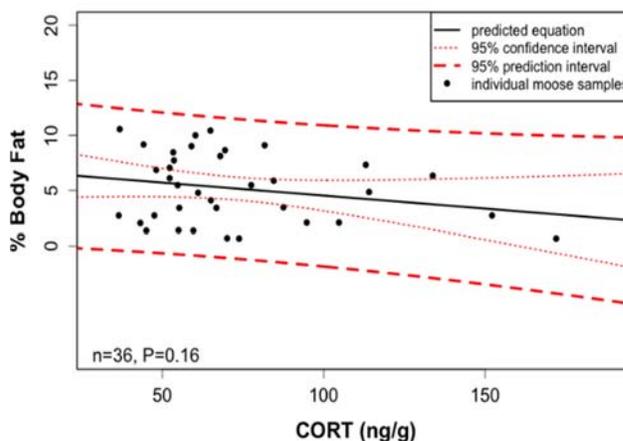


Figure 3. Relationship between percent body fat and fecal GC (CORT) concentrations.

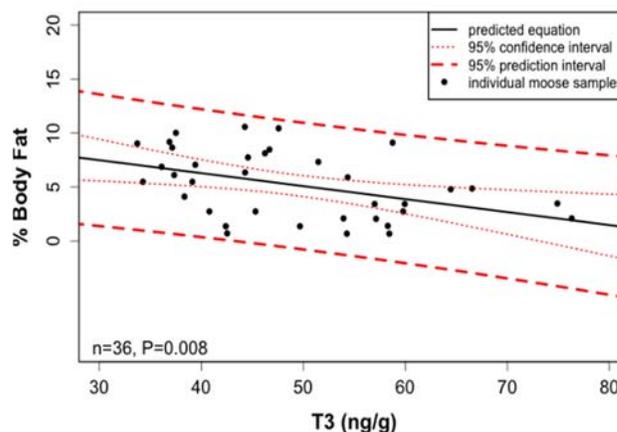


Figure 4. Relationship between percent body fat and fecal T3 concentrations.

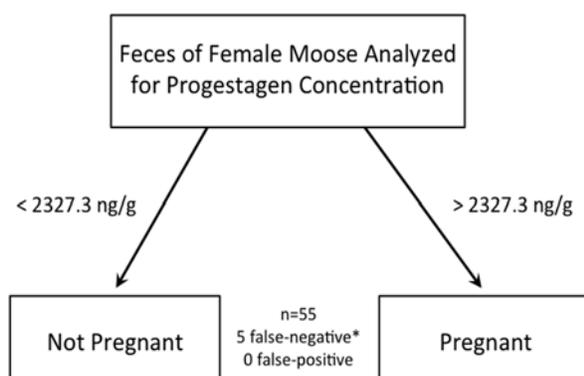


Figure 5. Graphical representation of the classification tree used to calculate the fecal progesterone threshold for determination of pregnancy status. * See Figure 6 and discussion for additional dialogue regarding the 5 misclassified (false-negative) individuals.

Fecal progesterone threshold for pregnancy determination

CART revealed a fecal progesterone threshold of 2327.3 ng/g (Figure 5). This threshold resulted in a 91% (50/55) accurate assessment of pregnancy based on fecal progesterone, indicating a clear fecal progesterone threshold for determination of pregnancy status. All five misclassifications were false-negatives (Figure 6), suggesting possible fetal reabsorption (Cook et al. 2002; see discussion). Logistic regression indicated a strong relationship between fecal progesterone concentration and pregnancy status ($n=55$, $P<0.001$). Even though a threshold of 2327.3 ng/g resulted in the misclassification of 5 individuals, quantitative ELISA assessment of PSPB may support the notion that some or all of our 5 false-negatives are indeed cases of fetal reabsorption, resulting in an increase in fecal-based pregnancy detection of 93%-100% (see discussion).

◆ DISCUSSION

Fecal GC measures may offer a non-invasive metric for assessing nutritional condition of populations or subpopulations, but not individuals. Our results indicate that fecal GC concentrations vary considerably at given levels of nutritional condition (i.e., percent body fat; Figure 3). The variability of GC across the gradient of nutritional condition we observed is likely due to the overall energetic environment the animal is experiencing, including both endogenous energy reserves and exogenous energy availability (McEwen and Wingfield 2003). Because nutritional stress and GC levels are not expected to rise dramatically until individuals cannot

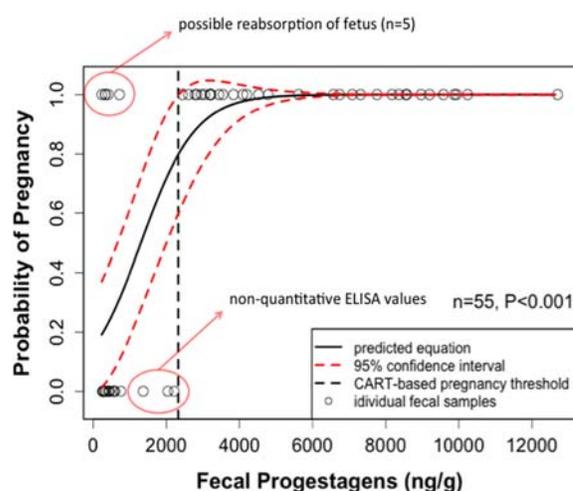


Figure 6. The relationship between fecal progesterone concentrations and pregnancy. Note the 5 false-negatives (upper left corner of plot) and that not all serum samples analyzed for PSPB used quantitative ELISA methods (bottom left corner of plot), which may induce inaccuracy in pregnancy status determination. See discussion for further details.

meet metabolic needs from a combination of both endogenous and exogenous sources, forage quality and availability interact with nutritional condition to determine the GC response (McEwen and Wingfield 2003). Hence, it will be difficult for researchers and managers using fecal-based approaches to disentangle whether elevated GC levels are caused by poor nutritional condition of the animal, deficits in protein or caloric intake, or a combination of these factors. Moreover, large herbivores carry over nutritional reserves from seasonal range to seasonal range (Middleton et al. 2013, Monteith et al. 2013), making the use of GC levels to identify condition of seasonal habitats unreliable. Whereas previous research has demonstrated statistically significant relationships between GC and nutritional condition (e.g., Kitaysky et al. 1999, du Dot et al. 2009, Schultner et al. 2013), our research indicated only weak correlation between GC levels and nutritional condition (coeff.= -0.23, 95% CI= -0.057, 0.009). Despite the non-significance of our GC model, a more robust sample size will likely yield statistical significance, suggesting that GC levels may serve as a proxy for nutritional condition in comparisons of populations or subpopulations.

Nutritional condition was correlated more strongly with fecal T3 than GC in our study (coeff.= -0.12, 95% CI= -0.207, -0.033). Similar to the relationship between GC and nutritional condition, T3 varied considerably within individuals in nearly identical nutritional condition (Figure 4).

Interestingly, the relationship between T3 and nutritional condition, however strong, did not concur with our biomedical and microcosm-based prediction.

This apparent contradiction has been observed in other free-ranging large mammals (Gobush et al. 2014), and thus deserves further attention. T3 levels were observed to be less variable at given levels of nutritional condition than GC (Figs. 3 and 4). Therefore, once a mechanistic understanding of why T3 levels are inversely related to nutritional condition in large mammals is reached, T3 may serve as a better proxy to population and subpopulation level nutritional condition than GC.

Pregnancy was determined by fecal progesterone concentrations in mid-February (Figure 5). Our results are consistent with previous reports of fecal progesterone thresholds in pregnancy studies of moose (Monfort et al. 1993, Berger et al. 1999, Murray et al. 2012). In this study, CART appears to provide a simple, objective and accurate means of calculating a threshold for fecal pregnancy tests. The CART-based threshold resulted in only a 91% (50/55) accuracy rate, with the 5 misclassified individuals all represented as false-negatives. These 5 misclassifications may have been non pregnant and had aborted fetuses or were in the process of reabsorbing fetuses (Cook et al. 2002), exhibiting low fecal progesterone levels, while ELISA detected the presence of PSPB. Reevaluation of PSPB via quantitative ELISA measures is needed to confirm the 91% accuracy rate as we would like accuracy to be >95%. Despite the <95% accuracy rate, the reported threshold of 2327.3 ng/g should perform well for comparing pregnancy rates between populations or subpopulations in nutritional studies and when aiming to assess habitat-performance relationships (Eberhardt 2002, Bowyer et al. 2005).

We have shown evidence that fecal-based measures of T3 and progesterone provide a non-invasive method for assessing nutritional condition and pregnancy rates in free-ranging populations of moose. Our pilot study was hindered by modest sample sizes and will benefit from augmentation. Despite this limitation, however, we believe that ample evidence has been provided to support continued allocation of time and monies to the validation and refinement of these techniques. Studies occurring in national parks and other settings where capture and handling of animals is undesirable will benefit greatly from the continued pursuit of non-invasive methods for monitoring nutrition and reproduction (Berger et al. 1999). Furthermore, non-invasive tools aimed at aiding our understanding of habitat-performance relationships and life history

characteristics will aid researchers and managers in assessment of bottom-up and top-down limitation (Bowyer et al. 2005).

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SPATIO-TEMPORAL ECOLOGICAL AND EVOLUTIONARY DYNAMICS IN NATURAL BUTTERFLY POPULATIONS (2013 FIELD SEASON)



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♦ INTRODUCTION

The study of evolution in natural populations has advanced our understanding of the origin and maintenance of biological diversity. For example, long term studies of wild populations indicate that natural selection can cause rapid and dramatic changes in traits, but that in some cases these evolutionary changes are quickly reversed when periodic variation in weather patterns or the biotic environment cause the optimal trait value to change (e.g., Reznick et al. 1997, Grant and Grant 2002). In fact, spatial and temporal variation in the strength and nature of natural selection could explain the high levels of genetic variation found in many natural populations (Gillespie 1994, Siepielski et al. 2009). Long term studies of evolution in the wild could also be informative for biodiversity conservation and resource management, because, for example, data on short term evolutionary responses to annual fluctuations in temperature or rainfall could be used to predict longer term evolution in response to directional climate change. Most previous research on evolution in the wild has considered one or a few observable traits or genes (Kapan 2001, Grant and Grant 2002, Barrett et al. 2008). We believe that more general conclusions regarding the rate and causes of evolutionary change in the wild and selection's contribution to the maintenance of genetic variation could be obtained by studying genome-wide molecular evolution in a suite of natural populations. Thus, we have begun a long term study of genome-wide molecular evolution in a series of natural butterfly populations in the Greater Yellowstone Area (GYA). This study will allow us to quantify the contribution of environment-dependent natural selection to evolution in these butterfly populations and determine whether selection consistently favors the same alleles across space and through time.

The focal species, *Lycaeides idas*, is one of five nominal species of *Lycaeides* butterflies that occur in North America (Figure 1; Nabokov 1949, Guppy and Shepard 2001, Gompert et al. 2006). These species are descended from one or more Eurasian ancestors that colonized North America about 2.4 million year ago (Vila et al. 2011). *Lycaeides idas* hybridizes with a second species, *L. melissa*, in the GYA (Gompert et al. 2010, 2012). *Lycaeides idas* is a holarctic species that is found in Alaska, Canada, and the central and northern Rocky Mountains of the contiguous USA (Scott, 1986). *Lycaeides idas* is univoltine and adults generally fly from mid-July to early August. In the GYA *L. idas* populations often occupy mesic forest and montane habitat at elevations ranging from 2000-3500 m above sea level. Most populations of *L. idas* in the GYA feed on *Astragalus miser* as larvae, but some populations feed on other native legumes (most notably, other species of *Astragalus* and *Lupinus*; Gompert et al. 2010). We selected *L. idas* as the focal species for this study because of our experience with this species, extensive data on the location and natural history of *L. idas* populations, the availability of genomic resources for this species, and several key aspects of this species's natural history (e.g., *L. idas* have non-overlapping generations with one generation per year, well-defined populations, and modest genome sizes, and *L. idas* are found in various different habitats that might experience different environment-dependent selection pressures).

The specific goals of this study are to: (i) quantify genetic variation and molecular evolution in *L. idas* and their relationship with population size and environmental variation across space (i.e., different populations) and through time (i.e., from generation to generation), and (ii) test the hypothesis that the nature and strength of environment-dependent selection varies among populations and over generations and

that this variation is sufficiently large to contribute to the maintenance of genetic variation in *L. idas*. This report documents the results from the second year of this study (2013), during which time we continued collecting *L. idas* for DNA sequencing and distance sampling to estimate population sizes (population size is an important parameter for our evolutionary models).



Figure 1. Photograph of a *L. idas* butterfly perched on its host plant (*Hedysarum*) on Rendezvous Mountain.

◆ METHODS

We began this long-term study in July of 2012. This report covers the second year of the study: July and August 2013. We collected 524 adult *Lycaeides idas* butterflies from 10 locations (Table 1). We are storing these whole adult butterflies at -80°C for DNA extraction and sequencing. In addition, we conducted a pilot study to evaluate a distance sampling protocol to estimate adult population densities and sizes in *L. idas*. Distance sampling involves counting individuals and recording their distance from a transect line or point (Buckland et al. 2001). This distance information is used to estimate a detection function that accounts for imperfect detection away from the transect line. We included four sites in this study: Bull Creek (BCR), Blacktail Butte (BTB), Bunsen Peak (BNP), and Garnet Peak (GNP). We randomly designated 10, 100-meter linear transects at each of the four sites (Figures 2 and 3). Two trained observers (ZG and LKL) slowly walked along each transect (about one pace per second) and measured and recorded the distance of each observed *L. idas* perpendicular to the transect line. We also observed and recorded the sex of each butterfly and the presence or absence of the larval host plant (*Astragalus miser*) near the transect line. We conducted these population surveys from July 6th until July 30th, and we only performed transect counts between 10:00 am and 2:00

pm under sunny or partly sunny skies. We visited BTB three times to quantify variability in population size over the flight season.

We estimated population densities (adult butterflies per square kilometer [km²]) using the *distsamp* function in the *unmarked R* package. We binned the detection distances of butterflies into 1-meter bins prior to analysis (e.g., 0 to 1 m, 1 to 2 m, etc.). We used a half-normal detection function and estimated the detection function and density model parameters using maximum likelihood (Royle 2004). This model assumes the latent transect-level abundance distribution is Poisson and that the detection process is multinomial with a different detection probability for each distance class or bin.



Figure 2. Photograph of a transect for distance sampling. The white line is the transect line and yellow flags indicate the location of observed *L. idas* butterflies.

◆ RESULTS

We observed and recorded distances for 122 butterflies across the four sites and 40 linear transects. Based on these observations our estimates of adult *L. idas* population density were: 0.00896 butterflies per square meter (standard error [se] 0.00196) at BCR, 0.00308 butterflies per square meter (se 0.00103) at BNP, 0.00528 butterflies per square meter (se 0.00153) at GNP, and 0.00241 (visit 1), 0.00415 (visit 2) or 0.00428 butterflies per square meter at BTB (se 0.00101 to 0.00154). We converted these density estimates to estimates of peak census population size based on rough estimates of each population's range (we identified suitable habitat from ground surveys and satellite images). Peak population size estimates were 793 butterflies (BCR), 211 butterflies (BNP), 373 butterflies (GNP), and 165-292 butterflies (BTB).

Because adult *L. idas* eclose (i.e., emerge following pupation) over a period of several weeks, these peak population size estimates are underestimates of the total adult population size at each site (perhaps by a factor of about three or four times given a one month flight season and a rough estimate of adult survival time in the wild of seven to ten days). We obtained peak population size estimates in 2012 that were higher on average than those from 2013: BCR = 794 butterflies, BNP = 721 butterflies, BTB = 2375 butterflies, and GNP = 206 butterflies.

Table 1. Population identification, locations, and number of adults (m = male, f = female) collected at each site for DNA sequencing. Sites within National Park boundaries are noted (GTNP = Grand Tenon National Park, YNP = Yellowstone National Park).

Population	Latitude	Longitude	Sample size
Blacktail Butte (GTNP)	43° 38' N	110° 41' W	25 m, 25 f
Bull Creek	43° 18' N	110° 33' W	34 m, 20 f
Bunsen Peak (YNP)	44° 56' N	110° 43' W	25 m, 25 f
Garnet Peak	45° 26' N	111° 13' W	37 m, 28 f
Hayden Valley (YNP)	44° 41' N	110° 29' W	25 m, 25 f
Mt. Randolph	43° 51' N	110° 24' W	40 m, 10 f
Periodic Springs	42° 45' N	110° 50' W	41 m, 10 f
Rendezvous Mountain (GTNP)	43° 36' N	110° 53' W	25 m, 25 f
Ski Lake	43° 31' N	110° 55' W	23 m, 29 f
Upper Slide Lake	43° 35' N	110° 20' W	40 m, 11 f

◆ DISCUSSION

Because we have just begun this long-term study and we have not yet sequenced the DNA from the sampled butterflies, we cannot yet make any conclusions about the rates or causes of molecular evolution in these study populations. But we have already learned a few things from the distance sampling surveys and analyses over the past two years.

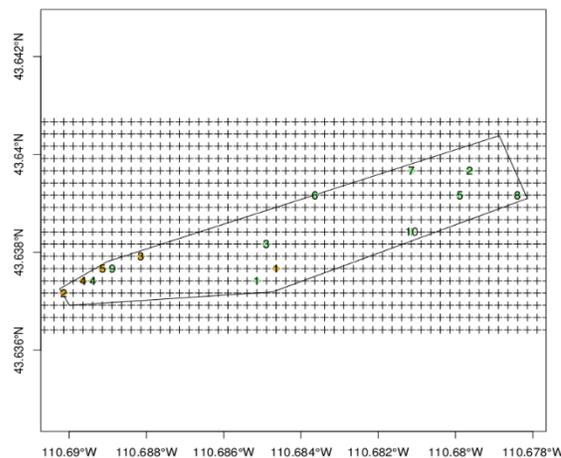


Figure 3. This plot shows the approximate boundary of the *L. idas* BTB population and the start points of transects (numbers and colored points). The cardinal or ordinal direction for each transect was chosen randomly but with the constraint that transect lines could not cross or leave the polygon boundary.

These initial analyses indicate that the four focal sites sustain adult *L. idas* populations of hundreds to thousands of individuals. These are the first population size estimates for this butterfly species. Based on these moderate population size estimates we predict that both genetic drift and selection are important drivers of evolution in this system (Lynch, 2007). The lower population size estimates in 2013 than 2012 are potentially interesting and could reflect demographic variability between years, but could also be an artifact caused by a change we made in how we designated transects. We also observed variation in the population size at BTB over the course of the summer, in particular our estimate from the first visit was about half that of the second and third visits. This is not surprising as the first visit was early in the season, and thus before the peak size. The consistency of the population size between the second and third visits (which were separated by about 10 days) indicates that the population remains at its peak size for more than a week.

We will continue this study during the 2014 summer field season. During this and subsequent field seasons, we will collect samples and estimate population sizes at all 10 sites listed in Table 1. We will also begin collecting weather and habitat data that will be useful for fitting causal models of molecular evolution. We plan to begin DNA sequencing of the collected *L. idas* after one or two additional field seasons.

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PICTORIALISM IN THE AMERICAN WEST

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♦ ABSTRACT

Early twentieth century (1900-1945) photography of northwestern Wyoming (including the Teton and Yellowstone areas) fits into a paradigm of regional photographic production that either conforms to the documentary or pictorial aesthetics most common in the era. Pictorial photography, especially, links the region to larger trends in the nation and can be analyzed to uncover previously unexamined assumptions about the value of photographic aesthetics and regional production within the milieu of fine art photography in the United States prior to WWII.

♦ INTRODUCTION

Photographic pictorialism in the American West was an aesthetic movement, coterminous with the rise of regionalism, which reached its height in the late 1920s and 30s. The photographic style as a product of the regionalist impulse goes largely unexplored for many reasons. First, pictorialism was an approach to photography that was overthrown (seemingly) by the modernist movement, in America first mounted in art photography by Alfred Stieglitz and his famous image, *The Steerage*, from 1907. Second, the hegemony of New York and the upper East Coast in the early twentieth-century American art world seemed close to absolute. In the third and fourth decade of the century, despite an interest in western lands by many artists - most notably Georgia O'Keeffe, Edward Weston, Ansel Adams and Group f/64 - the West was still considered a cultural backwater, its precise attraction for many modernists. Finally, that pictorialism in the West is not a common scholarly subject has to do with the nature of regionalism—the conceptual home for amateur and hobbyist pictorialists—that was splintered and decentralized by definition.



Stieglitz, *The Steerage*, 1907

Aesthetically, pictorialism was an approach to photography that emphasized romantic artfulness. Through the use of soft focus lenses, textured paper, and self-conscious compositional techniques borrowed from trends in painting and printmaking, the style was originally an effort to legitimize the mechanical medium of photography. Begun in the late nineteenth century in Europe by Henry Peach Robinson and encouraged through organizations like the Brotherhood of the Linked Ring, pictorialism was for a time associated with the avant-garde of the fine arts. While never really accepted in the nineteenth century as artists equal to painters, pictorialists aggressively co-opted their fine art technique and conceptual approach. For example, the craftsmanship



Harrison Crandall, Panorama View of Teton Range

of a pictorialist photograph was a response to the pervasive Arts and Crafts Movement that championed high quality workmanship and an insistence on aesthetic beauty. Moreover, the approach to photography drew heavily on symbolist sentiment in avant-garde art from the turn of the century; imagery in pictorial photography emphasized archetypes and favored universal motifs.

The regional aesthetic in the visual arts of the American West in the first decades of the twentieth century was considered thoroughly provincial in the cultural sphere of artistic visual production. That provinciality episodically provided much needed cultural isolation for the burgeoning modernists, but even the artistic centers such as Los Angeles and Toas/Santa Fe in the early twentieth century were anomalous and not fully acknowledged centers of anything. In the 1920s and 1930s, when regionalism and its kin emerged in response to WW I and the Great Depression and then was largely crushed by the post-war American art market, western centers of art that had expanded to include San Francisco and other major cities were still peripheral to the hegemony of the upper East Coast.

As early as 1900 photography critics took note of “a too definite desire...to overestimate and encourage the work of a very small circle” and “a very pronounced effort of the Eastern leaders to discourage any other salon, save the ones in which they personally figure.”⁷⁰ Western pictorialism, indeed western photography in general does not have to be considered a shadow of East Coast art, but as a regional stylistic incarnation that spawned and continues to spawn

artistic approaches, interpretations and aesthetics that are profoundly meaningful for the history of the United States.

◆ METHODS

My research relies heavily on primary sources, both textual and visual. These sources, I believe, are the best way to enter into past discussions and debates. In addition to artist archives and manuscript collections, photographic periodicals such as *Camera Craft*, *The American Amateur Photographer* and many others are a rich and under-utilized resource. Secondary scholarship also usefully offers new approaches. Of particular importance to this project is Christian Petersen’s *After the Photo-Secession* (1997), and scholarship in the increasingly dynamic field of Regional Studies, including Douglas Reichert Powell’s *Critical Regionalism* (2007) and Robert Dorman’s *Hell of a Vision: Regionalism and the Modern American West* (2012).

Conceptually the “interaction and intersection” model for understanding cultural forces is a more appropriate research methodology for this study as opposed to seeing changes in cultural production as a result of a binary/dichotomous tension. This approach was first introduced to me in Glenda Riley’s “Writing, Teaching, and Recreating Western History Through Intersections and Viewpoints,” (2000) and guides my research question that will consider alternatives to the more canonical model.

⁷⁰ Arthur Hewitt, “The Pictorial Movement: An Afterword,” *The Photographic Times*, Nov. 1, 1900 32/2 pg.481.

The Teton Historical Society and Museum, and the photography collections of the Grand Teton National Park are repositories that hold collections that exemplify regional production across the American West. The photographs of unknown photographers in the region as well as the more well-known work of Teton photographer Harrison Crandall provides support for my investigation into regional photographic production as a phenomenon.

◆ PRELIMINARY OUTCOMES

My preliminary investigation in NW Wyoming is part of a larger project. *Pictorialism in the American West* will be the first wide-ranging book length study to address the broad concerns of pictorialism in the West from 1900-1945. The manuscript is divided into four sections that will cover the following topics: (1) Defining American Pictorialism, (2) Pictorialism in the American West, (3) Pictorialism and Native America, and (4) From Pictorialism to Modernism.

To date I have accomplished archival research at the Center for Creative Photography, Arizona State History Museum, Arizona State Historical Society, Arizona State University's Special Collections, the Getty Research Institute (with a grant from the University of Wyoming), University of Wyoming American Heritage Center, and Utah Museum of Fine Art. With the help of a Charles Redd Center for Western Studies grant, I have been able to visit the following repositories: University of Washington Special Collections, Buffalo Bill Center of the West, Center for Southwest Studies in Durango, Colorado, and the Palace of the Governors Photo Archive. I will also be a scholar in resident at the Georgia O'Keeffe Research Center from January to May, 2015.

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NUTRIENT LIMITATION AND UPTAKE RATES IN STREAMS AND RIVERS OF THE GREATER YELLOWSTONE AREA

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✦ ABSTRACT

Nutrient pollution of aquatic ecosystems is a growing concern as the influence of human activities continues to increase on the landscape. Headwater streams have long been shown to process nutrients via the biofilm community growing on the bottom of streams. The growth and activity of these biofilms is often limited by the availability of nitrogen (N), phosphorus (P), or co-limited by both N and P. Although small stream nutrient dynamics are relatively well understood, comparatively little is known about larger, non-wadeable rivers. Biofilms on the river bottom are likely still nutrient limited, but there becomes an increased potential for light limitation as rivers increase in depth. In addition to biofilms on the bottom of rivers, free-living microbial communities suspended in the water column also occur in rivers and process nutrients - a component of nutrient processing largely ignored in streams. In summer 2013 we worked in streams and rivers of the Greater Yellowstone Area (GYA) to establish the nutrient limitation status of minimally-impacted rivers, as well as the role of the water column in processing nutrients as streams increase in size. For both the nutrient limitation and water column uptake studies, we are using the GYA sites in addition to systems from other regions of the US to establish what controls the various aspects of nutrient dynamics in rivers. Our results from the GYA, in addition to Midwest and Southwest US rivers, will provide water quality managers with new strategies for improving water quality downstream, and clarify mechanisms controlling nutrient retention in rivers.

✦ INTRODUCTION

Biofilms made up of algae, bacteria, and fungi colonize virtually every surface of stream and river bottoms (i.e., benthos). This bioreactive assemblage drives numerous ecosystem functions,

including primary production and nutrient retention (Cummins 1974, Peterson et al. 2001). These biofilms, and their ability to perform these ecosystem functions, may be limited by the availability of nitrogen (N), phosphorus (P), or co-limited by both N and P (Pringle et al. 1986, Tank and Dodds 2003, Johnson et al. 2009). Although N or P may limit benthic biofilms, co-limitation by both N and P is the most common in freshwater ecosystems (Francoeur 2001, Elser et al. 2007, Harpole et al. 2011). The nutrient limitation status of biofilms can be used as a metric to characterize stream and river health (Bunn et al. 1999, Johnson et al. 2009), and is an important mechanism regulating nutrient retention in stream networks (Hill et al. 2010).

Nutrient limitation of a system strongly influences the ability of stream networks to retain nutrients exported from the terrestrial landscape. Streams that are more nutrient limited are more likely to be 'retentive', thus reducing nutrient export to sensitive downstream ecosystems. Nutrients retained within a stream network may alleviate eutrophication in downstream ecosystems (Alexander et al. 2000). Nutrient processing by benthic biofilms in headwater streams, and the nutrient limitation of these biofilms has been the primary focus of stream ecology due to the predominate role of benthic biofilms and headwater streams at regional scales (Peterson et al. 2001, Alexander et al. 2007).

In contrast to headwater streams, which make up the majority of stream miles throughout a stream network (Alexander et al. 2007), ecosystem function in larger rivers may be driven by a free-living, suspended biological community rather than the biofilms attached to the stream bed. This shift from the benthos to the water column is driven by shifts in the physical environment of a stream as it increases in size and becomes a river (Vannote et al. 1980). As streams increase in size, they become wider and deeper, increasing the light reaching the water's surface (due

to decreased canopy cover) but reducing the light reaching the benthos (due to deeper, and potentially more turbid, waters). This physical change in the river environment is predicted to shift the biological community to a more lake-like, pelagic community (Vannote et al. 1980). If the biological community indeed moves to the water-column, pelagic processes should also become more important for nutrient retention. Unfortunately, there have been very few studies performed in non-wadeable rivers (Tank et al. 2008); ecologists have primarily focused on small streams, or very large rivers (e.g., the Hudson River (Caraco et al. 2006)). The lack of empirical research in moderately sized, non-wadeable rivers has led to the false dichotomy of either benthic or pelagic processes dominating flowing waters. In reality, there is likely a transition zone in which rivers of a certain size exhibit both benthic and pelagic ecosystem processes.

For the past few decades ecosystem ecology of flowing waters has focused primarily on small, headwater streams (Mulholland et al. 1985, Peterson et al. 2001, Hall et al. 2009). This is reflected by a preponderance of nutrient uptake studies occurring in small streams (Ensign and Doyle 2006, Tank et al. 2008), and is likely due to a combination of the methodological challenges of working in larger river systems (Mulholland and Webster 2010) coupled with the high value, and extreme sensitivity of headwater streams (Peterson et al. 2001). While incredibly valuable, this focus on headwater streams has led to a knowledge gap surrounding non-wadeable rivers. Indeed, an improved understanding of riverine nutrient cycling should be a priority for stream ecologists (Mulholland and Webster 2010).

To achieve a better understanding of riverine nutrient dynamics, and as part of a larger, NSF-funded project, we have quantified riverine uptake of ammonium (NH_4^+), nitrate (NO_3^-), and phosphorus (P) in 15 rivers across the United States. In 2010, we studied five of these rivers located in or near the Greater Yellowstone Area (GYA) (Snake, Buffalo Fork, Henrys Fork, Green at Seedskadee, and Salmon). During this work we found that rivers in the GYA are biologically active, and indeed process nitrogen at rates comparable to, or even higher than, rates found in small streams located within Grand Teton National Park (GTNP) (Hall and Tank 2003, Tank et al. 2008, Tank et al. in prep). This result reinforced the idea that rivers deserve increased scientific attention and led to the research we performed in 2013.

Although our work in 2010 quantified nutrient uptake rates in these rivers, the processes driving uptake were treated as a black box. In 2013, we set out to measure some potential drivers of nutrient uptake in rivers of the GYA and to identify where the transition from benthic to pelagic dominated rivers occurs. Data collected in 2013 will be combined with studies from the Southwest and Midwest US to describe nutrient processing in the pelagic zone, and nutrient limitation in the benthic zone, in a wide variety of river systems.

◆ STUDY AREA

Our 2013 work was conducted in five rivers throughout the GYA as well as three streams in GTNP. We determined benthic nutrient limitation in four of the five rivers we studied in 2010. We substituted the Teton River near Driggs, ID for the Salmon River because (1): traveling to the Salmon River was financially and logistically unfeasible, and (2) we contracted with the Idaho Department of Environmental Quality (ID-DEQ) to study nutrient limitation in the Teton River near the site of a new waste-water treatment plant. In addition to the non-wadeable rivers where we measured nutrient limitation, we measured pelagic nutrient uptake in Ditch Creek near the Teton Science School, lower Spread Creek approximately 1 km upstream of its confluence with the Snake River, and Pacific Creek where it flows under US-287.

◆ METHODS

Pelagic nutrient uptake

We measured pelagic nutrient processing using the *in situ* chamber incubation approach of Reisinger et al. (in prep). Briefly, we filled 3 L clear polycarbonate chambers (n=15) with depth-integrated river water. We then amended each chamber with one of three solutes (NH_4^+ , NO_3^- , or SRP) to a target concentration of $30 \mu\text{g L}^{-1}$ above background. After this amendment, we homogenized each chamber by inverting three times. We immediately collected an initial water chemistry sample to represent time zero within each chamber. We then suspended chambers at the surface of the water column to insure ambient temperature conditions and provide maximum ambient light availability over the course of the 4 h incubation (Figure 1). Starting with time zero, we collected a water sample from each chamber every hour over the course of the incubation, amounting to a total of 5 water chemistry samples from each chamber.



Figure 1. An example of a pelagic nutrient uptake incubation experiment performed in the Green River at Seedskaadee National Wildlife Refuge.

We collected water chemistry samples throughout all incubations by removing 60 mL of water from the chamber, filtering 20 mL of the sample through a 0.2 μm SUPOR filter (Pall Corporation, Port Washington, NY, USA) into a sterile 50 mL centrifuge tube (VWR, Radnor, PA, USA) as a rinse. After rinsing, we filtered the remaining 40 mL of sample into the tube and stored samples on ice until return to the laboratory, where we stored samples frozen until analysis. We quantified dissolved NH_4^+ using the phenol-hypochlorite method (Solorzano 1969), NO_3^- using the cadmium reduction method (APHA 1995), and P using the ascorbic acid method (Murphy and Riley 1962) on a Lachat Flow Injection Autoanalyzer (Lachat Instruments, Loveland, CO, USA). To quantify nutrient uptake, we calculated the first order decay rate of nutrients over time (k ; h^{-1}) and then converted this decay rate to volumetric uptake (U ; $\text{mg m}^{-3} \text{h}^{-1}$) by multiplying by background concentration.

Benthic nutrient limitation

We quantified benthic nutrient limitation using nutrient diffusing substrata (NDS). We constructed NDS using 30 mL polycarbonate cups filled with a 2% agar solution amended with 0.5 M NH_4Cl (NH_4^+ treatment), 0.5 M NaNO_3 (NO_3^- treatment), 0.5 M KH_2PO_4 (PO_4^{3-} treatment), 0.5 M of both NH_4Cl and KH_2PO_4 (NH_4^+ and PO_4^{3-} treatment), 0.5 M of both NaNO_3 and KH_2PO_4 (NO_3^- and PO_4^{3-} treatment), or no amendment as a control (C treatment; Tank et al. 2006). We then topped NDS with either inorganic

fritted glass disks or organic cellulose sponge cloth (Johnson et al. 2009) for a total of five replicates for each treatment and substratum type. The use of both inorganic and organic substrata allowed us to examine nutrient limitation of both autotrophic and heterotrophic biofilm components (Tank and Dodds 2003, Johnson et al. 2009). Once the agar had solidified and disks were placed on top, we attached the cups to PVC L-bars using cable ties. We attached the L-bars to a cinder block at each site, which we then placed in the main channel as near to the main current as we could reach with the NDS remaining upright (Figure 2). Based upon NDS deployment in other rivers, we elevated the L-bar on cinder blocks in order to minimize the potential for burial of NDS by fine sediments.

After incubating for 14 days, we retrieved NDS from the river. Substrata were placed in 50 mL centrifuge tubes. We immediately performed metabolism incubations on the substrata within these centrifuge tubes. First, we measured the initial temperature and dissolved oxygen (DO; as both $\text{mg O}_2 \text{L}^{-1}$ and % saturation) of a 20 L bucket of unfiltered river water (to serve as the initial DO for the incubation). We then filled the tubes containing NDS substrata with unfiltered stream water in the bucket, capping the tubes underwater to insure no air bubbles were present. We also filled three centrifuge tubes with river water only to serve as a water-column control. To measure ecosystem respiration (ER), we covered the tubes with dark sleeves, made of aluminum foil and duct tape shaped to tightly cover the centrifuge tubes. We performed ER incubations in the river at ambient temperature for 2 h. After the incubation period was over, we measured the final temperature and DO in each tube. The difference between initial and final DO provides ER ($\text{mg O}_2 \text{h}^{-1}$), which was then scaled areally based upon the known surface area of the substrata.

Following ER incubations, we emptied the water from all of the tubes, and refilled them from a bucket of fresh river water. Following the same protocol as the ER incubations, we measured net primary production (NPP) as the change in DO over a 1.5 h incubation with no sleeves covering the tubes. The light incubations provide net primary production (NPP) under ambient light and temperature. We calculated gross primary production (GPP) as:

$$\text{GPP} = \text{NPP} + \text{abs}(\text{ER})$$

where GPP is gross primary production, and abs (ER) is the absolute value of ecosystem respiration (traditionally expressed as a negative due to the

decrease in oxygen caused by respiration). All metabolic variables are expressed as $\mu\text{g O}_2 \text{ cm}^{-2} \text{ h}^{-1}$.

Upon completion of light incubations, we removed NDS substrata from the incubation tubes, wrapped them in aluminum foil, and stored them frozen until they were returned to the lab where we quantified algal biomass on each substratum as chlorophyll *a* (chl *a*). We analyzed substrata for chl *a* using the cold methanol fluorometric method (Wetzel and Likens 2000), but chl *a* results are not included in this report.

Statistical analysis

To quantify the nutrient limitation status of autotrophic and heterotrophic biofilm productivity, we ran two-way analysis of variance (ANOVA) on GPP and R of both inorganic and organic disks using the metabolic rate as the response variable and the presence of N and/or P in the NDS as the factors (Tank and Dodds 2003). As we had two different forms of N

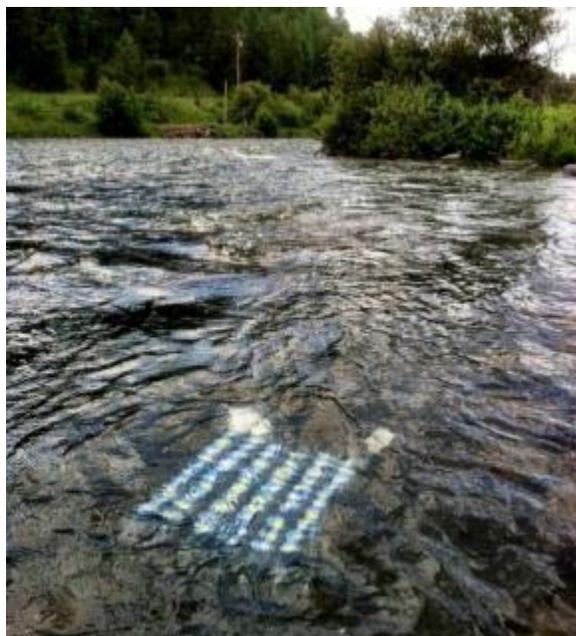


Figure 2. Nutrient diffusing substrata were deployed in five rivers throughout the GYA.

added to different NDS, we ran ANOVAs using NH_4^+ and NO_3^- amended NDS separately to determine if N form added to NDS altered limitation patterns. To establish the controls of pelagic nutrient processing in streams of different size, we ran a simple linear regression with nutrient uptake of each solute as our response variable and different potential environmental factors as our predictor variables. We initially ran regressions using only GYA sites, but

realized that we did not have enough variation and/or statistical power to find significant patterns, and therefore included all 15 study sites we have for our study of pelagic nutrient uptake across streams of different sizes. Therefore, for these regressions we have 15 different study sites: the three streams analyzed in 2013, pelagic nutrient uptake measured in the Snake and Buffalo Fork in 2010, and 5 sites each in moderately and highly human influenced Midwest US watersheds. For nutrient limitation, only results from the 2013 work will be presented in this report, but these results will be combined with work from the Midwest (spanning 2011 - 2014) and Southwest (2012) resulting in three separate manuscripts: (1) Pelagic nutrient processing along a stream size gradient (in prep to be submitted to *Biogeochemistry* by Summer 2014), (2) Pelagic nutrient uptake in 15 rivers spanning a nutrient and turbidity gradient (in prep to be submitted to *Ecology* by Fall 2014), and (3) Spatial and temporal variation of benthic nutrient limitation in rivers (still collecting data from Midwest rivers).

◆ PRELIMINARY RESULTS

Nutrient limitation

Benthic biofilms in the five study rivers within the GYA all exhibited some sort of nutrient limitation, regardless of functional response. When analyzing NH_4^+ as the N treatment, GPP of autotrophic biofilms was N limited at three rivers, P limited at one river, and co-limited by N and P at one river (Figure 3A). In contrast to NH_4^+ , when using NO_3^- as the N treatment, biofilm GPP was co-limited by N and P at four rivers, and N limited at one river (Figure 3B). Ecosystem respiration of heterotrophic biofilms was primarily N limited at the majority of rivers, regardless of which N treatment we analyzed. First, when using NH_4^+ as the N treatment, ER was N limited in four of the five rivers and co-limited by N and P at one river (Figure 3C). When using NO_3^- as the N treatment, ER was N limited at all five rivers studied in the GYA (Figure 3D).

These results are consistent with what we would expect from rivers in the GYA. The relative lack of human development in the region, coupled with the high P availability due to the underlying geology, makes the prevalence of N limitation unsurprising. The one site where we found any implication of solely P limitation was the Teton River near Driggs, ID. We were asked to study this river by the ID-DEQ as a new wastewater treatment plant is being installed to serve the city of Driggs and there is

already increased human development in this region relative to the other rivers in this study, so it makes sense that this river might exhibit different nutrient limitation patterns from the other four rivers.

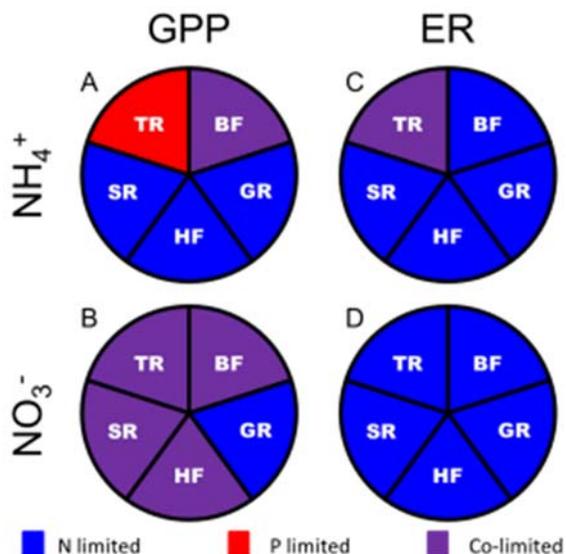


Figure 3. Nutrient limitation status of biofilm gross primary production (A, B) and ecosystem respiration (C, D) using either NH_4^+ (A, C) or NO_3^- (B, D) in five rivers in the GYA. Each slice of the pie represents one river: BF=Buffalo Fork, GR=Green River, HF=Henry's Fork, SR=Snake River, TR=Teton River. Each color represents a different nutrient limitation classification: blue=N limited, red=P limited, purple=co-limited by N and P.

Water column nutrient uptake

We were able to measure nutrient uptake in the water column at all three streams we worked in during summer 2013. Unlike human impacted systems we have worked in previously, volumetric uptake of P was higher than either NH_4^+ or NO_3^- . Volumetric P uptake ranged from 0.62 $\text{mg m}^{-3} \text{h}^{-1}$. Ammonium uptake ranged from 0.15 to 0.31 $\text{mg m}^{-3} \text{h}^{-1}$, which was generally higher than nitrate uptake, which ranged from 0.01 to 0.17 $\text{mg m}^{-3} \text{h}^{-1}$. Although we only have a sample size of three streams from Summer 2013, it appears that P uptake decreased with background P concentration while NH_4^+ uptake appears to increase with background NH_4^+ concentration. These opposing trends could be suggesting that at lower P concentrations, water column biota assimilate whatever P is available, whereas higher P concentrations alleviates the need to assimilate P at high rates. This could be an example of luxury P uptake, which has been seen previously in

lake phytoplankton (Wetzel 1992), and is implicated in water column nutrient uptake in 15 rivers across the United States (Reisinger et al. in prep), but has not been seen previously in streams.

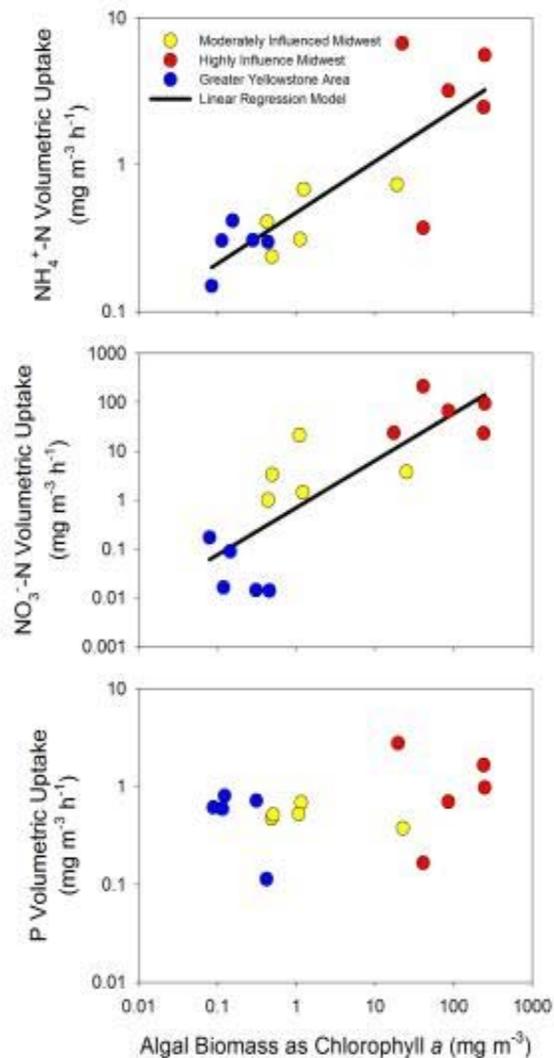


Figure 4. Volumetric uptake of NH_4^+ and NO_3^- increased with algal biomass, whereas P uptake did not respond to algal biomass. Different colors represent different watersheds (blue=GYA, yellow=moderately influenced, and red=highly influenced by human activities).

As part of a larger project based upon the hypothesis that pelagic uptake increases with stream size, we combined volumetric uptake measured in 3 streams in summer 2013 with measurements taken in summer 2010 at the Buffalo Fork and Snake. We did

not find any correlation between stream size (using watershed area as the stream size metric) and volumetric uptake of NH_4^+ , NO_3^- , or P. This was similar to the lack of any correlation between volumetric uptake and stream size in two Midwest watersheds (data not shown). We then attempted to find environmental factors that controlled volumetric uptake in GYA streams and rivers. However, the amount of variability in the environmental factors that we predicted would control pelagic uptake in the GYA was very low. Because of this low variability, we were unable to establish the controls on pelagic uptake in GYA streams and rivers. However, when we combined our measurements of pelagic uptake from GYA systems with measurements from both a moderately influenced, and a highly influenced Midwest watershed, after transforming data to meet assumptions of normality, we find that uptake of NH_4^+ and NO_3^- is positively correlated with chlorophyll *a* ($R^2=0.75$ and 0.68 , respectively, $p<0.01$ for both), whereas P uptake is not (Figure 4).

◆ MANAGEMENT IMPLICATIONS

Our research in the GYA had two primary objectives: (1) establish the nutrient limitation status of riverine biofilms in minimally impacted rivers; and (2) quantify pelagic nutrient uptake in headwater streams to inform a larger study on the response of pelagic nutrient processing to increasing stream size. The high degree of N limitation of riverine biofilms found in these rivers suggests that biofilms in rivers of this size are processing nutrients in similar fashion to those in headwater streams. This is in contrast to results of a study in rivers in the Southwest United States which also had low nutrients, but had high loads of suspended sediment - these 'muddy' rivers were typically not nutrient limited and instead were likely limited by light (Reisinger et al. unpublished data). This implies that if light availability were increased in human-influenced systems via reducing erosion and suspended sediment loads, nutrient retention should increase. In addition to the nutrient limitation results, our pelagic nutrient uptake results show that even in small, headwater streams, nutrients are processed in the water column. This is counter to previous research and provides an additional nutrient removal mechanism to be optimized by managers.

Although our results from summer 2013 only provide a snapshot of the big picture, serving as a 'minimally influenced' end point for our studies, we do find that rivers appear capable of processing nutrients in ways previously ignored. Incorporating the results from the GYA into the bigger picture in the

coming years will reveal processes and controls on the multitude of nutrient processing mechanisms in rivers, providing water quality managers with new strategies for improving downstream water quality.

◆ ACKNOWLEDGEMENTS

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EFFECTS OF CLIMATE AND BIOTIC FACTORS ON LIFE HISTORY CHARACTERISTICS AND VITAL RATES OF YELLOWSTONE CUTTHROAT TROUT IN SPREAD CREEK, WYOMING

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◆ ABSTRACT

The Upper Snake River represents one of the largest remaining strongholds of Yellowstone cutthroat across its native range. Understanding the effects of restoration activities and the diversity of life-history patterns and factors influencing such patterns remains paramount for long-term conservation strategies. In 2011, we initiated a project to quantify the success of the removal of a historic barrier on Spread Creek and to evaluate the relative influence of different climate attributes on native Yellowstone cutthroat trout and non-native brook trout behavior and fitness. Our results to date have demonstrated the partial success of the dam removal with large, fluvial Yellowstone cutthroat trout migrating up Spread Creek to spawn, thus reconnecting this population to the greater Snake River metapopulation. Early indications from mark-recapture data demonstrate considerable differences in life-history and demographic patterns across tributaries within the Spread Creek drainage. Our results highlight the diversity of life-history patterns of resident and fluvial Yellowstone cutthroat trout with considerable differences in seasonal and annual growth rates and behavior across populations. Continuing to understand the factors influencing such patterns will provide a template for prioritizing restoration activities in the context of future challenges to conservation (e.g., climate change).

◆ INTRODUCTION

The Greater Yellowstone Ecosystem is one of the largest intact ecosystems remaining in the lower 48 states (Koel et al. 2005). Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) are a vital component within this system serving as a food source for an estimated 42 species of birds and mammals (Varley and Schullery 1995). Additionally, the subspecies is highly valued as a recreational and cultural resource (Gresswell and Liss 1995, Varley and Schullery 1998).

It is estimated that Yellowstone cutthroat trout occupy approximately 42% of their historic range (May et al. 2007). About 54% of the current occupied stream length is in Wyoming (May et al. 2007). The decline of Yellowstone cutthroat trout has been attributed to the introduction of non-native salmonids and habitat degradation. Land uses such as resource extraction, grazing, and water diversion have impaired habitats and altered hydrologic regimes (Clancy 1988, Varley and Gresswell 1988, Van Kirk and Benjamin 2001). Introduced species, particularly brook trout (*Salvelinus fontinalis*), have led to displacement of native cutthroat trout species (Peterson et al. 2004, Shepard 2004). Rainbow trout (*O. mykiss*) pose a risk of hybridization (Allendorf and Leary 1988) and introgression may become prolific in systems where they co-occur with cutthroat trout (Thurrow et al. 1988, Henderson et al. 2000).

Many of the remaining genetically pure strongholds for this subspecies are on public land in mountainous areas that have not received the level of human disturbance that lower elevation systems have (Varley and Gresswell 1988). This has likely led to the resident life history form being more common than the fluvial form as it has with other salmonids (Nelson et al. 2002). However, headwater populations of Yellowstone cutthroat trout have not received the level of life history research that migratory populations from Yellowstone Lake and larger systems have (Gresswell et al. 1994, 1997, Kaeding and Boltz 2001). Much of the research pertaining to Yellowstone cutthroat trout in small systems has been on status assessments and factors influencing distributions (Kruse et al. 1997, 2000).

In addition to the current threats, global climate change may pose the most serious obstacle to the long term persistence of Yellowstone cutthroat trout (Williams et al. 2009, Haak et al. 2010, Gresswell 2011). Changes in air temperature and weather patterns are anticipated to alter thermal (Isaak et al. 2010, 2012b, Mantua et al. 2010) and hydrologic regimes (Adam et al. 2009). Moreover, many basins throughout the West have already exhibited the effects of climate change with shifts towards earlier timings of runoff in the spring and decreases in summer flows (Isaak et al. 2012a). The concurrent effects on biotic factors such as non-native species distributions (Wenger et al. 2011a, 2011b) and macroinvertebrate prey (Harper and Peckarsky 2006) are anticipated to play major roles in shaping future cutthroat trout distributions. However, there is still a lack of understanding about the influence that abiotic and biotic factors have on the diversity of life histories and population demographics of Yellowstone cutthroat trout.

Current and future management of the subspecies will be heavily focused on maintaining the current distribution as well as restoring populations where feasible (Gresswell 2011). To best direct resources for specific actions it is necessary to understand the extent of fine-scale diversity in populations as well as factors promoting this diversity. In this study we examined the effects of stream temperature, streamflow, food availability, and presence of non-native brook trout on life history characteristics of Yellowstone cutthroat trout in three tributaries in Wyoming. Our specific objectives were to: (1) document movement patterns of Yellowstone cutthroat trout and brook trout; (2) estimate survival rates of Yellowstone cutthroat trout; and (3) evaluate the effect of streamflow, stream temperature, food abundance, and fish densities on growth variability of Yellowstone cutthroat trout.

◆ STUDY AREA

Spread Creek is a third-order tributary to the Snake River in western Wyoming (Figure 1). A portion of the lower basin is located in Grand Teton National Park and the remainder is located on the Bridger-Teton National Forest. The basin is situated in the Mount Leidy Highlands region of the Gros Ventre mountain range. The geology is dominated by relatively unstable sedimentary rock and mass wasting is common (Ryan and Dixon 2007). The climate of this region is characterized by dry summers and cold winters with much of the yearly precipitation occurring as snowfall.

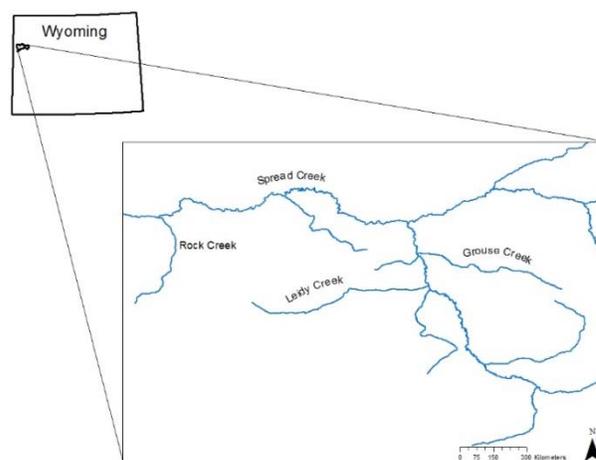


Figure 1. The location of the Spread Creek drainage in Wyoming and the location of the three study tributaries within the basin.

This system supports Yellowstone cutthroat trout, bluehead sucker *Catostomus discobolus*, Utah sucker *C. ardens*, longnose dace *Rhinichthys cataractae*, mottled sculpin *Cottus bairdii*, Paiute sculpin *C. beldingi*, and non-native brook trout.

Sampling was conducted in Rock, Grouse, and Leidy creeks (Figure 1). Leidy and Grouse creeks are 1st-order streams and Rock Creek is a 2nd-order stream. Trout-bearing stream length in Rock Creek is 4.5 km and flows from an elevation of 2500 to 2200m where it enters Spread Creek. Grouse and Leidy creeks flow from elevations of 2700 to 2400m where they enter South Fork Spread Creek. Trout-bearing stream length is 5.4 km in Leidy Creek and 5.7 km in Grouse Creek.

Rock Creek flows through a confined valley with conifers as the dominant riparian vegetation. The lower and middle portions of Leidy Creek flow through a wide valley dominated by a willow riparian

zone. The upper portion consists of a short, high-gradient coniferous forest section and a meadow-like reach directly below Leidy Lake. Grouse creek has a mixed willow/conifer riparian zone in the lower and middle sections and a conifer forested upper section. The majority of Grouse Creek flows through an unconfined valley (Figure 2).



Figure 2. Grouse Creek in the Spread Creek drainage (Photo R. Al-Chokhachy).

◆ METHODS

Where necessary, project methods have been approved by the respective permitting authority or oversight committee. Animal capture protocols have been approved by the Montana State University Institutional Animal Care and Use Committee (IACUC). In addition, relevant sampling permits have been issued by Grand Teton National Park and the state of Wyoming.

Fish capture and recapture

Fish sampling was conducted in 100m sampling reaches that were systematically distributed throughout the trout-bearing stream length for an overall sampling coverage of approximately 30% in each stream. Three reaches on Rock, Grouse, and Leidy creeks were block-netted and sampled with three-pass electrofishing to estimate capture efficiency. The remaining reaches were sampled with a single pass. Summer sampling commenced following runoff during the first week of July. All reaches were resampled at the end of September for summer growth estimates.

Fish were collected using a Smith Root LR-24 backpack electrofishing unit operated at voltages between 100 – 500 V, frequencies under 50Hz, and pulse widths less than 4 μ sec. After capture, trout were anesthetized with clove oil. Clove oil is an effective

method of fish anesthetization and is approved by the U.S. FDA, allowing for the immediate release of individuals back to the stream (Anderson et al. 1997). Once it was deemed that fish were sufficiently anesthetized, measurements of total length (\pm 1mm) and weight (\pm 0.01g) were taken on each individual. Newly captured trout with lengths 80-120mm were implanted with a 12mm passive integrated transponder tag (PIT-tag; half-duplex, Oregon RFID, Portland, OR) and individuals with lengths $>$ 120mm were implanted with a 23mm PIT tag. Tags were inserted into the body cavity through a small ventral incision made with a scalpel. The incision was slightly anterior to the pectoral fins. Adipose fins were removed to serve as a secondary tag. Captured individuals missing an adipose fin were placed under a hand-held PIT-tag scanner to check for a tag. If a tag was detected then the unique tag identification number was recorded. If no tag was detected after three attempts, the fish was recorded as having shed the tag and implanted with a new tag. Shed rate was low over the course of the study (4%). After processing, individuals were placed in a live well (plastic tub with holes that allow current to flow through) until they fully recovered and then were distributed throughout the sampling reach.

Movement

Prior to fish sampling, we installed passive instream antennae at the mouths of Grouse, Leidy, and Rock creeks. The antennae consisted of two loops laid on the substrate of the stream channel. Loops were separated by 5-10m and allowed for direction of movement to be determined. Detections were recorded by a half-duplex multiplexer (Oregon RFID, Portland, Oregon) powered by two 12-volt batteries charged by a solar panel.

After completion of fish sampling, we used mobile PIT-tag antennae to provide information on recapture and movement for all PIT-tagged individuals. We used continuous surveys in each of the three tributaries. We conducted the mobile surveys using 2 portable hoop antennae (\sim 0.3 m diameter) attached to a pole. This portable unit allowed the operator to cover the stream in a manner analogous to backpack electrofishing and detect fish as the wand passed over a tagged individual. Movement distances were calculated as the distance from the mid-point of the tagging reach to the point of relocation in ArcMap10.1 with the Network Analyst package.

Stream temperature and streamflow

Pressure transducers (Solinst Canada LTD, Georgetown, Ontario) and temperature data loggers (Onset Computer Corp., Pocasset, Massachusetts) were deployed near the mouth and top of the trout-bearing stream length in each stream to record water temperature (± 0.01 °C) and stage height (± 0.001 m) continuously at hourly intervals. Discharge was measured at least three times over the growing season at each pressure transducer to develop stage-discharge relationships. We estimated lapse rates from the lower and upper loggers to interpolate stream temperatures at all tagging reaches based on the elevation of the reach mid-point. Temperature data was used to calculate cumulative growing degree days (GDD). Average daily temperatures above 3°C were summed over the growing season to calculate GDD. The minimum temperature of 3°C was chosen because salmonids have exhibited growth down to 3.8°C in laboratory experiments (Elliot 1975) and we wanted to provide a buffer around this threshold to be conservative with the temperature cutoff.

Food availability

Food availability was measured with bi-weekly drift samples collected at one fixed sampling reach near the mouth of each stream from July through September. Each sample occasion consisted of a morning sample starting at one hour after sunrise and an evening sample starting at one hour prior to sunset. This regimen was chosen to capture the beginning of the crepuscular increase in drift density that is an important feeding period for salmonids (Elliott 1967, 1970).

Two drift nets (25 x 45cm, 500 μ m mesh) were deployed adjacently in the thalweg of a fast-water channel unit. Nets remained in the channel for one hour to maximize the volume of water sampled without risking backflow due to clogging. Nets were deployed at least 2cm off the substrate to prevent benthic macroinvertebrates from crawling into the nets and the tops of the nets were always above the water surface to capture drifting terrestrial invertebrates. Flow and water depth were measured directly after setting the nets and prior to retrieving them to calculate the volume of water sampled. The contents of the nets were transferred to storage jars and preserved with 95% ETOH.

In order to account for differences in total energy available due to differences in invertebrate community composition across streams, samples from 2012 were identified to the taxonomic level of order

and then dried in an oven at 103°C for four hours (Mason et al. 1983). Energy content was estimated using dry mass-energy equivalents (Curry et al. 1993). There was a strong correlation between total energy estimated from order-specific caloric content and total dry mass of the sample ($R^2 = 0.9$). Therefore, drift samples from 2013 were oven dried and weighed without partitioning taxonomic groups. Food availability comparisons across streams and years were based on total dry mass of the sample.

Growth analysis

Variation of individual summer growth rates of Yellowstone cutthroat trout was analyzed with linear mixed-effect models. We did not include brook trout in the analysis due to the small sample size and to avoid confounding factors because they were only present in Grouse Creek. Only trout recaptured within the same year were included in the analysis. Growth rates were estimated on a daily basis over the summer growing season as

$$G = (M_2 - M_1) (t)^{-1},$$

where M_1 is initial weight, M_2 is weight at recapture, and t is days between capture and recapture. Variation in growth rates was explored with the general model structure

$$G = RB + TL + MF + GDD + MF \times RB + GDD \times RB + MF \times GDD + MF \times TL + GDD \times TL + RB \times TL,$$

where RB is sample reach biomass calculated as total first pass biomass divided by average stream-specific capture efficiency, TL is the initial total length of the individual, MF is mean streamflow over the period between capture and recapture estimated from the lower level logger in each stream, and GDD is the cumulative growing degree days calculated as the sum of average daily temperatures above 3°C between capture and recapture estimated at the reach the trout was captured in. The effect of food abundance was not included in the model because there were little biologically or statistically significant differences in drifting biomass (mg/m^3) of invertebrates across streams or years (see results). A set of candidate models were developed that were nested structures of the global model to assess support for the hypothesized effects. Analyses were conducted in Program R (R Core Team 2013) using the package nlme (Pinheiro et al. 2013). All models included a nested structure of random effects for stream and sample reach. We used Akaike's information criterion corrected for small sample size (AIC_c) to rank competing models.

Survival analysis

We used a Barker model in Program MARK (White and Burnham 1999) to estimate survival rates of Yellowstone cutthroat trout. This model incorporates information from recapture occasions as well as dead recovery and live resightings of tagged individuals between occasions. In addition to survival (S), the Barker model estimates recapture probability (p), the probability of recovering the tag of a dead individual between occasions (r), the probability of recapturing an individual alive between occasions (R), the probability of recapturing an individual alive before it dies between occasions (R'), the probability that an animal at risk of capture at time t is at risk of capture at time $t + 1$ (F), and the probability that an animal not at risk of capture at time t is at risk of capture at time $t + 1$ (F').

We used data from 2011 through 2013 for the analyses (Table 1.). No recapture events took place in 2011 so all sampling occasions (July 26 – September 16) were combined into the first sampling occasion. Individuals were split into two size classes (80-120mm and >120mm) for analyses. Individuals of the smaller size class were automatically moved into the larger size class in the following year. Stream and size class was incorporated into the analysis as a group variable.

Models were ranked by AIC_c scores. We chose to model emigration as random ($F=F'$) because movement data from the portable PIT antennae surveys revealed that the median range moved by fish was greater than sampling reach lengths which would likely make the probability of a fish being within the sample reach during a sampling event random. To find the best structure for the other parameters we held survival as the global structure and compared different structures of a parameter of interest and selected the best structure based on AIC_c . While comparing structures of a given parameter we kept all other parameter structures modeled as the global structure. Once we found the most supported structure of each parameter we maintained those structures while testing for the best structure to model survival. We assessed over dispersion using the median c-hat procedure in MARK. There was minor evidence of over dispersion (c-hat = 1.344) and all models were adjusted accordingly. We used QAIC_c to rank the candidate survival model structures and calculate the relative QAIC_c weight of each model. We chose to use model averaging to develop the best estimate of survival rate to use for comparisons across streams, size classes, and time intervals.

◆ PRELIMINARY RESULTS

Stream temperature and streamflow

Across the three tributaries, there were considerable differences in discharge during 2012 and 2013 (Figure 3.). Stream discharge was highest in Leidy Creek in 2012 and 2013 (Table 2). Discharge in Grouse Creek was higher than in Rock Creek in 2012, but was very similar during 2013 (Table 2). Summer discharge was lower in 2013 than in 2012 for Leidy and Grouse Creeks, but higher in 2013 than in 2012 in Rock Creek. Stream temperatures were similar in Rock and Grouse Creeks and slightly cooler in Leidy Creek during both years.

Food availability

There were little biologically relevant or statistically significant differences between the drifting biomass of invertebrates during the summer months across the three streams (Figure 4). In Leidy Creek the average invertebrate biomass in the drift was 0.18 mg/m³ (SD = 0.10) in the morning and 0.26 mg/m³ (SD = 0.12) in the evening during 2012 and was 0.55 mg/m³ (SD=0.58) in the morning and 0.39 mg/m³ (SD=0.14) in the evening during 2013. In Grouse Creek, the average drifting biomass was 0.14 mg/m³ (SD = 0.12) in the morning and 0.50 mg/m³ (SD = 0.53) in the evening during 2012 and was 0.30 mg/m³ (SD= 0.15) in the morning and 0.67 mg/m³ (SD=0.35) in the evening during 2013. In Rock Creek, the average drifting biomass was 0.15 mg/m³ (SD = 0.10) in the morning and 0.20 mg/m³ (SD = 0.14) in the evening during 2012 and was 0.24 mg/m³ (SD= 0.08) in the morning and 0.16 mg/m³ (SD=0.07) in the evening during 2013.

Growth

Average growth rates varied among streams and between years (Figure 5). In general, brook trout in Grouse Creek consistently demonstrated high growth when compared to Yellowstone cutthroat trout in Grouse Creek and each of the other tributaries. In 2012, there were no significant differences between growth rates of brook trout and Yellowstone cutthroat trout in Grouse Creek, nor between cutthroat trout in Grouse and Leidy Creeks. Yellowstone cutthroat trout in Rock Creek had significantly lower growth rates than observed in both Grouse and Leidy Creeks. There were no significant differences in growth rates of cutthroat trout across the three tributaries in 2013.

Table 1 – Sampling dates and methods used to capture, recapture, and resight trout in Grouse, Rock, and Leidy creeks. During primary sampling occasions live captures and recaptures were done with backpack electrofishing units and live resights during intervals between primary occasions were done with passive instream antennae (PIA) at the mouths of each creek as well as portable PIT antennae (PPA) surveys in the three streams.

Sampling Date	Resight Interval (months)	Number Marked	Live Recaptures	Live Resights	Dead Recoveries	Sampling Method
Jul 26 – Sep 6, 2011		115				Electrofish
	10			51	2	PIA + PPA
Jul 2-18, 2012		217	8			Electrofish
	3			170	1	PIA + PPA
Sep 22 – Oct 5, 2012		311	51			Electrofish
	9			293	4	PIA + PPA
Jul 1 – 18, 2013		140	41			Electrofish
	3			235	37	PIA + PPA
Oct 5-11, 2013		192	50			Electrofish
				154	16	PIA + PPA

Table 2 - The average (standard deviation) daily discharge (m^3/s) and stream temperature ($^{\circ}\text{C}$) measured near the mouths of Grouse, Leidy, and Rock Creeks during the period of July 1 to September 30 in 2012 and 2013.

Stream	2012		2013	
	Temperature	Discharge	Temperature	Discharge
Grouse Creek	9.99 (2.81)	0.08 (0.02)	10.25 (2.84)	0.06 (0.02)
Leidy Creek	9.11 (2.13)	0.34 (0.09)	9.15 (2.23)	0.17 (0.05)
Rock Creek	9.92 (2.65)	0.02 (0.02)	10.48 (2.68)	0.07 (0.02)

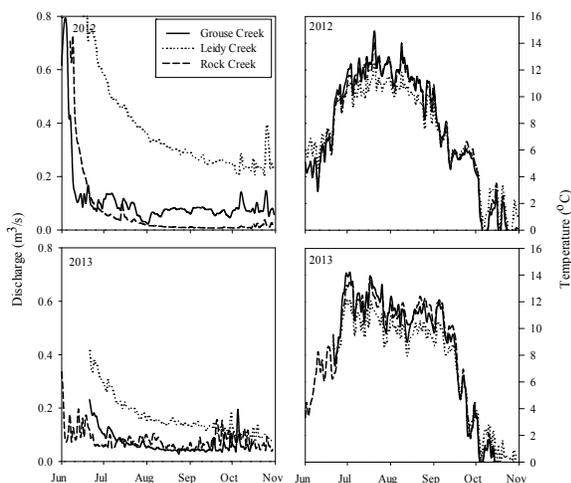


Figure 3. Average daily discharge (left) and average daily temperature (right) in Grouse, Leidy, and Rock creeks during the summer of 2012 (top) and 2013 (bottom).

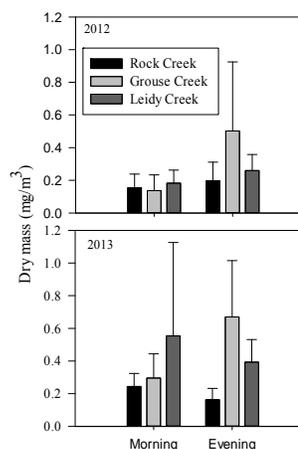


Figure 4. Average dry mass of invertebrates drifting in the water column during the morning and evening sampling events in the three tributaries in 2012 (top) and 2013 (bottom). Error bars represent 95% confidence intervals.

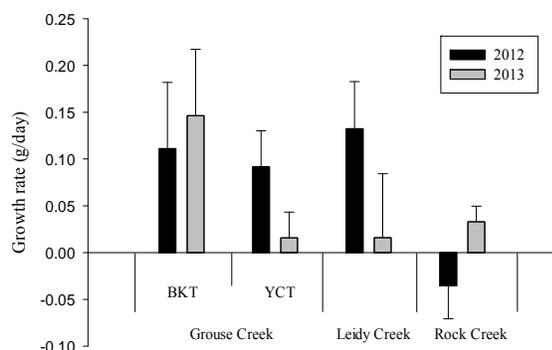


Figure 5. Average growth rates (g/day) in Grouse, Leidy and Rock Creeks for brook trout (Grouse Creek only) and Yellowstone cutthroat trout in 2012 and 2013. Error bars represent 95% confidence intervals.

Growth rates of brook trout in 2013 were significantly greater than Yellowstone cutthroat trout in Grouse Creek. Cutthroat trout in Grouse Creek exhibited significantly lower growth rates in 2013 than in 2012. Cutthroat trout in Leidy Creek also had a decrease in growth rates from 2012 to 2013, but this was not significant. In Rock Creek, cutthroat trout had significantly higher growth rates in 2013 than in 2012.

Stream temperature, streamflow, and fish length were all strongly associated with variation in summer growth rates as the most supported model contained the main effects of these factors (Table 3). There were also significant interactions between streamflow and temperature, streamflow and length, and temperature and length. At all temperatures within the range observed throughout the study, higher streamflow was associated with higher growth rates (Figure 6). Increased accumulation of degree days throughout the growing season was associated with decreased growth rates. The effect of streamflow was greater at lower accumulations of degree days. The effects of streamflow and temperature were greater for larger fish than smaller fish. There was minimal support for a reach biomass effect as the best model containing this effect was 2.58 AIC_c units away from the top model and only had 16% of the support in the data (Table 3).

Movement

Monthly displacement distances were different across seasons and streams (Figure 7). The range of movement in Rock Creek declined considerably after high flows subsided in July, but trout in Leidy and Grouse creeks continued to exhibit a high range of mobility throughout the summer and fall. Yellowstone cutthroat trout in Grouse Creek were more mobile than brook trout except for the fall

interval when they exhibited very similar movement patterns.

In general, Grouse Creek had the greatest amount of fish moving in and out of the stream during both years, Leidy Creek had the least amount of movement, and Rock Creek had considerable variability across years (Figure 8). In 2013 there was a substantial difference in the number of fish detected moving over the antennae in each stream.

There were 57 trout (44 cutthroat and 13 brook trout) detected in Grouse Creek, 24 trout (22 cutthroat and 2 brook trout) detected in Leidy Creek, and 32 cutthroat trout detected in Rock Creek. Frequency of detections differed across months and across streams. Cutthroat trout in Grouse Creek had peak movements in July and October as well as consistent movements throughout the summer. Movements over the Rock Creek antennae peaked in July then remained low for the remainder of the season. Leidy Creek had the least amount of detections as well as no clear seasonal pattern.

Survival

There was overwhelming support for a model that contained the additive effects of size class, time interval, stream, and the interaction of size class and time interval ($W_i = 97.3\%$, Table 4). However, model-averaged survival estimates were not significantly different between size classes or across streams (Figure 9). During all time intervals monthly survival rates between size classes were not significantly different in any stream. During the summer of 2013, trout >120mm had significantly lower monthly survival rates compared with the other time intervals, whereas trout 80-120mm did not exhibit significantly lower survival rates (Figure 9). When estimates were expanded over the seasonal interval, survival rates for both size classes were generally lower in winter than in summer except for the summer of 2013 which was the lowest survival for individuals >120 mm (Figure 10).

Table 3- Set of linear mixed-effect models developed for comparison of growth rates (g/day) of Yellowstone cutthroat trout in three tributaries of Spread Creek, WY. Asterisks denote interactive effects. All models include nested random effects for reach and stream. K is the number of parameters for each model; AIC_c is Akaike's information criterion, corrected for small sample size; ΔAIC_c is the difference between a given model and the most supported model; W_i is the Akaike weight of the model. Model terminology is as follows: RB (reach biomass, g/m²), MF (mean streamflow, m³/s), TL (total length of individual at tagging, mm), and GDD (growing degree days).

Model	Structure	K	AIC_c	ΔAIC_c	W_i
1	MF + GDD + TL + MF*GDD + MF*TL + GDD*TL	10	-181.9	0	0.60
2	RB + MF + TL + GDD + MF*RB + MF*GDD + MF*TL + GDD*TL	12	-179.3	2.58	0.16
3	RB + MF + TL + GDD + MF*RB + MF*GDD + GDD*TL	11	-178.0	3.91	0.08
4	RB + MF + TL + GDD + MF*RB + MF*GDD + MF*TL + GDD*TL + RB*GDD	13	-176.4	5.51	0.04
5	RB + MF + TL + GDD + MF*RB + MF*GDD + MF*TL + GDD*TL + RB*GDD + RB*TL	14	-175.7	6.21	0.03

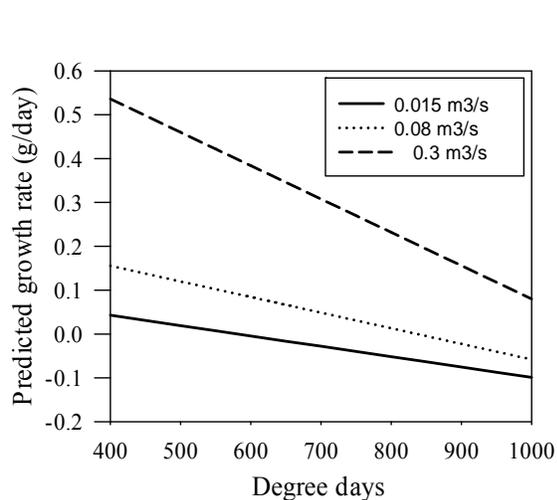


Figure 6. Variation in growth rate (g/day) in relation to temperature for three levels of discharge. Inference is from the best supported model and predicted growth is based on a fish length of 150mm. The relationship between growth rate and temperature is shown for the minimum (solid line; 0.015 m³/s), median (dotted line; 0.08m³/s), and maximum (dashed line; 0.3 m³/s) streamflows observed in this study.

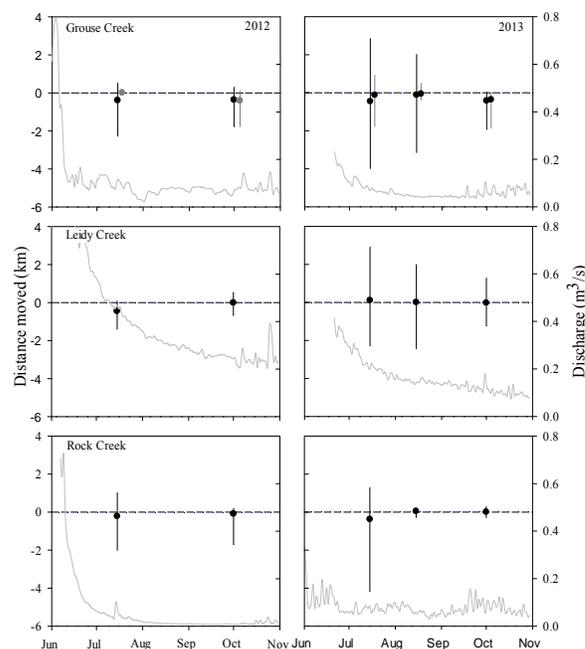


Figure 7. Monthly displacement distances (left y- axis) of Yellowstone cutthroat trout (black vertical lines) and brook trout (dark grey) and mean daily discharges (right y-axis) in 2012 (left column) and 2013 (right column). The circles represent the mean displacement distance during the interval and the vertical lines represent minimum and maximum distances moved; negative values represent distances moved downstream and positive values represent distances moved upstream. Note that the fall movement interval in 2012 is from July to November and in 2013 is from September to November.

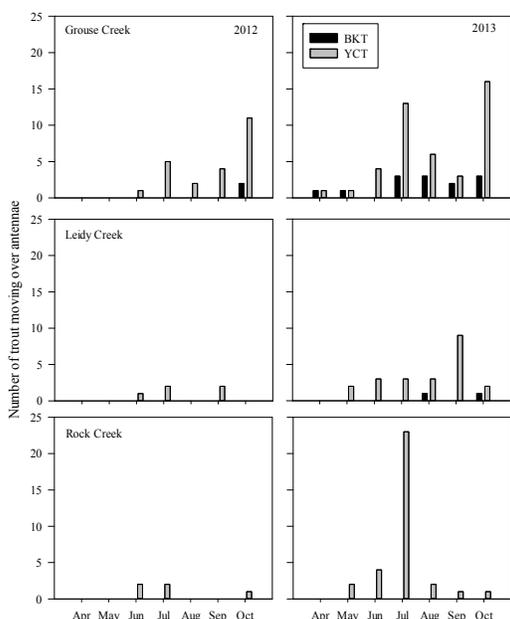


Figure 8 - Number of tagged Yellowstone cutthroat trout (grey bars) and brook trout (black bars) moving over the stationary antennae by month in 2012 (left column) and 2013 (right column). Note that no brook trout have been detected in Rock Creek. These are counts of the last known detection of a unique tag number within a year.

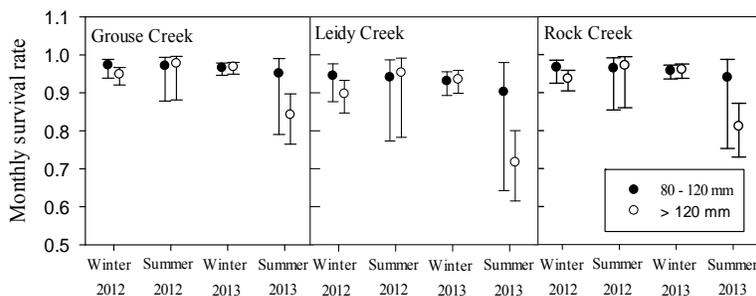


Figure 9. Model-averaged estimates of monthly survival rate (95% confidence interval) calculated from mark–recapture analyses of two Yellowstone cutthroat trout size-classes (80-120 mm, black circles; >120 mm open circles) in three tributaries of Spread Creek, WY, 2011–2013. The winter 2011 interval is from September 1, 2011 – June 30, 2012; the summer 2012 interval is from July 1 – September 30; the winter 2012 interval is from October 1st 2012- June 30th 2013; and the summer 2013 interval is from July 1st 2013 – September 30th 2013.

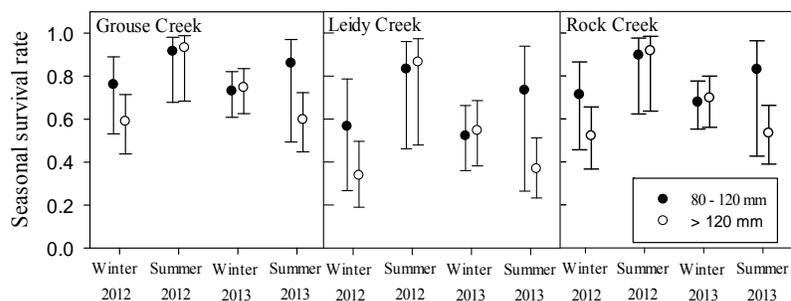


Figure 10. Model-averaged estimates of seasonal survival rate (95% confidence interval) over each time intervals calculated from mark–recapture analyses of two Yellowstone cutthroat trout size-classes (80-120 mm, black circles; >120 mm open circles) in three tributaries of Spread Creek, WY, 2011–2013. The winter 2011 interval is from September 1, 2011 – June 30, 2012; the summer 2012 interval is from July 1 – September 30; the winter 2012 interval is from October 1st 2012- June 30th 2013; and the summer 2013 interval is from July 1st 2013 – September 30th 2013.

Table 4 - Summary of model selection among Barker mark–recapture models used to estimate Yellowstone cutthroat trout survival rate (S) across two size-classes in three tributaries of Spread Creek, WY, 2011 – 2013. The Barker model includes six parameters: S ; capture probability (p), which was modeled as varying by size and stream; probability of recapturing a fish between sampling occasions (R), which was modeled as varying by time interval (t); probability of recapturing a fish before it dies between sampling occasions (R'), which was modeled as varying by season; probability of resighting a dead animal (r), which was modeled as varying with season; and the probability that a fish at risk of capture in time t is also at risk of capture in time $t+1$ (F), which was set equal to probability that a fish not at risk of capture in time t is at risk of capture in time $t+1$ (F') because it was assumed that emigration from the tagging reach was random. Quasi - Akaike's information criterion corrected for small-sample size (QAICc), the difference between a given model and the best supported model (Δ QAICc), number of parameters estimated by the model (K), Quasi-Akaike weight (W_i), and likelihood of each model are shown.

Model structure of S	K	QAICc	Δ QAICc	W_i	Model likelihood
size + stream + t + size*time	24	3118.79	0	0.97	1
stream + t	19	3126.88	8.10	0.02	0.0174
size + stream + t	20	3128.05	9.26	0.01	0.0097
Size + stream + year + size*stream	20	3135.15	16.36	0.00	0.0003

◆ DISCUSSION

Knowledge of intra-species diversity in life history characteristics and vital rates is an important consideration for long-term conservation planning (Schindler et al. 2010). In this study we documented variability in growth, movement, and survival of Yellowstone cutthroat trout from three tributaries within an intact headwater basin. Additionally, we quantified important stream factors and linked variability in growth rates to differences in stream temperatures and streamflows. We also compared growth rates and movement patterns between brook trout and Yellowstone cutthroat trout within one stream.

Growth

Salmonid growth is strongly regulated by stream temperature due to the direct control it exerts on metabolism (Swift 1961, Brett 1964). Studies conducted in a laboratory setting have revealed strong relationships between temperature and growth (Elliot 1975, Bear et al. 2007), but attempts to assess laboratory derived temperature relationships in a field setting have yielded mixed results (Lobón-Cerviá and Rincón 1998, Johnson et al. 2006, Xu et al. 2010a). We found that temperature had a significant effect on Yellowstone cutthroat trout growth, but it depended on fish length and streamflow. A similar relationship has been documented for variability of summer growth rates of brook trout in the Eastern U.S. (Xu et al. 2010a).

We found that increased streamflow was strongly associated with higher growth rates. Harvey et al. (2006) documented suppression of rainbow trout growth rates when streamflow was diverted from study reaches within a California stream. The mechanistic relationship between growth and streamflow is likely due to the control streamflow has on availability of suitable foraging habitat (Nislow et al. 2004).

Although we were unable to analyze growth variability for brook trout or test for an effect of brook trout presence on Yellowstone cutthroat trout growth due to confounding variables and small sample size, we found that brook trout had higher average growth compared with Yellowstone cutthroat trout within the same stream as well as populations in the other tributaries. Other studies have documented negative effects of introduced salmonid species on growth rates of native trout. Seiler and Keeley (2009) found cutthroat trout growth rates were significantly lower in sympatry with cutthroat-rainbow hybrids than in allopatry. McHugh and Budy (2005) observed Bonneville cutthroat trout *O. c. utah* had lower growth rates in sympatry with brown trout than in allopatry. In a laboratory experiment, brook trout significantly depressed growth rates of bull trout (McMahon et al. 2007). Further investigation is necessary to investigate the effect of brook trout density on Yellowstone cutthroat trout growth rates and what interaction it has with the other factors we investigated in this study.

Survival

Salmonids have age-structured populations, in which survival rates are dependent on size and age class (Xu et al. 2010b). Small increases in survivorship of juvenile age classes can elicit substantial responses in population growth, which can increase chances of persistence (Hilderbrand 2003). We did not detect significant differences between survival rates of two sizes of Yellowstone cutthroat trout. During the summer of 2013 the estimate of survival for larger trout was considerably lower than survival of smaller trout, but detection of a statistically significant difference was precluded by the imprecise survival estimate of smaller fish due to a small sample size of tagged trout in that size class. The decrease in survival of adult trout may be from low streamflows in 2013. Even though Rock Creek had slightly higher discharge in 2013, all three streams have been in a drought cycle and the associated decreases in baseflow may have negatively impacted survival of larger trout. Xu et al. (2010b) found that decreased streamflows reduced summer survival rates of brook trout in larger size classes.

Interestingly, we did not detect significant differences in survival across streams despite different hydrologic and thermal regimes. Although these differences are associated with variation in growth they may not be different enough to elicit changes in survival. Temperatures in these streams are generally optimal as the maximum average daily temperature throughout the summer never approached the critical upper thermal limit of 19.6°C, reported for the similar subspecies westslope cutthroat trout (Bear et al. 2007). Also, we may not be detecting effects on survival due to the size classes we investigated. Peterson et al. (2004) documented biotic and abiotic effects on survival of juvenile Colorado River cutthroat trout, but for age-2 and older there were no detectable effects on survival.

Movement

Movement can influence individual success by moving to more suitable locations and it can influence population dynamics through immigration and emigration. It wasn't until recently that mobility in headwater trout populations was found to be common, contrary to early thoughts (Gowan et al. 1994). We documented a wide range of movement patterns, with some fish exhibiting high mobility. There were trout present in each stream that moved distances greater than 3km. In Rock Creek displacement distances declined greatly after July. In Grouse and Leidy creeks, the widest range of movement was in July as well, but there was still a broad amount of mobility

through the late summer and fall. The high mobility documented during the July interval may be from trout making post-spawning movements. Other studies have found cutthroat trout movements to be greatest during the spawning season and decline considerably following post-spawning movements (Young 1996, Hilderbrand and Kershner 2000, Schrank and Rahel 2004).

It is largely documented that discharge is a key factor eliciting spawning movement for cutthroat trout (Brown and Mackay 1995b, Schmetterling 2001), but the role it plays in affecting movement patterns during other seasons remains poorly studied. We found mobility was greatest earlier in the summer when flows were higher as well as in streams with higher discharge profiles. Trout in Grouse and Leidy creeks had higher average displacement distances than trout in Rock Creek and this pattern was most pronounced after high flows subsided. Although Rock Creek had similar average discharge compared with Grouse Creek in 2013 it is characteristically a low discharge profile stream. This sharp decline in mobility on the descending limb of the hydrograph may be indicative of local adaption to a low discharge profile. Individuals that make long range movements may do so during higher flows to minimize risk of predation. In Grouse and Leidy Creeks baseflows are generally higher and individuals may be at less risk of predation and use mobility later in the summer to better exploit optimal foraging habitats within the streams (Gowan and Fausch 2002).

We observed a wider range of movement distances within each stream in 2013 compared with 2012 which may be due to a much larger sample size of tagged individuals during 2013. The average distances moved during each interval were not very different between years within each stream. Although we did not observe pronounced movement differences in response to inter-annual variability in discharge as was observed with Bonneville cutthroat (Schrank and Rahel 2006), we did see the general trend of higher mobility in response to higher flows when comparing across streams.

We found an increase in trout moving over the stationary antennae in Grouse and Leidy creeks during the fall, but not in Rock Creek. There was a slight peak in detections at the antennae in Leidy Creek during September and during October in Grouse Creek. These movements may be individuals seeking suitable over-winter habitat as westslope cutthroat have been documented making extensive fall movements coinciding with declining temperatures and formation of stream ice (Brown and Mackay 1995a, Jakober et al. 1998). There is documentation of

variation in fall movements among different subspecies as Bonneville cutthroat trout (Hilderbrand and Kershner 2000) and Colorado River cutthroat trout (Young 1998) did not display autumn movements. It is interesting that we found a similar pattern of variability across different populations of the same subspecies.

◆ CONCLUSIONS

Our research documented variability in growth and movement patterns as well as quantified survival rates of Yellowstone cutthroat trout. We found strong and interactive effects of streamflow and stream temperature on trout growth rates. Higher streamflows mediated the effects of increasing summer stream temperatures, whereas low streamflows exacerbated the impacts of warming temperatures. This underscores the importance of considering multiple climate-driven stream factors when predicting the effects of climate change on trout populations. We also found considerable differences in movement patterns within the basin that may be related to differences in stream discharge profiles. These results suggest that intra-basin variability in life history characteristics and vital rates should be considered when developing and implementing conservation strategies.

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INTERNS

UW-NPS WILDERNESS INTERNSHIP

SHANNON GLENDENNING ✦ UNIVERSITY OF WYOMING ✦ LARAMIE, WY



✦ INTRODUCTION

In the summer of 2013, projects regarding wilderness in the John D. Rockefeller, Jr., Memorial Parkway (Parkway) and Grand Teton National Park (Park) were researched and completed. The researcher worked under the direct supervision of Shan Burson, bioacoustics ecologist and wilderness coordinator for Grand Teton National Park, and with the staff of the Science and Resource Management Division of Grand Teton National Park. The main goal of the wilderness internship was the drafting of a wilderness eligibility assessment for the Parkway. Secondary tasks included research and recommendations for wilderness management in the Park.

✦ WILDERNESS ELIGIBILITY ASSESSMENT

All lands administered by the National Park Service are evaluated for their eligibility for inclusion in the National Wilderness Preservation System. It is a first, administrative look at the wilderness character

of a piece of land. Since the John D. Rockefeller, Jr., Memorial Parkway was established in 1972, an assessment was never completed. The Parkway is administered by Grand Teton National Park.

The initial steps of the study was finding and evaluating National Park Service documents relating to the establishment and management of the Parkway. Documents included the Environmental Impact Report from 1973 evaluating the impacts of the establishment of the Parkway; congressional hearings and reports on the establishment of the Parkway; the enabling legislation for the Parkway; the Foundation for Planning and Management for Grand Teton National Park and the John D. Rockefeller, Jr., Memorial Parkway; the General Management Plan; the Fire Management Plan, land management policies and designations for neighboring lands to the Parkway; visitation statistics, environmental assessments for various projects that have occurred in the Parkway; and many other documents relating to former and current management and activities occurring in the Parkway. These documents provided a basis for the assessment.

The second component of the assessment was evaluating the Parkway based on its wilderness character using 2012 NAIP imagery at one meter resolution. This imagery was used in coordination with existing Park GIS information to determine what types and levels of development had occurred in the Parkway.

Using this information, the wilderness character of the land in the Parkway was evaluated. Wilderness character is defined in the Wilderness Act of 1964 and subsequent National Park Service policies. Based on this analysis, a draft memo was prepared explaining the assessment process and the recommendation based on the guidance provided by the Wilderness Act and National Park Service policies and guidance. This was sent to the Park Superintendent for review and action.



◆ OTHER WILDERNESS PROJECTS

After the completion of the draft wilderness eligibility assessment additional work on wilderness management in Grand Teton National Park was completed. The Park does not manage any congressionally designated wilderness but manages recommended and potential wilderness, land managed to preserve its wilderness character.

For every action proposed to occur in wilderness a Minimum Requirement Assessment is required. Conducting a minimum requirement analysis follows the direction of both law and agency policy to assist land managers make better informed decisions. The Park's current Minimum Requirement Decision Guide (MRDG) was evaluated and revised as necessary based on feedback from the wilderness

coordinator and review of other guides used for the same analysis. Additionally, programmatic MRDGs were developed for ongoing administrative actions occurring in Grand Teton wilderness. Drafts include bridge replacements, sign replacements, food storage installations, and administrative and historic structure repair or restoration, and research activities in wilderness.

The Park is going through an internal process of writing a document to effectively integrate wilderness character in Grand Teton National Park into park planning through monitoring and understanding the resources in wilderness. The first two chapters of this document were drafted, describing the definition of wilderness character and purpose of monitoring, and the history of the Wilderness Act and wilderness in Grand Teton National Park.

◆ CONCLUSION

In the summer of 2013 significant work was completed for wilderness lands in Grand Teton National Park and the John D. Rockefeller, Jr., Memorial Parkway in Wyoming.



◆ ACKNOWLEDGMENTS

I would like to thank everyone at the UW-NPS Research Station. You all made the summer an amazing experience and made living in the Tetons, next to Jackson Lake, even better than I could imagine. Also a big thank you to Shan Burson and staff in the Science and Resource Management Division of Grand Teton National Park for this opportunity and great learning experience.

CLASSES



FIELD RESEARCH AND CONSERVATION



INSTRUCTORS ♦ CHUCK COLLIS ♦ JENNIFER ADAMS
CLAYTON HIGH SCHOOL ♦ CLAYTON, MO



♦ CLASS OVERVIEW

The Field Research & Conservation class emphasizes long-term field research experiences, examines ecosystem processes, and investigates the evolution of American perspectives about nature. Our time spent at the UW-NPS research station was divided between pursuing behavioral ecology research and exploring Grand Teton National Park and the surrounding area to gain understanding of how the region was shaped, both by geological and biological process as well as political processes that have been shaped by America's ever-changing conservation ethic.



This year we performed a preliminary field study on a population of sagebrush crickets (*Cyphoderris strepitans*) at Lower Deadman's Bar that investigated the role of female choice in the promotion of calling behaviors by males. To gather baseline data, we built a circular, 0.5 meter diameter pen around the "home sagebrush" of each of the twenty males in our study. Over four nights, we observed and scored the frequency of male calling and how quickly their calling resumed when disturbed. These data were then used to separate the males into two groups: bold and timid.



We hypothesized that the males' behaviors would be consistent with baseline data when a bold male, a timid male, and a female were placed in a pen together. We also hypothesized that females would mate with bold males more often than timid males. Paired t-tests indicate that neither bold nor timid males changed their recovery-from-interruption behaviors significantly ($p = 0.14$ and 0.17 , respectively) while in a pen together. However, timid males showed a significant increase in their calling frequency ($p < 0.04$) while bold males showed no significant differences in this regard ($p = 0.13$). Observations of the crickets in these compressed densities suggest that timid males are stimulated to call in response to the calls of a bold male nearby. Although females did mount bold males more often than timid males, chi-square analysis indicates the differences were not statistically significant ($p = 0.26$). We wonder if this was influenced by the increased calling frequency of the timid males.



Students read numerous articles from Behavioral Ecology, Animal Behaviour, Physiological Zoology, and other professional periodicals. After discussing articles in detail with their instructors, students used their newfound understandings to complete a poster of our major findings in 2013. Their poster was presented at the 2014 Phi Sigma Research Symposium hosted by Illinois State University.

Living within a community of research scientists had tremendous benefits to my students. On numerous occasions we conversed with researchers about their work and gained valuable insights concerning the design and implementation of scientific studies. More specifically, we were introduced to research involving disease transmission in local species of birds.

Aside from conducting research, we explored Grand Teton and Yellowstone National Parks while learning about ecosystem dynamics, the role of disturbance and succession, local flora and fauna, and the influences of geologic process in shaping landscapes and the communities that occupy them.



IOWA STATE UNIVERSITY FIELD TRIP REPORT: ECOLOGY AND EVOLUTION IN THE GREATER YELLOWSTONE ECOSYSTEM

DIANE M. DEBINSKI ✦ ROBERT KLAVER ✦ DEPARTMENT OF ECOLOGY, EVOLUTION AND
ORGANISMAL BIOLOGY ✦ IOWA STATE UNIVERSITY ✦ AMES, IA

JULIE BLANCHONG ✦ SUE FAIRBANKS ✦ DEPARTMENT OF NATURAL RESOURCES
ECOLOGY AND MANAGEMENT ✦ IOWA STATE UNIVERSITY ✦ AMES, IA



Figure 1. Iowa State University EEB Fieldtrip participants at UW-NPS Research Station, June 2013. In order from left to right: Jer Pin Chong, Lynne Gardner, Hannah Julich, Amy Podaril, Karri Folks, Bob Klaver, Julie Blanchong, Tatyana Flick, John Delaney, Ryan Williams, Brent Mortensen, and Melissa Telemeco (photo by Diane Debinski).

✦ COURSE DESCRIPTION

Iowa State University's graduate program in Ecology and Evolutionary Biology (EEB) requires that all graduate students participate in one field trip class during their graduate career. In this 2 credit class students learn about the ecology of the ecosystem that they will be visiting via seminars and lectures during the semester. The classroom teaching culminates in a field trip experience. During the field trip the students have an opportunity to meet local scientists, researchers, land managers and representatives from non-government agencies. They then write up a summary of their work and are graded on these activities.

The 2013 EEB fieldtrip was led by Drs. Diane Debinski, Julie Blanchong, Bob Klaver, and

Sue Fairbanks. Ten graduate students participated in the field trip focused on the Greater Yellowstone Ecosystem (Figure 1).

The Greater Yellowstone Ecosystem (GYE) is one of the largest intact ecosystems in the continental U.S. However, it faces pressures from extractive industries, ecotourism, disease, and burgeoning population growth. The goal of this course was to familiarize the students with some of the ecological, social, and political issues related to managing this ecosystem. We met during the 2013 spring semester as a seminar group to inform ourselves about some of these issues. Then in June of 2013, we took a 10 day field trip to the GYE to explore some of these lands and organisms. Our team was housed for four nights at the University of Wyoming-National Park Service Research Station. We also spent two nights in cabins

near Gardner, Montana interacting with staff of the Yellowstone Institute. From these sites, we conducted day hikes through a variety of habitat types (forest, alpine, riparian, geyser basins, etc.) and met with biologists and conservationists representing organizations such as the National Park Service, the U.S. Forest Service, U.S. Geological Survey, Northern Rocky Mt. Science Center, Teton Science School, Wyoming Game and Fish Department, and the Greater Yellowstone Coalition. Some of the issues that our group explored included:

- Management of brucellosis and chronic wasting disease relative to bison and elk both in the parks and within the surrounding landscape
- The status of the wolf reintroduction program - Case studies: trophic structure before and after wolves came back; delisting/hunting issues; sarcoptic mange
- Protection of genetic biodiversity housed in hot springs of Yellowstone National Park, birth place of *Thermus aquaticus*, used in PCR techniques
- Potential effects of global climate change in the GYE - Case studies: pine beetles, pikas, forest change, and grizzly populations

- Warming waters and native trout
- Invasive species
- The role of fire in maintaining biodiversity
- The debate over wilderness designation of national forest lands in the GYE
- Water quality issues and the protection of geothermal resources
- Phosphate and gold mining, oil extraction, and wind power - Case study: sage grouse.

✦ CONCLUSIONS AND ACKNOWLEDGEMENTS

The class went very well and we appreciated the opportunity to spend time at the UW-NPS Research Station and to interact with the broad array of researchers and managers who work within the ecosystem.

Field Trip Itinerary			
Date	Location	Event	Location for the night
May 31 (Friday)	ISU Transportation Services parking lot	Pack vehicles	Ames
June 1 (Saturday)	Ames, IA to points westward	Westward ho!	Cheyenne WY
June 2 (Sunday)	Point westward to Moran WY	Drive to UW-NPS	UW-NPS Research Station, Moran, WY
June 3 (Monday)	AMK Grand Teton National Park	Hank Harlow – morning welcome to AMK, hibernation physiology talk. Hike/canoe near station Deb Patla & Kelly McCloskey – wetland restoration & amphibians	UW-NPS Research Station, Moran, WY
June 4 (Tuesday)	Grand Teton NP	Renee Seidler 9 a.m. AMK - wolverines; Diane Debinski - climate change experiment Pilgrim Creek Aly Courtemanch -evening presentation, bighorn sheep and migration routes	UW-NPS Research Station, Moran, WY
June 5 (Wednesday)	Old Faithful, Hot Springs	Drive through YNP, stop at hot springs to learn about archeobacteria	UW-NPS Research Station, Moran, WY
June 6 (Thursday)	Hayden Valley, Norris Hot Springs	Drive through YNP, discussion with Paul Cross (USGS) at Mammoth (~2 p.m.) about bison, elk, and disease	Yellowstone Institute, Gardiner, MT
June 7 (Friday)	Yellowstone Institute	Yellowstone Institute Programming (wildlife viewing and hike in Lamar Valley)	Yellowstone Institute, Gardiner, MT
June 8 (Saturday)	Drive eastward	Drive from Gardiner, MT and stop in Chamberlin, SD	Chamberlain, SD
June 9 (Sunday)	Drive home	Drive SD to IA	Ames

NASA-NPS LANDSCAPE CLIMATE CHANGE VULNERABILITY PROJECT (LCCVP) TEAM MEETING AT AMK RANCH (UW-NPS RESEARCH CENTER)



LEADERS ✦ ANDY HANSEN ✦ TOM OLIFF
MONTANA STATE UNIVERSITY ✦ MISSOULA, MT



Figure 1. A portion of the team hiking up Cascade Creek.



A NASA-funded research team met May 19-22 at the AMK Ranch for a semi-annual team workshop.

Participants included:

Montana State University – Andy Hansen,
Tony Chang, Regan Nelson, Nate Piekielek
Woods Hole Research Center – Patrick Jantz,
Scott Zolkos

NPS Inventory & Monitoring Program –
John Gross, Bill Monahan
Great Northern LCC – Tom Olliff
NASA Ames – Forrest Melton, Jun Xiong
Guest – Steve Running (University of
Montana)
Chef – Jodi Stevens

The goal of the project is to demonstrate the four steps of climate adaptation planning in two US Department of Interior Landscape Conservation Cooperatives (LCCs) using NASA and other data and models. Objectives are:

1. Hindcast and forecast future climate and land use scenarios.
2. Assess the vulnerability of ecological processes and key habitat types.
3. Evaluate management options.
4. Design and implement management adaptation strategies.
5. Facilitate decision support.

Designation of DOI LCCs emphasizes the threat that climate and land use change pose to biological resources in national parks and federal lands. Developing strategies for management and adaptation requires the ability to forecast biological response under future scenarios, assess the vulnerabilities of biological resources, and designing multi-scale management strategies. This project focuses on portions of the Great Northern and Appalachian LCCs, which have already undergone climatic warming. Within the climate adaptation framework of Glick et al. 2011, we are using the Terrestrial Observation and Prediction System (TOPS) and the SERGoM land use change models to hindcast (2001-2010) and forecast (2010-2100) responses of

habitat types to future climate and land use scenarios. Results are being used to assess vulnerability and to place indicators into management classes: Low Risk (management not needed); Manageable (management effective and required); and Save at High Costs (management costly, high risk). For Manageable issues, the team is designing spatially and temporally explicit management strategies to improve resilience and/or adaptation. This project will help prioritize future activities within the two case-study LCCs and provide a demonstration that may lead to application nationwide.

The project is nearly half way through the 4-year funding period. The purpose of the team meeting was to review progress to date and plan for upcoming activities. We convened the evening of May 19 with a fascinating introduction to the AMK by Hank Harlow. This was followed by a discussion lead by climate scientist and global ecologist Steve Running. The group had a wonderful day-long hike up Cascade Creek in the shadow of the Grand Teton on May 20. Our main work session was on May 21 at the AMK, but we were careful to leave time for a short hike to Grand View Point in the evening. The workshop was concluded on May 22 with a meeting at Grand Teton National Park Headquarters with GTNP and Bridger Teton National Forest Staff. The AMK was an outstanding setting for stimulating creative thoughts and fostering group synergy. Meals by Chef Jodi Stevens were wonderful. More information on the study can be found at:

<http://www.montana.edu/lccvp/index.html>.



UNIVERSITY OF WYOMING OUTDOOR STUDIO ART CLASS



INSTRUCTOR ✦ PATRICK KIKUT ✦ UNIVERSITY OF WYOMING ✦ LARAMIE, WY



✦ CLASS OVERVIEW

Since its inception as a Summer Innovative Course in 2000, the Department of Art Summer Outdoor Studio class has been exceptionally grateful for the opportunity to stay and work at the AMK Research Station as part of the three week summer intensive course. For art students, the dramatic setting and accommodation are inspiring and it is a highlight of the experience. From the AMK Ranch, students have full access to Grand Teton NP, Yellowstone NP as well as the National Wildlife Museum in Jackson. Last year we scheduled a docent tour of the Wildlife museum and attended an informative lecture on Native Art in the National Parks at the Coulter Bay Visitors Center. Art students appreciate the interaction with student researchers from different science disciplines. Often those conversations have direct impact on the



creative work students produce during their stay. The AMK staff and, in particular, Professor Hank Harlow have offered us incredible hospitality and generosity. Professor Harlow's knowledge of the geology, biology, and history of Grand Teton National Park is invaluable to this course. Also, his enthusiasm for art and scientific research is infectious. Our stay at the AMK always culminates in an exhibition of student and faculty creative work, hosted by Hank Harlow, UW NPS Research Station Director.



AMK Boat House/ Studio



National Wildlife Museum

UTAH STATE UNIVERSITY WATERSHED SCIENCES GRADUATE STUDENT INDUCTION COURSE



INSTRUCTORS ✦ JOSEPH M. WHEATON ✦ PATRICK BELMONT
UTAH STATE UNIVERSITY DEPARTMENT OF WATERSHED SCIENCES ✦ LOGAN, UT



✦ CLASS OVERVIEW

Utah State University Department of Watershed Sciences runs an introductory course for all incoming graduate students (10 in fall 2013) immediately prior to each fall semester. The course is an intense, five day introduction to the fundamental concepts of Watershed Science, as well as the people of the Department of Watershed Science and the techniques they use in research. The course begins

with one day focused on water quality and wetlands at Cutler Reservoir in Logan, Utah, then one and a half days focusing on collection of fish, remotely sensed data, and topographic surveys in the Logan River watershed, followed by one and a half days discussing landscape organization and evolution and making field observations in the Grand Teton region. We use AMK Ranch for lectures, discussions, group dinners, sleeping quarters, and as a central base for Teton area activities, including rafting on the Snake River (photos above).

✦ CLASS OBJECTIVES

The general objectives of the course are to help incoming graduate students get acquainted with the nearby landscape, the people in the Department of Watershed Sciences, some of the broader concepts and questions that define Watershed Science, and some of the techniques that USU faculty use to answer those questions.

A sampling of the techniques demonstrated:
Terrestrial laser scanning, Real-time kinematic GPS, Collection of visible in IR aerial photography using drone aircraft, Field mapping, Soil evaluation, Collection and analysis of climate data, Fish and macroinvertebrate sampling, and Water quality monitoring.

