NATIONAL PARK SERVICE RESEARCH CENTER

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EDITED BY

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INTRODUCTION

2011 ANNUAL REPORT
DIRECTOR’S COLUMN

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 performed in national parks, monuments, and recreation areas in Wyoming and neighboring states. The UW-NPS Research Center solicited research proposals from university faculty or full-time governmental research scientists 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 distributed to nationally-recognized scientists for peer review and are also reviewed and evaluated by the Research Center’s steering 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 the middle to end of March to early April.

The UW-NPS Research Center also operates a NPS-owned field research station in Grand Teton National Park. The research station provides researchers in the biological, physical and social sciences an enhanced opportunity to work in the diverse aquatic and terrestrial environments 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.

Special acknowledgement is extended to Ms. Celeste Havener, Office Associate, for her skills and dedication to the Research Center which were a vital contribution to this publication.

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).
SEASONAL AND ALTITUDINAL VARIATION IN POLLINATOR COMMUNITIES IN GRAND TETON NATIONAL PARK

MICHAEL E. DILLON ♦ DEPARTMENT OF ZOOLOGY AND PHYSIOLOGY AND PROGRAM IN ECOLOGY ♦ UNIVERSITY OF WYOMING ♦ LARAMIE

ABSTRACT

Native pollinators are in decline across the globe, likely due to a combination of habitat loss, pesticides, invasive species and changing climate. Determining the independent effects of climate on pollinators has been difficult in part because we lack studies of pollinator populations in largely undisturbed areas. Early spring and alpine pollinators are most likely to be affected by changing climate. Using a standardized sampling protocol, I measured relative abundance of major pollinator groups (flies, beetles, bees, wasps, and butterflies) from early spring to late summer at sites ranging from 2100 to 3300 m elevation. Flies were most abundant in early spring and at high elevations. Bees were abundant throughout the season and across all elevations. These data suggest that flies and bees should be targeted for future monitoring because they may be particularly susceptible to changing climate, and their loss could cascade through the broader community.

INTRODUCTION

Global warming is likely having profound and diverse effects on organisms, including shifts in their distributions (Parmesan and Yohe 2003) and changes in the timing of life history events (“phenology”; Both et al. 2006). Differential effects of climate on phenology of community members can lead to “phenological mismatches” that may cause reductions or even extinctions of local populations (Memmott et al. 2007). Such phenological mismatches may have played a key role in the decline of insect pollinators in Europe (Biesmeijer et al. 2006) and the United States (Cameron et al. 2011) over the last 20-30 years. These pollinator declines are alarming not only because of their effects on agriculture (Berenbaum et al. 2007) and therefore human health (Eilers et al. 2011) but also because of their potentially substantial and far-reaching indirect effects on ecosystem services (over 85% of flowering plants depend on insect pollination; Ollerton et al. 2011).

Pollinator declines are undoubtedly tied to loss of habitat associated with changes in landscape use (Cameron et al. 2011), to nontarget effects of over- and misuse of common herbicides and insecticides (Henry et al. 2012, Whitehorn et al. 2012), and to pathogen spread from introduced species (Stout and Morales 2009). However, the effect of changing climate on pollinators is less clear because we have so little data on undisturbed pollinator populations (see Parmesan 2007), making it difficult to disentangle the effects on pollinators of climate vs other drivers (reviewed by Potts et al. 2010).

Given that long-term data on pollinator populations in undisturbed locations is rare, one approach to assessing potential impacts of climate-driven phenological mismatch is to identify pollinators whose phenology and life-history make them more likely to be impacted by changing spring temperatures (Memmott et al. 2007). In particular, pollinators that emerge in early spring and specialize on particular plant species may be more susceptible to phenological mismatch (e.g. Kudo et al. 2004). Similarly, pollinators in alpine ecosystems may be particularly vulnerable to changing climate because the short and unpredictable growing season increases the probability of mismatch with floral resources (Burkle and Alarcon 2011), and because mountains
have experienced the most extreme temperature changes (IPCC 2007). Furthermore, alpine plants are more strongly dependent on pollinators for reproduction (García-Camacho and Totland 2009), making the potential community-wide effects of phenological mismatch pronounced in alpine ecosystems.

Knowledge of seasonal and altitudinal abundances of pollinators in undisturbed habitats provides important data on which groups and species are most likely to be affected by shifting climate. However, community-wide studies of altitudinal and seasonal variation in pollinators are rare (Cruden 1972, Macior 1974, Arroyo et al. 1982, Primack 1983, Inouye and Pyke 1988, Warren et al. 1988). In general, bees tend to dominate the pollinating fauna but often diminish in importance with altitude (Primack 1983, Warren et al. 1988 but see Arroyo et al. 1982), where they are often replaced by flies and butterflies (Macior 1974, Inouye and Pyke 1988). Unfortunately, the limited data available are largely based on non-standardized sampling techniques, making interpretation of the relative abundance data problematic. Therefore, these data are of limited utility for identifying pollinators most at threat from ongoing climate change.

To address this gap, here I report preliminary data on insect pollinator communities in Grand Teton National Park. The study area is attractive because it has remained largely undisturbed in terms of anthropogenic impacts unrelated to climate (e.g. land use changes and agricultural chemicals) and because the large elevation gradient within the park facilitates altitudinal transects. Newly available standardized sampling protocols allow for unbiased assessment of seasonal and altitudinal variation in insect pollinator populations.

Methods

Study sites

I sampled pollinators at 13 sites in Grand Teton National Park (GTNP), Wyoming, USA during three separate trips in 2011: June 24 - July 1, July 16-23, and August 12-19 (Table 1). One site was near the UW-NPS Research station on the AMK Ranch, five sites were spaced roughly every 250 m in elevation from 2100-3050 m along the Paint Brush Canyon Trail and 6 sites were spaced roughly every 250 m in elevation from 2100 to 3300 m along the Death Canyon trail (Figure 1, Table 1). All sampling sites were open meadows with abundant flowers. Flower abundance and community composition varied seasonally and with altitude among sites but was not explicitly measured (Shaw 1968 for description of area flora).

![Figure 1. Pollinator collection sites within Grand Teton National Park. Point colors indicate altitude from low (red) to high (blue).](image)

Collections

At each site, I collected pollinators in bowl traps (Southwood and Henderson 2009), which are an effective, unbiased and standardized method for sampling insect pollinators (Dafni 1992; Berenbaum et al. 2007), including flies, beetles, bees, butterflies, and wasps (Dafni 1993, Berenbaum et al. 2007). Bowl traps were made from 5 oz polystyrene vials (40 dram, Thornton Plastic Co., Salt Lake City, Utah, USA) painted white, fluorescent yellow, and fluorescent blue, colors that are attractive to a diverse assortment of pollinating insects (Dafni 1993). Bowl triplets (one of each color) were mounted on rebar stakes at approximately the height of the surrounding flowers (10-40 cm above ground). Stakes were placed in a straight line roughly 6 m apart to avoid effects of neighboring bowls on capture rates (Droege et al. 2010). Bowl traps were filled ~3/4 full with soapy water (1 tsp. Dawn Original Blue ® dish soap per gallon distilled water) to minimize surface tension and therefore maximize captures of visiting insects. Bowls were left out for a ~48 hour sampling period before cup contents were poured through coffee filters to separate collected insects for transport to the lab. In the lab, collections were sorted by taxonomic group and counted, using a binocular scope when necessary. All collections were done under permit GRTE-2011-SCI-0011 (Study # GRTE-00219).
Table 1. Pollination sampling sites.

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<th>Site</th>
<th>Location</th>
<th>Elevation (m)</th>
<th>Description</th>
</tr>
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<tr>
<td>AM2100</td>
<td>43.9359 N, 110.6369 W</td>
<td>2087</td>
<td>Between Leek's marina and UWNPS research station</td>
</tr>
<tr>
<td>DC2100</td>
<td>43.6537 N, 110.8057 W</td>
<td>2050</td>
<td>Death Canyon trail SW of junction with Phelps lake trail</td>
</tr>
<tr>
<td>DC2350</td>
<td>43.6608 N, 110.8264 W</td>
<td>2364</td>
<td>Death Canyon trail below lip before ranger cabin</td>
</tr>
<tr>
<td>DC2600</td>
<td>43.6694 N, 110.8292 W</td>
<td>2597</td>
<td>Alaska Basin trail before 5th switchback</td>
</tr>
<tr>
<td>DC2850</td>
<td>43.6713 N, 110.8206 W</td>
<td>2831</td>
<td>Alaska Basin trail at 2nd switchback on Albright west slope</td>
</tr>
<tr>
<td>DC3050</td>
<td>43.6720 N, 110.8163 W</td>
<td>3053</td>
<td>Alaska Basin trail just before Albright-Static saddle</td>
</tr>
<tr>
<td>DC3300</td>
<td>43.6800 N, 110.8183 W</td>
<td>3314</td>
<td>Alaska Basin trail just north of static peak divide</td>
</tr>
<tr>
<td>PB2100</td>
<td>43.7998 N, 110.7316 W</td>
<td>2103</td>
<td>Leigh Lake trail past spillway to String Lake</td>
</tr>
<tr>
<td>PB2350</td>
<td>43.7999 N, 110.7657 W</td>
<td>2358</td>
<td>Paintbrush Canyon trail just below lower campsites</td>
</tr>
<tr>
<td>PB2600</td>
<td>43.7942 N, 110.7832 W</td>
<td>2579</td>
<td>Paintbrush Canyon trail below last shelf before Holly Lake</td>
</tr>
<tr>
<td>PB2850</td>
<td>43.7867 N, 110.7940 W</td>
<td>2830</td>
<td>South fork of PB Canyon trail near lake (not Holly)</td>
</tr>
<tr>
<td>PB3050</td>
<td>43.7926 N, 110.8089 W</td>
<td>3055</td>
<td>Paintbrush Canyon trail just below Paintbrush Divide.</td>
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**PRELIMINARY RESULTS**

During 2011, ~6063 hours of sampling (30315 cup hours) yielded 4680 insects. Overall, flies dominated cup collections (67% of all insects) followed by beetles (21%), bees (7%), wasps (4%), and butterflies making up just over 1% (Figure 2). The 2011 season was an unusually cold and wet year such that altitudinal representation varied with season and I was unable to reach the highest elevation sites until mid-August (Figure 3). I therefore subset the data to compare pollinator fauna among seasons and altitudes.

Seasonal variation in pollinator communities

When the data were restricted to the lowest elevation sites (AM2100, DC2100, PB2100; see Table 1, Figure 3), the number of pollinators captured per cup hour of sampling tended to increase across the season (ANOVA, \( P=0.053 \)), but the response varied among sites (ANOVA, interaction effect, \( P=0.052 \)), with AMK and Death Canyon having increased catch in August (Figure 4, black and red points) but Paintbrush Canyon showing no seasonal trend (Figure 4, blue points). These low elevation sites were dominated by beetles (47%) followed by flies (32%), bees (12%), wasps (5%), and butterflies (<1%).

Figure 2. Taxonomic composition of pollinators caught in bowl traps across all sites and sampling periods.

Figure 3. Seasonal and altitudinal sampling during 2011. Points are dates on which cups were collected from sites after ~48 hours of sampling. Point color indicates sampling area (black: AMK Ranch, blue: Paintbrush Canyon, red: Death Canyon) and points are scaled by total number of insects collected (see inset legend).
The pollinator fauna in early spring was dominated by beetles (45%), followed by bees (27%) and flies (27%), whereas in late summer flies (39%) and beetles (38%) dominated, with bees also accounting for a sizable portion of cup collections (12%). Wasps and butterflies never accounted for more than 7% of collections. These seasonal patterns in pollinator community composition were driven by an increase in fly abundance across the season (ANOVA, $P=0.032$; Figure 5A), a marginal decrease in beetle abundance (ANOVA, $P=0.062$; Figure 5B), and no change in bee abundance across the season (ANOVA, $P=0.744$; Figure 5C).

Altitudinal variation in pollinator communities

Because of limited sampling at high altitudes early in the season (Figure 3), I only compare altitudinal variation in pollinator communities for the late summer sampling dates (Figure 3). Late season samples were dominated by flies (70%), followed by beetles (19%), bees (6%), wasps (3%), and butterflies (<2%). There was a non-significant trend for the total number of pollinators...
per cup hour to increase with elevation during the final sampling period (ANOVA, \( P=0.085 \)). This may be due to the interaction between season and altitude: this was late in the season for the low altitude sites and early to mid season for the high altitude sites. Flies and beetles dominated at 2100 m (39% and 38% of captures, respectively), followed by bees (12%). Mid-elevation (2850-3050 m) sites were ~95% flies. Beetles dominated the 3300 m site (64%), followed by flies (17%) and bees (14%). These patterns in pollinator community composition were driven by altitudinal increases in flies up to 3050 m (ANOVA, \( P<0.001 \)), altitudinal decreases in beetles (ANOVA, \( P=0.003 \)), and relatively constant bee abundances across altitude (ANOVA, \( P=0.111 \); see Figure 6). Wasps and butterflies were particularly rare at high elevations but never made up more than 7% of the samples at any elevation.

## CONCLUSIONS

Preliminary analyses suggest that flies are under-appreciated pollinators. Not only were flies by far the most abundant pollinators overall (Figure 2), they were proportionately more abundant in early spring (Figure 5) and at high elevations (Figure 6) than the next most common pollinators, beetles and bees. Recent pronounced declines in pollinating flies (Biesmeijer et al. 2006) combined with their prevalence in early spring and at high elevations documented here suggests that flies may be particularly susceptible to changing climate. However, flies tend to be generalist pollinators, able to harvest resources from a wide variety of flowers (Willmer 2011), perhaps buffering them from potential climate-induced phenological mismatch. From the plant perspective, flies often have short dispersal distances and limited capacity to carry pollen (Willmer 2011), potentially making the community-wide implications of reduced fly populations less severe.

Beetles are also common in early spring (Figure 5), but tend to be rare above 2600 m (Figure 6). However, like flies, they tend to be generalist feeders and (usually) less effective pollinators (Willmer 2011).

Although they can be important pollinators in other systems, wasps and butterflies were always rare in these collections. For butterflies, which are often one of the most common pollinators collected, bowl traps may be an inappropriate sampling technique. The relatively large size of butterflies may make it difficult to capture visitors in the small cups. Butterflies have also been one of the most important groups for documenting the biological effects of changing climate (Parmesan and Yohe 2003), therefore future work should include alternative sampling methods for estimating butterfly populations.
Although bees were not the most abundant pollinators, they were present in sizable numbers across all seasons and altitudes (Figures 5, 6). Given that: 1) bees are active early in the spring and at high altitudes, 2) that flower specialization is particularly common among bees (reviewed by Willmer 2011), and 3) that bees are effective pollinators of diverse plants then bees may be particularly susceptible to changing climate and reductions in bee populations are likely to reverberate through the broader community.

**FUTURE WORK**

Beyond the abundance data presented here, we are also exploring other characteristics of insect pollinators that may change seasonally and altitudinally and that may also alter their importance as pollinators. Body size can vary with geographic and seasonal shifts in temperature (see, Bishop and Armbruster 1999, Brehm and Fiedler 2004, Dillon et al. 2006) and also has important implications for pollinator efficiency and floral specialization. We are currently measuring body size of identified native bee specimens to test for seasonal and altitudinal variation in body size among this diverse group of important pollinators.

**ACKNOWLEDGEMENTS**

I thank the UW-NPS Research Station for financial support, my collaborators Carlos Martinez del Rio and Scott Shaw for discussions and advice, Linda Franklin and Sue Consolo-Murphy for facilitating collection permits, John Bruno, Olivia Nater, Christine Bell, and Shelby Oelklaus for help in the field and lab, and Hank Harlow and Celeste Havener for facilitating station arrangements.

**LITERATURE CITED**


GRAND TETON NATIONAL PARK
A long time ago, in 1922 to be exact, a man and his young bride packed all their possessions into a Model T Ford truck, and navigated the primitive road eastward across Teton Pass. Harrison and Hildegard Crandall were undertaking an adventure to live out their American dream. They intended to raise a family in Jackson Hole, and interpret their “ideal landscape”—the Teton country—in oil paintings and photographs. Like so many energetic Americans before them, the Crandall family had the fortitude and perseverance to make their dreams come true. There were many tough years of dry homesteading in Jackson Hole, building and running an art business during the Great Depression, and weathering the controversies of frontier life during turbulent times. Nonetheless, the Crandall family successfully operated their art studio for 34 years near Jenny Lake in the Grand Teton National Park. They also operated a studio in the shadow of Jackson Lake Dam at the old village of Moran. Today, we can celebrate the Crandall family legacy by studying Harrison’s many fine paintings and photographs that are found in collections and homes far and wide.

Harrison Crandall was “Official Photographer” of the Grand Teton National Park from the Park’s establishment in 1929 until his retirement in the 1960s, which gave him a unique opportunity to photograph many early Park scenes. Thousands of photographic negatives were produced of Grand Teton landscapes, local ranch life, tourists, and officials. A customary part of any photographic business is to file all negatives in a safe place for future use. Harrison’s irreplaceable negative archive had grown to fill several filing cabinets. However, the routine storage process was destined to become a legendary story filled with elements of photographic tragedy, insight and conservation.

On Christmas Eve 1954, Harrison’s log studio-workshop building where the negatives were stored was mysteriously engulfed in fire. The studio was adjacent to the Crandall’s home, which was located near Moose, Wyoming. The Crandalls their visiting daughter, Nancy, and her husband, Chuck Cooper, were to help celebrate the holiday with resident co-workers, Quita (Harrison’s other daughter), and her husband, Herb Pownall. When the fire was discovered, fire fighters were summoned from Park Headquarters, which was located a few miles away at Moose. It took precious time for the responders to take drained and dry firefighting equipment from storage. Water was found for a pump truck in nearby Ditch Creek, but a thick layer of ice prevented quick access. There was too little time to save the burning structure, and only a small portion of the Crandall negative file could be rescued.

The aftermath of the studio-workshop fire was no time to grieve over the irreplaceable losses, which also included some of Harrison’s oil paintings and camera equipment. The rescued negatives were soaked! Herb recognized that if the wet negatives were not immediately separated and dried, they would perish within a few days from physical and/or mildew damage. Herb understood the sensitivity of the negatives because he was a photographic expert himself, and worked for many years as Harrison’s
darkroom technician and studio manager. Harrison, Herb, and Chuck raced to separate the wet negatives and hang them in the air to dry. Hastily strung drying lines became a chaotic profusion of images. In the rush to save as many negatives as possible, some potentially salvageable images without identifying notes were lost in the charred ruins under foot. In all, about 1,200 negatives were rescued (mostly 3.25” x 4.25” and a few 4.75” x 6.75”).

Many rescued negatives were slightly damaged around the edges from partial melting of the plastic base and emulsion layers. Some negatives had minor warping and lifting of emulsion within the prime image area. Remarkably, most of the rescued images remained in somewhat useable condition. In the end, the surviving negatives were rescued thanks to the foresight and quick action of Harrison, and the dedicated assistance of other family members. The dried negatives were placed back into bulk storage where they rested for nearly half a century. Despite the heavy losses, Harrison remained undaunted. At the age of 67, his vigorous constitution drove him to rebuild. Out of the ashes, he built a larger studio-workshop, and continued his life-long quest to create art and photographs of his favorite place on earth for show at his Jenny Lake studio.

The surviving Crandall negatives resurfaced during the “Creating a Vision of Grand Teton National Park” research project (see Barrick 2008, 2009). Initially, the study of Harrison Crandall’s work involved locating photographic “prints” from private collections, the Grand Teton National Park archive, and the national archives. At the time, I did not fully understand the scope of the negative collection or the number of recorded subjects. Moreover, Herb initially underestimated the importance of the negatives for research because he believed that the fire damage made them very difficult to print using standard photographic technology. In fact, Herb tried to make some contact photographic prints years ago, but that project was abandoned, in part, due to the incredible amount of darkroom time that would have been required to avoid extreme handling damage and to print all of the images. In 2010, I was invited to visit the Pownalls in order to scan some Crandall prints, and during that process, Herb brought out a negative and showed it to me. I was pleasantly surprised to learn that the negative exhibited far less damage and warping than I expected. It was clear that digital scanning equipment would accommodate the negatives without causing further damage, and provide a high-quality digital image (in any event, the edges were likely to be cropped somewhat during most printing applications). Quita and Herb Pownall graciously agreed to allow me to digitally scan the surviving Crandall negatives for use in my research and publications. The digital negatives are easily converted to positive images using standard photographic editing software.

The rescued negatives had a storied history, but their journey was not yet complete! The digitization process opened up another important part of the story. The Pownalls, buoyed with a renewed sense of the historic and research value of the images, gracedly decided to donate the negatives, and the digital copies, to the American people through the Grand Teton National Park archive. In a very real sense, the negatives were now destined to close a circle—a major visual archive of Harrison and Hildegard Crandall’s life work, including images of the Grand Teton National Park’s founding activities, was going to reside in perpetuity with the National Park that they loved. Moreover, since most future use of the images will be based on digital technology, the donated digital copies will help the Park conserve the images by reducing the need to handle the fragile negatives. Curator of the Grand Teton National Park, Alice Hart, arranged for funds to place the negatives in archival sleeves, and to include them in the National Park Service’s photographic inventory system. The Crandall negatives are now in safe, permanent, temperature-controlled storage at the National Park Service’s photographic archive facility at Tucson, Arizona.

The Crandall negatives were appraised by Terry Winchell of Fighting Bear Antiques (Jackson, Wyoming), in consultation with other experts that have evaluated the collected works of early western photographers. In 2011, the appraised value of the Crandall negative collection and associated digital scans was determined to be $185,000. While the appraisal provided an expert assessment of the current “market” value of the donation, it is not customary for such appraisals to capture the considerable “nonmarket” value that is associated with historically important art collections. In nonmarket terms, it is fair to say that the negatives are now part of the priceless heritage of the American people. The negatives (and images they record) will provide an enduring benefit through their role in future research and interpretation of Grand Teton National Park. These nationally important images will be appreciated and remembered as a treasure that will be enjoyed by generations to come.

The following figures (1-20) are a selected sample of the images contained in the Crandall
negative collection, which is now part of the Grand Teton National Park archive. The images speak for themselves.

**ACKNOWLEDGEMENTS**

The Crandall research was graciously supported, assisted, and reviewed by Quita and Herb Pownall (Harrison Crandall’s daughter and son-in-law—both worked in Crandall Studios). The Curator of Grand Teton National Park supported the field and archive research. Valuable assistance was provided by the staff of the AMK Ranch and the University of Wyoming—National Park Research Center. The research was conducted under Grand Teton National Park research permit GRTE-2008-SCI-0067.

![Harrison R. Crandall posing with his camera near the family homestead, now located in Grand Teton National Park (photo by Harrison R. Crandall, Grand Teton National Park archive).](image1)

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![“Teton Range” #1017 (photo by Harrison R. Crandall, Grand Teton National Park archive).](image2)

![“Mirrored Granite Peaks” #1095 (photo by Harrison R. Crandall, Grand Teton National Park archive).](image3)

![“Broken Fog” #1034 (photo by Harrison R. Crandall, Grand Teton National Park archive).](image4)
Figure 5. A pack train.  (photo by Harrison R. Crandall, Grand Teton National Park archive).

Figure 6. The set of a western-theme movie production in action  (photo by Harrison R. Crandall, Grand Teton National Park archive).

Figure 7. Canoeing on Jenny Lake  (photo by Harrison R. Crandall, Grand Teton National Park archive).

Figure 8. Among the Tetons  (photo by Harrison R. Crandall, Grand Teton National Park archive).

Figure 9. Margaret Smith (Craighead)—Harrison often asked local people to model in his staged photographs—here among the wildflowers.  (photo by Harrison R. Crandall, Grand Teton National Park archive).
Figure 10. Tossing horseshoes at camp under the Tetons (photo by Harrison R. Crandall, Grand Teton National Park archive).

Figure 11. The big fish of Jackson Lake (photo by Harrison R. Crandall, Grand Teton National Park archive).

Figure 12. Branding cows (photo by Harrison R. Crandall, Grand Teton National Park archive).

Figure 13. Cowboy at rest (photo by Harrison R. Crandall, Grand Teton National Park archive).
Figure 14. Kitty Lee and Powder River Jack (photo by Harrison R. Crandall, Grand Teton National Park archive).

Figure 15. Native Americans at Powwow (photo by Harrison R. Crandall, Grand Teton National Park archive).

Figure 16. Bow training at powwow (photo by Harrison R. Crandall, Grand Teton National Park archive).

Figure 17. Powwow pipes (photo by Harrison R. Crandall, Grand Teton National Park archive).
Figure 18. Horse portrait (photo by Harrison R. Crandall, Grand Teton National Park archive).

Figure 19. Meeting of dignitaries, including William Henry Jackson on left (photo by Harrison R. Crandall, Grand Teton National Park archive).

Figure 20. Little mountain climber (photo by Harrison R. Crandall, Grand Teton National Park archive).
Babesiosis Survey of Voles of Grand Teton National Park

**Purpose of the Study**

First described in 1885 by Viktor Babes, babesiosis was the first known arthropod vector-borne disease and the general term for the malaria-like infection due to protozoan parasites of the family Babesiidae of which there are on the order of 100 known species of worldwide distribution (CDC, Hunfeld et al. 2008). The overarching objective of this study is to examine the phylogenetic relatedness of the endemic strain(s) of Babesia microti isolated from voles (Microtus montanus, M. pennsylvanicus) in the Grand Teton National Park to previously described babesia species/strains. In the United States the rodent parasite B. microti is the etiological agent of babesiosis in areas of endemicity with the primary reservoir often described as the white-footed mouse (Peromyscus leucopus) and borne by the arthropod vector the black-legged tick (Ixodes scapularis) (Persing et al. 1992, Mitchell et al. 1996). The primary reservoir within the Grand Teton National Park region has been shown to be the meadow vole (Microtus montanus) and the montane vole (Microtus pennsylvanicus) (Watkins et al. 1991, Peck 1998). It is these reservoir host animals which the present research proposes to investigate. To this end, the research aspects specific to our IACUC proposal are to obtain blood samples for subsequent genotyping of B. microti samples for comparison to those previously isolated from wild populations of voles from the Grand Teton National Park region (Peck 1998). This research generally involves comparing DNA sequences from isolates to those of previously described strains focusing on the B-tubulin genes. This was selected to give a more particular phylogeny than was possible by previously employed methods such as immunoassay, which lacks sensitivity and suffers cross-reactivity, and 16s-ribosomal DNA of the past decade, which lacks specificity relative to the less highly-conserved B-tubulin. These samples will be genotyped by sequencing and comparison against the relatively more recent Genbank B-tubulin sequence data submissions for B. microti variants.

Whereas the precise identification of a host organism is an essential element of the taxonomic recognition of a potentially new species of parasite, exact identification and preservation of the host specimen from which a parasite specimen is collected is also important. The voucher specimens of voles thus obtained, upon return to Nebraska, will be appropriately prepared and placed in the University of Nebraska at Lincoln collection.

**Potential Value of the Study**

The value of this research in the specific elaboration of the regional distinction in B. Microti strain from voles lies primarily in the observation that the species-specificity and virulence, including human cases of the disease, appears to be highly dependent on slight variations in closely related babesia strains. Babesiosis in general is a worldwide disease of considerable economic consequence and an increasingly recognized cause of morbidity and mortality in humans. Some areas of the northeast and northern Midwest states have shown positive antibody titers to B. microti by up to 10% of the residents, apparently from sub-clinical infection (Krause et al. 2003) so the true incidence has only begun to be explored by epidemiologists. Human to human Babesiosis via blood-transfusion and maternal-fetal transmission has also been documented in a number of cases and therefore now poses an additional risk to individuals receiving blood products who by reason of other debility are...
more likely susceptible to serious infection. For these reasons, babesiosis is now recognized as an emerging zoonosis in the United States, most specifically among splenectomized or otherwise immune-suppressed persons and therefore of some public health concern as well (Saito-Ito et al. 2000, Shuster 2002) and a reportable infectious disease in some jurisdictions. The specific identification of host/parasite strain in particularly relation to increased human encroachment of natural habitat of voles and other rodents as a reservoir species will ultimately aid in assessing the breadth and likelihood of cross to other species, including humans, in endemic areas such as GTNP.

The primary objective of the present research is to specify the natural endemic strain of *B. microti* within these vole populations by the most specific current molecular genetics techniques. *B. microti* is an obligate intraerythrocytic protozoan parasite and cannot readily be cultured outside of a suitable host animal (Valois-Crus 2006, Bautista and Kreier 1979) thus necessitating larger blood-sample volumes than might be otherwise possible if small sample inocula could be cultured in-vitro. Natural infections in these populations typically manifest quite low parasitemias on the order of .1 to 2% (Watkins et al. 1991). Inasmuch as this is the study of a blood infecting organism, sufficient sample volume to provide enough *B. microti* DNA to reliably perform multiple experimental analyses would, unfortunately, render the animals unfit to return to the wild.

The current research follows and expands upon studies conducted for several years, 1987 to 1990 (Watkins et al. 1991) in Grand Teton National Park describing splenomegaly and reticulocytosis of voles and other rodents determined by microscopical detection of presumed *B. microti* piroplasms as the causative agent and Peck (1998) by analysis of ribosomal 16s-like subunit DNA sequence therefore necessitating study of the identical species to yield a meaningful comparison.

**RESEARCH DESIGN**

The essential design simply involves collection of a statistically useful number of wild voles (n=26) calculated to reasonably ensure that parasitized animals will be included in the survey. Relevant literature regarding infection prevalence in host populations is somewhat limited although typical reported infection rates range from approximately 16 to 35% (Watkins et al.), with values dependent upon location, season, predator populations, host population density and other factors.

In order to ensure sample size adequate to provide infected animals this is taken as a binomial distribution problem based on the lower reported infection incidence of 16%. As such, this means that in any sample size (n) the number of animals expected to be free of infection would be (1-.16)^n

To attain a 99% probability of the sample containing at least one infected animal:

Setting prob. of < 1 infected animal in sample = .01 so let .01 = (.84)^n where n = sample size.

So, 99% confidence level based on lower incidence estimate:

n = log (.01)/ log(.84) = -2.00/-.076 or n = 26 animals minimum sample size.

These will be assayed for infection of *B. microti* parasites by blood-smear examination and DNA amplification utilizing the Polymerase Chain Reaction technique and sequencing the parasite B-tubulin gene so that elucidation of the particular infectious strain of this organism within this previously studied vole population may be accomplished. The genomic sequence data will be analyzed to construct the phylogeny of this strain of *B. microti* as the ultimate goal of the research.

**RESULTS**

A first field collection near the Grand Teton National Park during August 2011 was limited, but successful. In 2011, unusually poor weather, with a very late spring and flooding, resulted in exceptionally poor habitat conditions that affected both small-mammal and tick populations. This limited the size and number of animals obtained, and these stressors are also presumably responsible for the observed high trap mortality. Despite these difficulties, some infected animals were collected, although not in numbers that would support robust statistical analysis. DNA from blood of these animals (containing the target babesial DNA) has been prepared, and these animals have been delivered to the Nebraska State Museum as voucher specimens for preservation and identification. The parasite genomic data are not yet available as this portion of the study is still underway.
This study was performed with the approval of the UNMC/UNO IACUC, protocol #11-048-06-EP.

The accompanying Excel spreadsheet summarizes the 2011 collection data in the format recognized by the Wyoming Game and Fish Department under state scientific collecting permit #33-816 (Table 1.)

**LITERATURE CITED**


Centers for Disease Control. Laboratory identification of parasites of public health concern; Babesiosis [http://www.dpd.cdc.gov/dpdx/HTML/Babesiosis.htm](http://www.dpd.cdc.gov/dpdx/HTML/Babesiosis.htm)


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IDENTIFYING TRIBUTARIES TO JACKSON LAKE IMPORTANT FOR SNAKE RIVER CUTTHROAT TROUT RECRUITMENT

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NEW MEXICO STATE UNIVERSITY ♦ LAS CRUCES

ABSTRACT

Across their range, native salmonid species are imperiled due to habitat loss, alteration, and competition with non-native salmonids. New challenges, such as the effects of climate change on stream flow and water temperature create new problems for these species and highlight the importance of understanding their juvenile and adult life histories. Specifically, identifying life history movement patterns as it relates to spawning sites and juvenile rearing streams. We measured strontium isotope values of 13 tributaries and mainstem waters of the lower Snake River and Jackson Lake as well as otoliths collected from resident/juvenile cutthroat trout to determine if we could find unique isotopic signatures throughout the watershed. Strontium isotope values were similar for otoliths and water samples collected at the same location. Strontium isotope yielded unique isotope values across the watershed and between tributaries and the Snake River and Jackson Lake. Only three tributaries were undifferentiated using strontium stable isotopes. These were Pilgrim, Dime, and Sheffield Creeks. Due to their close proximity geographically and their geologic similarities it is not surprising we were unable to differentiate these three tributaries from each other. Future work using trace element analysis might provide further differentiation between these three creeks. Using this new information, we can now begin to look at adult cutthroat from Jackson Lake and the Snake River and determine their natal origins and fidelity to spawning tributaries. Using this information, managers can guide conservation efforts for cutthroat trout in the Jackson Lake watershed.

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 has 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 to focus the investments of time and money that will result in the greatest impact on conservation and restoration efforts. This study proposes to use a relatively new, proven analytical tool, stable isotope analysis, that will be used 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 (Muhlfeld et al. 2005, Coghlan et al. 2007, Barnett-Johnson et al. 2008, Walther et al. 2008, Ziegler and Whittle 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 Greater Teton and Yellowstone National Parks. 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 et al. 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 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 biologist routinely use to age fish (Hubert et al. 1987; Figure 1). 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).

The geomorphology surrounding Jackson Lake reflects a high degree of heterogeneity (Figure 2). 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. Using this approach, we propose to: 1) characterize the strontium isotope signature of Jackson Lake and its tributary streams, 2) characterize the strontium isotope signature of fish living in these waters, and 3) use this information to link adult cutthroat trout in Jackson Lake back to their natal origins, investigate spawning site fidelity, and identify important tributaries of Jackson Lake important for Snake River cutthroat trout reproduction and survival.

Figure 1. Cross sections of otoliths reveal daily (A) growth bands, as seen in this hatch year fish and annual bands (B, alternating dark and light) we can use to age and extract life history movement information using strontium isotopes.

**METHODS**

**Water Sampling and Analysis**

During low flow conditions in mid to late August we sampled water from upper, middle and lower Jackson Lake. Additionally, we sampled tributaries above their confluence with Jackson Lake and when necessary above and below confluences of tributaries prior to their merging and entering Jackson
Lake. Sampling during low periods provides a strontium isotope characterization that is more reflective of the annual water chemistry that would be experienced by cutthroat trout in Jackson Lake and its tributaries during the largest period of the year (i.e. distinguished from pulsed from Spring runoff). Samples were analyzed for their strontium isotope composition at the Interdisciplinary Center for Inductively Coupled Plasma Mass Spectrometry at the University of California, Davis.

Figure 2. The geology surrounding Jackson Lake is highly variable. With Granites dominating along the western shore, volcanic in the north, and sandstones/limestones in along the eastern and southern shores. We can use this variation to differentiate trout that reside in streams within each of these geologic formations.

Fish Sampling and Otolith Analysis

Concurrent with water sampling, we collected five cutthroat trout from tributary streams of Jackson Lake using standard hook and line techniques and backpack electrofishing in cooperation with Park Service fisheries biologists and technicians during August, 2011. Our sampling efforts were guided and prioritized using a Wyoming Game and Fish Department administrative report detailing the distribution and occurrence of salmonid species in the upper Snake River basin; which includes Jackson Lake and its tributaries (Stephens 2008; Figure 3).

In cooperation with the Wyoming Game and Fish Department in Jackson, Wyoming, we also collected cutthroat trout and lake trout during annual Jackson Lake sampling work at the end of June, 2011 to obtain otoliths for isotope analysis. Lake trout were collected to characterize the isotopic signature of fish originating in Jackson Lake. Otoliths were cross-sectioned at the University of Wyoming using an Isomet® low speed bone saw. Sections were mounted on chem slides and strontium isotope analysis was performed at the Interdisciplinary Center for Inductively Coupled Plasma Mass Spectrometry at the University of California, Davis.

Figure 3. Map of Jackson Lake and associated watershed showing locations where we collected fish and water samples (red lines) and locations where only water samples were collected (yellow lines). Reprinted with permission from Wyoming Game and Fish Department (Stephens 2008).

Statistical Analysis

We used discriminant function analysis to determine how well strontium stable isotopes correctly classified trout from known collection sites.
Preliminary Results

Water samples and otoliths collected at the same location produced similar strontium isotopic signatures (Table 1). Initial discriminant function analysis was able to correctly classify 64% of fish to the correct tributary of origin (Table 2). After grouping Pilgrim, Dime, and Sheffield Creeks, the correct classification increased to 84% (Table 3).

Table 1. Strontium isotope values reveal a tight relationship between otoliths and water sampled at collections sites.

<table>
<thead>
<tr>
<th>Location</th>
<th>Otolith Sr87/Sr86</th>
<th>Otolith SE</th>
<th>Water Sr87/Sr86</th>
<th>Water SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pilgrim Creek</td>
<td>0.7102</td>
<td>0.00002</td>
<td>0.7103</td>
<td>0.000006</td>
</tr>
<tr>
<td>Arizona Creek</td>
<td>0.7099</td>
<td>0.00003</td>
<td>0.7092</td>
<td>0.000004</td>
</tr>
<tr>
<td>Lizard Creek</td>
<td>0.7102</td>
<td>0.00001</td>
<td>0.7093</td>
<td>0.000006</td>
</tr>
<tr>
<td>Dime Creek</td>
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<td>0.7103</td>
<td>0.000005</td>
</tr>
<tr>
<td>Sheffield Creek</td>
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<td>0.00005</td>
<td>0.7097</td>
<td>0.000004</td>
</tr>
<tr>
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<td>0.7120</td>
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<tr>
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<td>-</td>
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<td>Jackson Lake</td>
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<td>0.00002</td>
<td>0.7100</td>
<td>0.000005</td>
</tr>
</tbody>
</table>

Table 2. Results of discriminant function analysis reveal that Pilgrim, Dime, and Sheffield Creeks are difficult to distinguish isotopically from each other. Rows represent the correct tributary of origin. Columns represent the stream of origin:

Table 3. Results of discriminant function analysis after combining Pilgrim, Dime and Sheffield Creeks (Combined) increased correct classification of origin from 64% to 84%.

Management Implications

In the Jackson Lake watershed, the ability to identify and prioritize important streams utilized for spawning and as juvenile rearing habitat for cutthroat trout was identified as a priority research need by biologists within the Greater Teton National Park. Using strontium stable isotope analysis in the Jackson Lake watershed we were able to: 1) determine that fish isotopically resembled their stream of origin and 2) that we could uniquely identify streams and mainstem bodies of water, Snake River/Jackson Lake, from each other. Understanding which tributary streams contribute to juvenile recruitment and, if possible, whether or not this contribution is evenly distributed throughout the watershed is important for prioritizing the expenditure of time, manpower, and money to protect and conserve streams important to growth and survival of juvenile cutthroat trout. Data from this study builds the foundation that future studies can build upon so that: 1) natal origins and spawning site fidelity may be determined for adult cutthroat trout in Jackson Lake and the lower Snake River, 2) characteristics of these streams that make them ideal for juvenile recruitment can be measured and compared across the watershed, and 3) results from this and future studies can inform sound, science-based management decisions.

Table 3. Results of discriminant function analysis after combining Pilgrim, Dime and Sheffield Creeks (Combined) increased correct classification of origin from 64% to 84%.
Although a more thorough discussion of our preliminary results would at this point be premature, we expect that our analyses over the coming years will offer new insights to managers making conservation decisions for Snake River cutthroat trout.

**FUTURE DIRECTIONS**

This short study has provided the baseline data showing that we can differentiate tributaries and fish across the watershed. It is important to note that this study represents a small sample size from each location and water samples represent a snapshot of the isotopic value of the water. Future studies should build upon our results by: 1) increasing sample sizes of fish from each tributary, 2) sample adult cutthroat trout from Jackson Lake, 3) sample water at different locations from the top to the bottom of tributary streams, 4) include trace element profiles with isotope analysis to increase our ability to differentiate tributaries, and 5) investigate the use of non-invasive sampling techniques by comparing otolith and scale isotope values.

**ACKNOWLEDGEMENTS**

This project was supported by a grant from the UW-NPS Research Station. Field work was supported by Dianne Miller (WYGFD), Clark Johnson, Seth Newsome, and Hank Harlow. Technical assistance was provided by Rob Gipson and Tracy Stephens with the Wyoming Game and Fish Department and Shawn Lanning with the Wyoming GIS Center at the University of Wyoming.

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INFLUENCE OF SPRING WEATHER CONDITIONS ON BREEDING BIRD DENSITIES IN GTNP

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ABSTRACT

The thaw came very late to Jackson Hole in 2011, with snow melt-out on May 15th. This year shares with 2008 and 2010 the claim of the latest spring over recent decades. The spring snow melt-out is a function of both accumulated snowfall and spring temperatures. A second measure of the advent of spring is the accumulation of growing degree-days (GDD); GDD finally exceeded 225 (°F; 125 °C) on June 23rd, that value being a predictor of 90% leaf-out in aspens. As is usual in late years, overall species richness and total bird density were generally lower across most park habitats. In particular, the foliage insectivores of the deciduous habitats, such as warblers and vireos in willows, aspens and cottonwoods, were much reduced in density (by as much as 50%). Sagebrush habitats, where snow persists longer in late springs and where most species feed on the ground early in the breeding season, were the most impoverished. In two such monitoring sites, #4 (Jackson Lake Junction Grass-sage) and #6 (Airport Sage), there were 1/4 to 1/3 fewer species present respectively, and bird densities were reduced to 43% and 39% of long-term averages for the sites.

INTRODUCTION

The timing of spring events that signal the advent of a new breeding season and allow birds to choose and defend the locations where they will attempt to raise young is an important variable. How early the breeding season can start may determine how many breeding attempts are possible during the season, which in turn can have pivotal population effects on short-lived species with few breeding opportunities. In high-latitude and/or high-elevation locations, reasonably descriptive of Grand Teton Nation Park (GTNP), the breeding season may already be critically short, with adverse conditions in late spring and early fall constraining a short summer season. For migrant birds, the predominant species in short breeding season locations, the timing of their returns from wintering areas to summer breeding sites is an evolved, behavioral trait adapted to the average onset of conditions suitable for initiation of breeding, and the progression of the vegetation and food supplies that they imply. Thus, generally, migrant birds will not be able to make full use of early springs by beginning breeding earlier, although they may reap the advantages of elevated food levels, and possibly lay and raise larger clutches. On the other hand, both residents and migrants will be particularly disadvantaged by late springs that necessitate delayed reproduction and a shorter season. While resident populations will bear those costs, migrants may choose to seek suitable conditions elsewhere or over a wider geographical area rather than wait locally for productivity to ameliorate.

Spring conditions in GTNP are described simply by the average temperature and the total precipitation from March to May inclusive, SPRT and SPRP. Since 1950, SPRT has averaged 34 °F ± 2.5SD (see Figure 1), and ranged from a high of almost 42 °F to a low of 29.3 °F. Over the same 62 y time period, SPRP has varied much more widely, about six-fold, with a mean of 6.1” ±2.0SD, a high value of >12.0” and a low of <2.0”. Over this time interval, there has been no discernible trend in spring precipitation that is statistically robust, although there has been a tendency for spring precipitation to be
somewhat more variable over the last three-quarters of the record. Comparing years <1986 and >1985, unpaired samples t-test yields t = -1.25, p = 0.218. A series of six years of generally declining spring precipitation ended in 2008, and in 2011 the precipitation was the highest recorded during the 62 y interval.

Spring temperatures, while generally steadier than precipitation totals, do show a statistically significant trend, with higher temperatures higher in years 1986-2011 than in the earlier years 1950-1985 (unpaired samples, 2-tailed t-test, t = -5.14, p<0.001). This observation is in accord with the widely-recognized warming trend recorded over the western U.S. over the last 30+ years, over which GTNP spring temperatures have increased by some 2.8 °F (1.6 °C).

Figure 1. A sixty-two year record of spring (March-May) average temperature SPRT and total spring precipitation SPRP at Larry Robinson’s Jackson Lake Dam weather station. Summary statistics are given in the charts below, including separate summary figures for years pre- and post 1986; see text for further analysis.

Birds are likely to respond directly to environmental cues other than temperature and precipitation, particularly to cues associated with weather conditions in the recent past. Leaf-out of the deciduous trees and shrubs, such as willows, aspens and cottonwoods, will essentially reflect cumulative conditions throughout an advancing spring. Leaf-out may provide the cues for habitat selection based vegetation structure, and also signal food resource availability, since herbivorous insect activity will be tightly correlated with leaf-out dates. Another obvious environmental cue for birds seeking breeding sites is the presence or absence of snow on the ground. This variable also is a cumulative picture of past spring conditions, both temperature and precipitation, during the seasonal advance from winter toward summer. Snowpack depth will clearly affect what exposed vegetation serves as foraging sites for early spring birds, and how melting snowpack of decreasing depth would reveal bird breeding habitats, in sequence, from willows, then sagebrush, then grass- and sedge-land, in GTNP. Snow that persists late into the spring is particularly critical for ground-foraging birds, a large category that includes both passerines such as sparrows, larks, blackbirds and corvids, as well as non-passerines such as cranes, geese, plovers and sandpipers. I refer to two variables that indicate the earliness or lateness of spring in GTNP: First, the snow meltout date (SMOD), measured below Jackson Lake Dam at the Moran 5 WNW weather station, is the Julian date at which the snowpack has dwindled to zero; it averages APR 19. Second, the leaf-out date, measured by the Julian date by which growing degree-days (GDD) has reached a value of 125 (°C) or 225 (°F), averages JUN 8 at Moran 5 WNW. GDD 125 is established in the literature as the degrees >5 °C (accumulated over days) that predicts 90% leaf-out in aspens Populus tremuloides.

Both variables, SMOD and GDD125, include aspects of spring temperature and spring precipitation, but different aspects, since they are but weakly correlated (r = -0.36, R² = 13%; see Figure 2).

Figure 2. Variation in two relatively independent indicators of the arrival of spring in GTNP. a) Julian date of GDD125 (ordinate: the number of growing degree-days [125] required for 90% leaf-out in aspens), and b) SMOD (abscissa: Julian date by which the winter snowpack dwindles to zero near Jackson Lake Dam). Only one-eighth of the variation in one of these variables is accounted for by variation in the other. SMOD is related more to spring precipitation that temperature, whereas the reverse is true for GDD125.
SMOD is inversely correlated to SPRT (r = -0.43), and more strongly related to SPRP (r = 0.59). GDD125, as one might expect, is closely related to spring temperatures (r = -0.729), but also it increases (i.e. delayed leaf-out) with increased precipitation (r = 0.395). Thus, there are two sorts of late springs, one driven largely by high precipitation (SMOD) and another related to slow spring warming rates (GDD125). Note that, over the years, there is a 40 d variation between the earliest and latest aspen leaf-out dates, and a similar interval between the earliest and latest snow melt-out dates. Note also that the three very late springs (upper right in Figure 2) fall in the last four years.

Methods, Study Sites, Concepts

For the purposes of this report, I use long-term breeding bird census data from four of the ca. 30 sites in GTNP for which such data exist. The rationale for this particular selection is that these four sites are within 1 km of the weather station site near Jackson Lake Dam, secondly that the four sites are within 0.5 km of each other, and thirdly that they represent quite different habitat types, all of which are important to the vegetational diversity of GTNP. The sites are, respectively, Site #2: Jackson Lake Junction (JLJ) Grass-sedge-field; Site #4: JLJ Grass-Sage; Site #10: JLJ Wet Willows, and Site #11: Oxbow Aspen-Willow. They have been censused in 18, 21, 20, and 19, respectively, of the 21 years since 1991. The census data record which species are using the site in a specific year, and how many pairs are breeding within the site. The census protocols were established at the time of initial selection of the sites, early 1990s, and have been followed since that time; previous reports to the Research Center will specify those details.

Table 1 lists 20 common bird species that breed in the selected four study sites, about half of them breeding in more than one site of the sites. The database on breeding densities over the years will be used to test hypotheses about which species and which habitats might show responses, via shifts in breeding densities, to variation in spring’s advent as measured by SMOD and GDD125 dates.

Of course, bird breeding densities are likely influenced by a plethora of factors beyond whether spring arrives early or late. Some of these, amongst many others, are last season’s reproductive output, overwintering success, the state of the vegetation and the food resources it produces, the level or proximity of predation threats, pressures from competitors, and disturbances both natural and unnatural. Therefore, any effects from the timing of spring are likely to be masked, to a greater or lesser extent, by other processes and pressures in the breeder’s environment. This means that relationships, if they exist, are expected to be loose or imprecise, and discernible if at all by primitive statistical standards. Some possibilities are illustrated in Figure 3, where ordinates correspond to breeding density of a species, and abscissas are measures of spring timing; SMOD or GDD125. In Figure 3, parts A and B depict generally positive and negative relationships (densities increasing and decreasing, respectively, with the lateness of the spring season. In parts C and F, high densities occur only with late seasons, with early seasons precluding the lowest densities (C) or the highest densities (F). In parts D and E, high densities are recorded in years with early spring seasons, and late seasons preclude (D) or allow (E) some high density counts.

![Fig. 3. Possible patterns of breeding density (ordinate) as a function of the advent of spring events (abscissa), early on the left to late on the right. See text for discussion.](image-url)
**RESULTS**

**Species Unaffected by Spring Timing**

There are a number of species in Table 1 that are evidently not influenced by the timing of spring. Not included in Figure 3 is the null option, in which there is no support for the hypothesis that the timing of spring affects breeding densities. The reality of this option is reinforced by species that occur in two different habitats, in neither of which is there any clear pattern in density and spring timing. Calliope Hummingbird _Stellula calliope_, Willow Flycatcher _Empidonax traillii_, Wilson’s Warbler _Wilsonia pusilla_, and Song Sparrow _Melospiza melodia_ all breed in both sites 10 and 11, and are examples of the null option. In addition, Vesper Sparrow _Pooecetes gramineus_ of Site 4, and Black-headed Grosbeak _Pheucticus melanocephalus_, House Wren _Troglodytes aedon_, Black-capped Chickadee _Poecile atricapillus_, and MacGillivray’s Warbler _Oporornis tolmiei_ of site 11 also vary year-to-year in breeding densities, but they do so without relation to spring timing. The only common species of Site 2, the grass-sedge field, is Savannah Sparrow _Passerculus sandwichensis_, and while it varies in breeding density >3-fold among years (0.65-2.20 pr/ha), this variation is not related to the timing of spring. Willow Flycatcher densities in sites 10 and 11 are plotted against SMOD and GDD in Figure 4.

Willow Flycatcher, like its congener Dusky Flycatcher, is a long-distance migrant, as are the two warblers, the hummingbird, and grosbeak, while the sparrows (Song, Vesper, Savannah) are shorter distance migrants, the first mentioned even wintering locally; the chickadee is a year-round resident.

**Species with Density Responses to a Single Spring Timing Measure**

Two of the species tested (Table 1) respond to a single measure of spring timing, GDD125, and not at all to the second measure (SMOD). These are Common Yellowthroat _Geothlypis trichas_ and Wilson’s Snipe _Gallinago delicata_, both species of wetlands. These wetlands remain wet even in dry years, and this may account for an independence from SMOD, which is largely determined by spring precipitation. Wilson’s Snipe, in both sites 10 and 11, display higher breeding densities in late years than in early years (Figure 5); the pattern is similar for Common Yellowthroat. Here breeding density has been standardized for each census site, since snipe densities average 4X higher at Site 10 than at Site 11 (nine times higher for the yellowthroat). Why these two species, sharing little except a preference for wetlands as a breeding habitat, should both respond positively to late years invites speculation. Both are migrants, with the snipe wintering in the southern United States into Mexico, the yellowthroat from Mexico south into Central America. One possibility, quite without any solid foundation, is that migrants returning north are “siphoned off” into productive habitats as they are encountered. As GTNP is fairly close to the southern end of the breeding range in the central U.S., perhaps the option of moving further north in late springs is less attractive, with the result that birds are retained in the southern parts of the range to a greater extent than in early spring years. The assumption that a late GTNP spring corresponds to a late spring in e.g. the Yukon remains to be tested.

One other species has a distinct density response to one measure of spring timing, SMOD, but not to the other—GDD125. Brewer’s Sparrow _Spizella breweri_ is often the commonest breeding bird in the grass-sage of Site 4, but in years with late snow melt-out the species can be entirely absent. Zero density counts have been recorded at Site 4 for Brewer’s Sparrow five times since 1991. The plot of density vs. SMOD is highly significant for this species, as shown in Figure 6. Note that, in locations where SMO dates are earlier, as in the southern end of Jackson Hole (e.g. near the Moose weather station; over a week earlier), Brewer’s Sparrow densities (e.g.
at Site 6, Airport Sage) are not nearly as sensitive to SMOD as they are at Site 4, at the northern end of the Hole. On the Antelope Flats road east of Blacktail Butte, Site 5 census data reveal that dependence on SMOD there is intermediate between Moran and the Airport.

Figure 5. Standardized breeding densities of Wilson’s Snipe in sites 10 and 11, as a function of GGD125. Snipe are present at significantly higher densities in late springs.

Figure 6. Brewer’s Sparrow breeding densities in Site 4 show a strong dependence on snow melt-out dates (SMOD); the species is rare or absent in late years.

Species with Density Responses to Spring Timing in One Habitat but Not Another.

Several species in Table 1 show a density response to the timing of spring events in one GTNP habitat, but not in another. Examples are three species that breed in Site 11, Aspen-Willows, where their densities are independent of measures of spring timing, and breed also in Site 10, the Wet Willows, where they all have been recorded at lower densities in late springs, whether measured by SMOD or GDD125, and in greater numbers in earlier springs. These are Lincoln’s Sparrow *Melospiza lincolnii*, Fox Sparrow *Passerella iliaca*, and White-crowned Sparrow, *Zonotrichia leucophrys*. All three species forage on the ground, a behavior not feasible before snow melt-out (average Moran date APR 19), and presumably more productive in years of higher spring temperatures that accelerate insect productivity at ground level (lower GDD125; average Moran date JUN 8). Again speculatively, it would seem that habitats with taller vegetation (i.e. aspens at Site 11) would become occupiable by these sparrows earlier in the year than lower willows-dominated habitats. In mid-winter, only the bare tops of a few of the taller willows reach above the level snowpack in Site 10, whereas in Site 11 the snow depths are much more variable, and the trees provide various opportunities for snow-free or at least snow-shallow areas, which melt out sooner and permit sparrow foraging earlier. Such a difference might explain why the several sparrow species are adversely affected by late springs in the willows but not in the aspens.

Song Sparrow is a breeding species in both of these habitats (Sites 10, 11), but its densities are not responsive to the timing of spring (see above). In GTNP, Song Sparrows are found almost exclusively along water courses, especially the shallow drainage channels that run through both Sites 10 and 11. These habitat features are apparently hospitable to the sparrows even where the surrounding snowpack remains or vegetative regrowth is delayed by low temperatures.

One other emberizine, Savannah Sparrow, shows early spring effects (enhanced densities) in one habitat but not another. In Site 2 no such effects have been detected, but in Site 4, a sagebrush-grassland mix that is much drier than Site 2, Savannah Sparrows are common in years of early springs, but in late springs, when the grass component they preferentially select has barely begun to grow by mid-summer (e.g. in 2011; Cody 2013), Savannah Sparrows are scarce or absent. Figure 7 illustrates decreasing breeding densities with later spring timing in Savannah and Fox Sparrows, at Sites 4 and 10 respectively. These plots are typical of those of the other species mentioned in this section. In Fox Sparrow, White-crowned and Lincoln’s Sparrows, SMOD may be substituted for GDD with the same result (negative slope), but not so in Savannah Sparrow. Another species of Site 11, American
Robin *Turdus migratorius*, also a ground foraging species, responds similarly to both measures of spring timing, SMOD and GDD125. In years with SMOD <105 (Julian Date; n = 7), robin densities at the site average 0.45 ± 0.081 pr/ha, whereas in the 7 years with the latest SMOD values the robins reached an average density of just 0.299 ± 0.189 pr/ha (t = 1.99; df = 12, p = .069). In 2011, with the latest SMOD in the last 25 y, no robins bred at Site 11; clearly, robins do better when spring arrives early.

Species with Non-linear Density Responses: Higher Numbers in Average Years.

The last pattern to be mentioned here is of species that exhibit their highest densities in average years. This is characteristic of species that a) are long-distance migrants, such as Yellow Warbler *Dendroica petechia* and Warbling Vireo *Vireo gilvus*, and b) are foliage insectivores and thus dependent on foliar insects, the availability of which is in turn regulated by the leaf-out dates of the deciduous habitats in which these birds are predominant: willows, aspens, and cottonwoods. The optimal strategy for migrant birds with a strong dependence on foliage insects is to time their return to breeding habitats coincident with the average leaf-out date of the vegetation, and a broad literature attests to this. The subject was discussed by Cody (2011), and thus will not be developed here.

**CONCLUSION**

While the density responses of bird species to the timing of spring are varied, over species, habitats, and foraging behaviors, the dominant pattern among the GTNP breeding birds is decreased densities in years of later springs. Thus, it would seem that the warming trend predicted to continue for many decades over western North America, and evidenced in GTNP by elevated spring temperatures, will, at least initially, be beneficial to many of the Park’s birds.

**LITERATURE CITED**


INVESTIGATING LIFE HISTORY TRADEOFFS IN AN OPPORTUNISTIC BREEDING SONGBIRD, THE RED CROSSBILL (*Loxia curvirostra*) IN GRAND TETON NATIONAL PARK

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**ABSTRACT**

Because available energy is finite, organisms must be selective with how and when energetic resources are allocated to demanding physiological processes such as reproduction or self-maintenance like immune function. Historically, research to understand how organisms orchestrate their annual cycles with respect to these costly and conflicting 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 seasonal and interannual variation in environmental conditions (temperature, precipitation, food supply) and investment patterns in survival and reproduction in a reproductively flexible songbird, the red crossbill (*Loxia curvirostra*), which can reproduce opportunistically in both summer and winter in Grand Teton National Park. In addition, crossbills provide a perfect model to investigate these environmental and physiological interactions. Preliminary results from this study have indicated that food availability may play an important role in determining how much crossbills will invest in survival (specifically immune function) and reproduction; e.g., crossbills will invest more in innate immunity and reproduction when food availability is high. 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**

Understanding how organisms allocate limited resources between survival and reproduction is one of the most fundamental problems in biology (e.g., Zera and Harshman 2001; Martin et al. 2008). Nearly all environments on earth are dynamic, thus organisms must adjust physiology, morphology and behavior to adaptively allocate resources as selective pressures shift (Sinclair and Lochmiller 1999; Nelson and Demas 1996). Seasonally breeding taxa provide insight into ways that multiple demanding processes can be maintained in the annual cycle (Zera and Harshman 2001). Generally, these species 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; Lochmiller and Deerenberg 2000). However, such taxa provide limited opportunities to reveal how physiological costs of different organismal processes may interact with environmental conditions to influence the evolution of investment strategies, mainly because certain combinations of conditions and organismal activities never occur in these species (e.g., breeding in winter). Consequently, our knowledge of how harsh environmental conditions and reproductive effort may interact to shape investment in survival remains limited. Thorough evaluation of this interaction would benefit from a study system where investment in reproduction and survival is facultative across extremely divergent environmental conditions, allowing for a more direct assessment of how demands imposed by physiological processes and environmental fluctuations influence the evolution of life history-related investments. Additionally, more long-term field studies of free-living organisms are essential as they provide a more ecologically relevant context than the more common captive studies and may illuminate novel, transformative environmental or physiological variables that should be considered when designing future studies focusing on these tradeoffs.

Red crossbills (*Loxia curvirostra*, Figure 1) are temperate zone songbirds that display exceptional temporal flexibility of breeding, despite highly seasonal changes in weather (Adkisson 1996), and can be found in Grand Teton National Park every year (Kelsey 2009). In years of high food availability (i.e., conifer seed availability) these birds can breed on the shortest days of the year when conditions are extremely thermally challenging, and on the longest days of the year when thermal conditions are benign (Benkman 1987; Hahn 1998). In contrast, they may not breed at all in either season if food availability is low. Investment in reproduction is therefore facultative and is more closely related to annual changes in food availability (i.e., conifer seed abundance) than seasonal changes in thermoregulatory challenges (Benkman 1987, 1990; Hahn 1998). Energy costs and selective pressures, however, are sure to differ across seasons, making crossbills ideal for exploring how changing environmental conditions (i.e., temperature and food resources) and physiological costs (i.e., breeding, immune function, etc.) influence the balance of investment in reproduction versus survival.

**ENVIRONMENTAL CONDITIONS**

Large seasonal fluctuations in day-length, temperature and precipitation characterize the north-temperate zone and contribute to low food availability during the short, cold days of winter. Energy demands of thermoregulation are higher in the winter and may prohibit investment in reproduction in many species (Nelson and Demas 1996). Crossbills, however, specialize on conifer seeds which typically increase in availability throughout summer as new cones develop, peak in early autumn as cones mature, and then decline throughout the winter and spring as seeds fall from the cones and are consumed by seed predators (Adkisson 1996). The quantity of new cones produced is highly variable across years (Fowells 1965). Crossbills, therefore, depend on a food supply that is variable and often uncoupled from seasonal changes in temperature or precipitation (Benkman 1987; Hahn 1998).

**Reproduction**

Reproduction is very energetically costly in birds and mammals but is essential to fitness (Nelson and Demas 1996; Speakman 2008). 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).

**Survival-enhancing processes**

Many processes contribute to survival in animals. Some of these, however, are particularly sensitive to resource allocation adjustments. These include:

**Immune Function:** The immune system can be categorized along an innate (nonspecific)-acquired (specific) axis and a constitutive (noninduced)-induced axis (Schmid-Hempel and Ebert 2003). An organism’s optimal immune defense strategies can vary among or within these axes depending on the current health of the individual and the current environmental conditions (Schmid-Hempel and Ebert 2003; Martin et al. 2008). For example, stress caused by inclement weather and low food availability during winter can be immunosuppressive, so animals may counteract these effects by investing more heavily in immunity and
foregoing reproduction (Sinclair and Lochmiller 2000; Nelson and Demas 1996). Preliminary data on red crossbills indicate a trade-off between one aspect of innate immune function and reproduction in the summer during low cone years but not in high cone years. Thus, an interactive effect between reproduction and resource availability may be present even outside of thermally challenging conditions (Schultz unpublished data).

**Plumage Molt:** Animals must also allocate energy to the maintenance of the integument (e.g., plumage, pelage), which is critical for thermoregulation and predator avoidance. (Ling 1970). Approximately 30% of the entire body protein content is replaced in birds during molt.

Molecular and energy resources are in high demand and generally constrain molt to occur post reproduction and prior to the onset of migration or low winter temperatures (King 1978). Growth rates, however, can be adjusted if breeding occurs later in the summer or during times of food stress (Dawson 2004). Such adjustments may allow investment in other processes but may also affect survival if feather quality is diminished, particularly in non-migrant, north-temperate species that face harsh winters (Hinsley et al. 2003). These types of trade-offs are evident in crossbills. Preliminary data show that crossbills investing heavily in body molt have lower innate immunity than crossbills not in body molt (Schultz unpublished data).

**RESEARCH APPROACH**

The Hahn lab has studied how cardueline finches orchestrate their annual schedules of various demanding and potentially conflicting processes to contribute to survival and/or reproductive success for over twenty years. To contribute to this ongoing long-term study of the annual schedules of cardueline finches, this project includes direct assessment of patterns of investment in immune function in red crossbills. How crossbills regulate investment in a survival-enhancing process like immune function when breeding, not breeding, and while molting under diverse environmental conditions is not currently known. To evaluate these hypotheses we are employing multiple field and lab techniques including: 1) longitudinal field survey of crossbills during two environmental extremes in winter and summer, 2) reproductive physiology measured by a) size of cloacal protuberances and brood patches in males and females, respectively, b) a lavage of the cloacal protuberance to collect semen and measure presence of spermatozoa, and c) utilizing hormone profiles (androgens and estradiol) extracted via a competitive binding radio-immuno assay (RIA) from blood samples, 3) two immune function assays to measure immunocompetence and to assess parasite load, and 4) investment in plumage molt measured by examining the presence of growing primary, secondary, and body feathers. This research addresses two hypotheses (described in detail below) including the environmental constraint and physiological constraint hypothesis- all of which aim to answer how both external environmental (Objective 1) and internal physiological states (Objective 2) affect the timing and nature of investment in reproduction and survival.

**Hypotheses tested:**

**Environmental Constraint Hypothesis:** Temporal and spatial variation in availability of resources and in environmental challenges are the primary determinants of the survival/reproductive investment balance.

**Physiological Constraint Hypothesis:** Limits to physiological capacity are the primary determinant of the survival/reproductive investment balance.

**STUDY AREA**

In Grand Teton, crossbills can be located throughout the park, but tend to be concentrated in areas of specific conifer densities (Kelsey 2008). The park’s dominant conifers are lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), blue spruce (*Picea pungens*), and subalpine fir (*Abies lasiocarpa*). Specifically, we catch crossbills in areas that vary in the relative dominance of the conifers that are important food sources for types 2-5 of red crossbills: lodgepole pine, Douglas-fir, and Engelmann and blue spruce. Data were collected in 2010 and 2011 in the areas of Jenny Lake, Death Canyon, Signal Mountain, String Lake, and at the UW-NPS AMK Ranch.

**METHODS**

The respective permitting authority has approved project methods. Animal capture and manipulation protocols have been approved by the University of California, Davis Institutional Animal Care and Use Committee (IACUC) and is conducted
Objective 1: How do external environmental conditions constrain the timing and nature of investment in reproduction or survival? To assess the effect of local environmental conditions on physiological investment patterns in the crossbill, we are measuring three key environmental variables: 1) average daily temperature, 2) precipitation levels, and 3) food availability during two environmental extremes where crossbills are likely to reproduce: winter and summer.

Capture Methods: We attract crossbills using live caged decoys. Decoys call loudly when they hear birds of their own type (Groth 1993), and birds are caught in mist nets when they approach the decoys (See Figure 2). We also supplement vocalizations from the decoy with playbacks of crossbill vocalizations. From each bird captured, we collect approximately 200 μL of blood into a pre-sterilized, heparinized capillary tubes and centrifuge the blood and freeze plasma at -20°C until hormone and immune assays.

Local Weather Conditions: Average daily temperatures and precipitation for the Grand Teton area are gathered from the NOAA High Plains and Western Regional Climate Centers. The NOAA/NWS Cooperative Observer 15-minute Precipitation Network is an example of a NOAA climate center that provides us with local weather information. The NOAA/NWS routinely collects 15-minute observations of precipitation from Fisher-Porter and Universal rain gages operated by cooperative observers located throughout the US (53 in Wyoming). These data are archived at NOAA/National Climatic Data Center (NCDC).

Cone Crop (food availability assessment)

Cone crop size is scored for all conifer species at each location and trap site (at 12 different long-term point-count sites established in 2006 by T. R. Kelsey and maintained annually since then) on a cone abundance index of 0 to 5 as used by the U.S. Forest Service. We score the cone crop on 10 trees of each species within each of four directional quadrants (NE, SE, SW, NW) from every place of capture.

Investment in Survival:

1. Immune Function: For this field study, we are measuring innate immune defense and constitutive adaptive defense using two different assays that probe different aspects of the immune system.
2. Plumage Molt: Pre-basic molt occurs seasonally in red crossbills (e.g., June through November) and may be arrested during summer breeding (Adkisson 1996). Molt of the nine primary flight feathers proceeds sequentially from wrist to wingtip. Molt progress will be scored as the nearest tenth of the most distally growing feather on a scale from 0.0 (not yet begun) to 9.0 (last primary fresh and finished growing) (Hahn 1995). We define active molt as having at least one feather growing (feather dropped,
Assessing Reproductive Investment:

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). 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 scores a 2; a bare, vascularized breast with full edema scores a 3; and a bare and wrinkly breast scored a 4 (i.e., post-full edema) (Cornelius 2009).

Assessing Physical Condition:

We calculate body condition by regressing body mass against physical size. Physical size is determined by measuring individuals for wing and tarsus length, keel, bill length, bill depth, and bill width using digital calipers and compiled by a principle component analysis (PCA). A positive residual between body condition and physical size is assumed to indicate higher body condition than negative residuals (Nolan and Ketterson 1983). Additionally we take measures of hematocrit from the blood, which can be interpreted as a measure of physiological condition and performance (Mills et al. 2008).

Objective 2: How does internal physiological state constrain the timing and nature of investment in reproduction or survival?

To measure the effect of an individual’s internal physiological conditions on its investment in either reproduction or survival (these methods described in detail above), we use parasite load, body condition, and innate immune function.

Assessing Parasite Load: We use approximately 5 μL of blood to make one blood smear per individual, which is stained (Wright-Giemsa) for later inspection for blood parasites such as Haemoproteus, Microfilaria, and Leukocytozoan. Recent data have indicated that Haemoproteus is the most prevalent blood parasite and has wide variation in infection rate among individual red crossbills caught in Grand Teton National Park (Figure 5).


Figure 5. Haemoproteus prevalence across individuals in summer 2010.

Figure 6. Immune Parameters from high (2011) and low (2010) cone years. Analyses corrected for Julian date and sex.
In summer of 2010 and summer and fall of 2011, Schultz (co-PI) ran a hemolysis-hemagglutination assay on the blood plasma of 32 and 68 red crossbills, respectively. 2010 was an extremely low cone year (cone crop score 0-1), while 2011 was a very high cone year (cone crop score 4-5). 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 (Matson et al. 2005). When comparing a low to high cone year, in a low cone year (N=32), the average lysis score (complement level) of crossbill plasma was significantly lower (p=0.03) than in a high cone year (N=68), which could indicate that crossbills are able to maintain higher innate immunity in years with large cone crops (Figure 6). Agglutination levels were significantly lower in 2011 (p=0.001), which given that natural antibodies (agglutination score) serve as recognition molecules that initiate the complement enzyme cascade by agglutinating foreign cells, which ends in cell lysis, higher agglutination levels in 2010 do not equate to higher immunity (Matson et al. 2005). Crossbills caught in 2010 had significantly higher white blood cell/ red blood cell ratios (p=0.02). Elevated white blood cell/ red blood cell ratios can indicate an inflammatory response (Campbell 2007), which taken together with the lysis and agglutination scores can indicate that crossbills had lower innate immunity in 2010. Lastly, parasite loads (levels of Haemoproteus) were not significantly different between years (p>0.5), indicating that birds were similarly infected with these blood parasites regardless of year and immune status.

When comparing male reproductive potential and their average lysis score, males with high reproductive potential (large cloacal protuberances, see methods above) experienced a significant (p=0.04) tradeoff with innate immunity (lysis score) only in low cone years, suggesting that it may be more costly to breed in years with low cone availability for males (Figure 7). While female red crossbills are incubating eggs and nestlings, males feed not only themselves but also their incubating female (Adkisson 1996). Thus, having to spend significant more time foraging for food could increase the energetic demand placed on males during reproduction, which could potentially explain why this tradeoff is more pronounced in males than in females.

![Figure 7](image_url)

**Figure 7.** Average lysis score increases with male reproductive potential in 2011 and decreases in 2010 (p=0.04). No significant difference in females (p=0.469). Agglutination, WBC/RBC, and Parasite Load did not vary significantly (p>0.1) with reproductive condition in either year in males & females.

**+ CONCLUSIONS**

The data presented above best support the **environmental constraint hypothesis**, which states that temporal and spatial variation in availability of resources and in environmental challenges are the primary determinants of the survival/reproductive investment balance. 2011 had higher food availability (higher cone crop score) than 2010, and crossbills caught during 2011 had overall higher innate immunity than those caught in 2010, suggesting that when resources are plentiful, crossbills are able to allocate more energy to survival (immune function), even while in reproductive condition.

**How red crossbill physiological investment in plumage molt affects investment in innate immunity in a high cone year (2011).** As mentioned above, plumage molt is an energetically expensive time for birds, particularly body molt. No significant differences in immune function were found among birds molting their primary or secondary feathers (p > 0.5), but significant differences were found among birds molting their body feathers (p=0.05, n=17) than those not molting their body feathers (N=50) in 2011 (Figure 8). Specifically, crossbills in body molt had significantly lower lysis scores than those not in body molt, indicating a potential trade-off between two survival-enhancing processes.

The data presented above best support the **physiological constraint hypothesis**, which states that limits to physiological capacity are the primary determinant of the survival/reproductive investment balance. Even during a year of high food availability (2011), crossbills molting their body feathers invested...
less in innate immunity (lower lysis score) than those not molting their body feathers, suggesting that how much a crossbill invests in immunity (survival) is limited by this physiological process.

**Broader Impacts**

The timing and investment in various life history stages have been more extensively investigated in seasonally breeding organisms, with most of these studies focusing on captively breeding animals (Martin et al. 2008; Nelson and Demas 1996; Lee 2006). Historical emphasis on captive, seasonal breeders may have led to misconceptions regarding whether trade-offs alone can explain fluctuations in physiological processes such as immune function in natural systems (Martin et al. 2008). Thus, we are limited in our ability to answer questions that involve how demanding environmental conditions may affect investment decisions specifically in regards to reproduction because seasonally breeding animals typically breed only when environmental conditions are benign. By studying organisms that are able to reproduce in harsh environmental conditions such as opportunistic breeders, we will gain more insight into potentially alternative physiological mechanisms that regulate the timing and investment in survival and reproduction. Finally, understanding how species effectively allocate resources to competing physiological processes is becoming increasingly important in light of recent anthropogenic changes. Anthropogenic effects such as habitat and climate modification can either accelerate the rate at which life history strategies evolve or hasten the extinction of species that are not able to quickly adapt (Wuethrich 2000; Hughes 2000).

**Acknowledgements**

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**ABSTRACT**

During the summer 2011 field season, the University of Wyoming American Studies Program conducted a field school at the AMK Ranch to develop a *Preservation Treatment Guide* for the property's historic buildings. Students and faculty documented and assessed the condition of each building on the property, researched and analyzed a range of historic preservation treatments, tested log cleaning techniques, and compiled the results of their field work, research and analysis into a 150-page document designed to guide National Park Service and University of Wyoming property managers in making decisions regarding historic buildings.

**BACKGROUND**

The AMK Ranch is listed on the National Register of Historic Places for its significance in the settlement of the Jackson Hole valley from 1890 to the modern era. The property is also significant for its well preserved buildings constructed in the Rocky Mountain Rustic style. The buildings retain integrity of materials, workmanship and design, and along with the landscape that surrounds them they convey the feeling and association of an early 20th century vacation property in Grand Teton National Park.

Because of their historic and architectural significance, the buildings and structures at the AMK Ranch, as well as the property as a whole, warrant special consideration in order to preserve their character-defining features. Because the AMK Ranch is a federal property that is listed on the National Register of Historic Places, any proposed work on the buildings must be reviewed by the Wyoming State Historic Preservation Office (WYSHPO) for compliance with the *Secretary of the Interior's Standards and Guidelines for Treatment of Historic Properties*. Property managers at this and other historic properties in the park need clarification on how to apply the standards to specific building conservation issues.

The *Preservation Treatment Guide* was developed by students and faculty in a 3-credit, upper-level undergraduate course entitled “Field Studies in Historic Preservation.”

The course was taught by University of Wyoming Research Scientist Mary Humstone, with assistance from building conservation specialist Harrison Goodall of Langley, Washington, and Grand Teton National Park Cultural Resource Specialist Katherine Longfield. Four University of Wyoming students enrolled in the course and contributed to the research and writing of the report (Figure 1).

![Figure 1. Project team, consisting of students, instructors and National Park Service staff, at a site visit to the Lucas-Fabian cabin in Grand Teton National Park (Mary Humstone, 2011)](image-url)
**Methodology**

The four students enrolled in the course conducted several days of research on historic preservation and building conservation methods before traveling to Grand Teton National Park. The research team stayed at the UW-NPS Research Center (AMK Ranch) for nine days, most of which were spent on site.

Under the guidance of Harrison Goodall, the team completed *Building Condition Assessment Forms* for each of the 16 historic buildings and two historic structures on the property. The forms are designed to record the important character-defining features of each building as well as overall condition, and the condition of the roof, exterior walls and finish, foundation, windows and doors, porches and steps, site drainage and grade, and surrounding vegetation.

While most of the building assessments were based on visual inspection, the team also conducted moisture-level testing in crawl spaces below buildings, checked logs for interior rot, and checked for lead paint on surfaces such as window sills (Figure 2). The team took documentary photographs of each building and structure noting both character-defining features and areas of deterioration.

![Figure 2. Student Cassie Loveland emerges after conducting moisture-level tests underneath the Berol Lodge at AMK Ranch. (Mary Humstone, 2011).](image)

Following the initial assessment, the team interviewed Research Center director Hank Harlow and caretaker Rich Viola to learn about past and current maintenance procedures and building conservation challenges (Figure 3). The team identified several problems that were common to most of the buildings on the AMK Ranch, including improper roof flashing, improper site drainage, vegetation adjacent to buildings, varmints (bats and ants) and areas of wood rot.

![Figure 3. Students meet with Rich Viola, caretaker at AMK Ranch, to discuss maintenance and conservation issues. (Mary Humstone, 2011)](image)

Once the problems were identified, the focus turned to solutions. The team spent a full day visiting other historic properties in the park to learn how other historic log buildings were being maintained and repaired. Their field visits included meeting with staff and touring the Western Center for Historic Preservation at the White Grass Ranch.

Although on-site time was limited, the team was able to conduct testing to determine the best procedures for cleaning logs. They also conducted training for on-site personnel in replacing daubing in log buildings.

Drawing from the expertise of Harrison Goodall, coupled with evidence from buildings at the AMK and other historic properties in the park and research on current rehabilitation practices and products, the team developed treatment procedures to address the major problems encountered in conserving historic buildings at the AMK Ranch.

**Case Study: Logs**

One area of particular concern to Research Center director Hank Harlow and caretaker Rich Viola was the black fungus that was growing on the building logs. The research team determined that, due to the application of a preservative made up of linseed oil, turpentine, and paraffin every few years, the log buildings at the AMK Ranch were generally...
in good condition, especially compared with other log buildings in the park that have been painted, whitewashed, treated with other finishes or left untreated. However, while the linseed oil protects the logs, it acts as a food source for fungal growth which in turn causes the logs to darken (Figure 4). Additionally, linseed oil breaks down in ultraviolet (UV) light and flakes off, leaving logs unprotected. Because of these negative factors, it was determined this treatment should be discontinued, and replaced with application of borate (a natural log preservative, fungicide, and insecticide) and a UV-blocking preservative.

![Figure 4. Black fungus growth on logs as a result of treatment with linseed oil. (Mary Humstone, 2011)](image)

Unfortunately, the layers of linseed oil must be removed for the necessary treatments of borate and UV blocker to be effective. The team conducted a series of log-cleaning tests, using different products and different methods of abrasion (Figures 5 and 6). Care was taken to choose cleaning solutions that are non-toxic, such as vinegar, baking soda and biodegradable detergents.

**CASE STUDY: BATS**

Bats are a perennial problem at the AMK Ranch, especially the Berol Lodge, where they can be found in any dark, warm corner of the building, including along the ridgepole and purlins in the living room and the curtains in the hallway. Pests, including marmots, pine martens, ants and birds as well as bats, can cause serious damage to buildings from digging, nesting, urinating and otherwise inhabiting the buildings, both inside and outside. Bat guano can cause damage to any fibrous material, such as wood, carpet, furniture, and curtains. Bat guano and urine can cause health issues such as histoplasmosis, a lung disease, and bats have also been known to carry rabies.

![Figure 5. Team members prepare a log wall for testing to compare the effects of different log cleaning techniques. (Mary Humstone, 2011)](image)

![Figure 6. UW student Andrea Lewis cleans logs with abrasive brush after applying a cleaning solution. (Mary Humstone, 2011)](image)

Because the AMK Ranch is within Grand Teton National Park, park-approved procedures for pest removal must be followed. Pests must be trapped and removed without harming them. Bats and other creatures should be removed when they are least likely to be impacted, which generally means avoiding mating and nesting seasons and waiting for offspring to mature.

Careful inspection of the Berol Lodge revealed the places where bats were entering and exiting the building. The team noted that the existing bat netting around the chimney had been improperly installed and therefore was ineffective. The team studied what methods of bat exclusion had been tried in the past and failed, and researched and analyzed alternative methods for excluding bats in order to come up with a recommended procedure for the AMK Ranch (Figure 7).
RESULTS

The product of this research project is a Preservation Treatment Guide for AMK Ranch that includes photographs and building condition assessments for 16 buildings and 2 structures, procedures for remedying the major conservation problems, and a maintenance checklist. The guide will be used by University of Wyoming and National Park Service personnel, not only at AMK Ranch but at other locations in the park (Figure 8).

Figure 8. Cover of Preservation Treatment Guide (2011).

The Preservation Treatment Guide for the AMK Ranch provides building-by-building information as well as general treatment procedures for the most common historic preservation problems. The Introduction provides background information about the history and significance of AMK Ranch, and defines the general protocols for work on a National Register-listed property. This section includes The Secretary of the Interior’s Standards for the Treatment of Historic Properties, customized for the AMK Ranch, and guidelines for proper documentation of preservation work (Figure 9).

Figure 9. Documentation of log daubing at the AMK Ranch boat house. (Mary Humstone, 2011)

Chapter 2, Historic Buildings at the AMK Ranch, contains an illustrated list of the character-defining features of each of the eighteen historic buildings and structures in the AMK Ranch Historic District, and an analysis of maintenance and repair problems and recommended solutions for each property (Figure 10). This section was designed to be used by property managers to create building-by-building files to document and monitor building conditions and treatments.

Figure 10. Page from Preservation Treatment Guide showing character-defining features of the exterior of the Berol Lodge.

Chapter 3, Addressing Problem Areas, provides specific procedures for the recommended solutions outlined in the previous section.
Recommendations address issues such as exterior log maintenance, including cleaning, finish, daubing, replacing sill logs, splicing and repairing log crowns and faces (Figure 11); repairing roofs and chimneys; correcting faulty ventilation, flashing, grading and drainage; removing vegetation around buildings; maintaining and repairing windows and doors; snow removal and winterization; and controlling pests, including ants and bats. Specific problems relating to drainage around the Berol Lodge and repair of the southwest porch of the Berol Lodge are included in this chapter (Figure 12).

Chapter 4, Regular Inspection and Maintenance Tasks, lists tasks that should be performed annually, such as cleaning roofs, gutters, and valleys, cleaning the interiors and exteriors of each building, painting any surfaces where paint is peeling and chipping, hanging screens and storm windows as needed, blowing out log checks, and trimming vegetation around buildings. This chapter also explains use of the Building Condition Assessment Form to record annual building inspections. Regular inspections help identify maintenance problems, making deferred maintenance less likely. As soon as problems are identified, repair should be scheduled.

The Appendix includes a CD with completed Building Condition Assessment Forms (2011) and blank forms for future use, as well as additional photographs and information on National Park Service policies.

Figure 11. Harrison Goodall shows student Cassie Loveland how to apply daubing to the logs of the boathouse at AMK Ranch. (Mary Humstone, 2011)

Figure 12. Page from Preservation Treatment Guide with step-by-step instructions for improving drainage at the Berol lodge. (2011)

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Harrison Goodall, Conservation Specialist and Katherine Longfield, Cultural Resources Manager at Grand Teton National Park, provided expertise in conservation of historic log buildings. Special thanks go to Dr. Hank Harlow, director of the UW-NPS Research Center, for supporting our research and field schools, and to caretaker Rich Viola for his care of the historic buildings at the AMK Ranch.

CHECKLIST OF PRESERVATION DOCUMENTS


MEASURING THE MORPHOLOGY AND DYNAMICS OF THE SNAKE RIVER BY REMOTE SENSING

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ABSTRACT

The Snake River is a central component of Grand Teton National Park, and this dynamic fluvial system plays a key role in shaping the landscape and maintaining a diversity of habitat conditions. The river’s inherent variability and propensity for change complicate effective characterization of this important resource, however; conventional, ground-based methods are not adequate for this purpose. Remote sensing provides an appealing alternative that could facilitate resource management while providing novel insight on factors influencing channel form and behavior. This study evaluates the potential for using optical data to measure the morphology and dynamics of a large, complex river such as the Snake. More specifically, we assessed the feasibility of estimating flow depth from multispectral satellite images acquired in September 2011. Our initial results indicate that reliable maps of river bathymetry can be produced from such data. We are also examining channel changes associated with a prolonged period of high flow during the 2011 snowmelt runoff season by comparing these satellite images with digital aerial photography from August 2010. An extensive field data set on flow velocities provides some hydraulic context for the observed morphodynamics. More sophisticated hyperspectral and LiDAR data sets are scheduled for collection in 2012, along with additional field measurements.

INTRODUCTION

A defining feature of the Teton landscape, the Snake River plays an important role in the geomorphology and ecology of Jackson Hole and provides visitors to Grand Teton National Park with abundant recreational opportunities. This dynamic fluvial system collects water and sediment from a large, mountainous drainage basin and conveys these materials across the valley floor via various mechanisms of flow and sediment transport. These processes interact to produce coherent patterns of sediment transfer and storage that are manifested as distinctive landforms - channels, bars, floodplains, and terraces. These geomorphic surfaces are colonized by vegetation but eventually reclaimed as the river shifts laterally, incises new channels, or reoccupies former flow paths. This perpetual reworking of the riparian zone creates a patchy mosaic of habitat conditions that supports a diversity of terrestrial and aquatic organisms, including such iconic species as bald eagles, beaver, native trout, and moose. The potential to view such wildlife, along

Figure 1. Cataraft and kayak used for field data collection along the Snake River. Photo by Chip Rawlins.
with the unique scenery in part created by the Snake, makes this fluvial environment a source of considerable enjoyment by the public, for whom the river and surrounding National Park have been protected and preserved.

Managing these natural resources is the responsibility of the National Park Service, but this important task is complicated by the same variability and dynamism that make the Snake River such a vibrant element of the landscape. Basic information on the river's form and behavior are needed for resource assessment and monitoring purposes, but the logistical constraints associated with conventional field methods make even sparse data difficult to obtain. Measuring channel and floodplain topography, flow conditions, and streamed characteristics over long reaches is simply not practical in such a heterogeneous riverine environment. Moreover, the channel changes that occur during each spring's snowmelt imply that maintaining an accurate, current database would require annual surveys. Information of this kind would facilitate various ongoing ecological and geomorphic investigations while enabling the Park Service to more readily achieve certain management objectives. For example, studies of native cutthroat trout would benefit from a more detailed knowledge of the physical habitat conditions (e.g., depth, velocity, and bed material grain size) preferred by these species during different life stages. Similarly, research on the effects of flow regulation on floodplain inundation, bed mobility, and general channel stability, along with related efforts to develop reach-scale sediment budgets, would benefit from more extensive, higher resolution topographic data. For resource management, current information on channel depths, the distribution of bars, and the location of obstructions (e.g., accumulations of large woody debris) would allow navigability by rafts to be assessed more easily and could help recreational boaters to avoid potentially hazardous situations. For many reasons, then, an enhanced capacity to characterize the morphology and dynamics of the Snake River would be of great value.

Remote sensing techniques could provide such a capacity by enabling more efficient measurement of several key river attributes. A quantitative, remote sensing-based approach would have several distinct advantages in this context: 1) a synoptic perspective that allows long segments of broad riparian zones to be mapped in a matter of hours rather than weeks, 2) continuous, high-resolution data that capture the spatial variability of the riverine environment far more effectively than traditional methods based on isolated cross-sections, and 3) more frequent coverage that could not only facilitate monitoring but also lead to an improved understanding of the fluvial processes that drive channel change and thus create, modify, and maintain diverse terrestrial and aquatic habitats.

Research on the application of remote sensing to rivers has progressed rapidly over the past decade (Marcus and Fonstad 2010). For example, our earlier work demonstrated the feasibility of mapping flow depth from optical data (Legleiter et al. 2004, 2009). Field measurements and digital aerial photography collected along the Snake River in August 2010 also indicated that reasonably accurate depth estimates could be derived from relatively basic images of this kind (Legleiter, forthcoming 2012a). Our results thus suggest that integrated, spatially explicit analysis of remotely sensed data could enable scientists and managers to more efficiently characterize complex river systems like the Snake.

Research hypothesis and specific aims

The primary goal of our research in Grand Teton National Park is to apply remote sensing methods to an important problem that is not only of scientific interest but also of direct relevance to current management needs: characterizing the morphology and dynamics of the Snake River. This effort will yield insight on factors influencing channel form and behavior and facilitate the Park Service's efforts to protect this resource. We have a more general research interest in the remote sensing of rivers, but the Snake River is one of our primary field sites for developing and testing new methods. This dynamic fluvial system provides an opportunity to critically evaluate the feasibility of mapping a large, braided river from various types of image data. This project is also consistent with our overarching research objective: to understand the mechanisms by which flow, sediment transport, and channel form interact to direct a river's morphologic evolution. Motivated by these goals, our efforts over the past year have focused on the following specific aims:

1) Obtain field measurements of reflectance and water column optical properties to more rigorously assess the feasibility of spectrally-based depth retrieval in this environment.

2) Acquire a new multispectral satellite image of the Snake River and evaluate the utility of these remotely sensed data for bathymetric mapping.

3) Quantify the channel changes that occurred during the 2011 runoff season by comparing aerial photographs from 2010 to the 2011 image data.
4) Collect field data on flow depths and velocities to provide some hydraulic and geomorphic context for the observed dynamics.
5) Identify future research needs and develop a plan for collecting additional remotely sensed data and field measurements that will advance our understanding of the Snake River.

**STUDY AREA**

This effort to characterize channel form and behavior via remote sensing focuses on the Snake River in Grand Teton National Park. This dynamic fluvial system is well-suited for such an investigation because the river encompasses a range of channel morphologies, valley floor environments, and disturbance regimes that not only pose a challenging test of remote sensing methods but also will allow us to examine various factors controlling river morphology. For example, the Snake includes both meandering and braided segments that are influenced by variations in slope and sediment supply, differences in streambank composition and riparian vegetation, a post-glacial legacy, and a strong tectonic signal. Field measurements and image data from the Snake thus allow us to draw comparisons among a variety of stream reaches in terms of both their amenability to remote mapping and their geomorphic controls. In addition, the Snake is an attractive site for study because the river features, 1) clear water conditions conducive to remote sensing of flow depths, 2) a pair of stream gages that provide a continuous record of river discharge, 3) relatively little direct human impact, apart from flow regulation by Jackson Lake Dam, and 4) a well-documented history of channel change based on archival aerial photography (Schmidt and Nelson, 2007). In any given year, a sizable portion of the Snake River could experience significant morphologic adjustment as a result of high snowmelt runoff; both existing and planned remotely sensed data sets provide an effective means of characterizing these dynamics.

Our 2011 field campaign involved extensive data collection along the Snake River and encompassed a broad range of channel configurations. We covered the segment from Pacific Creek downstream to Moose, with much of our effort focused on a pair of meander bends: 1) Swallow Bend, located at 537500 m E, 4851200 m N and 2) Rusty Bend, located at 535160 m E, 4849650 m N (UTM Zone 12N). In addition to these two detailed study sites, we performed a longitudinal survey using a specially designed cataraft outfitted with equipment for measuring flow depths, velocities, and various optical properties.

**METHODS**

For 2011, the general strategy of our investigation was to: 1) Make field measurements of flow conditions and optical properties along the Snake River, 2) Obtain multispectral satellite images of the riparian corridor, 3) Develop and evaluate image processing methods for retrieving water depth from remotely sensed data, 4) Combine the new satellite imagery with previously acquired aerial photography to examine the channel changes associated with high flows during the 2011 spring runoff and, 5) Interpret the observed dynamics in terms of flow and sediment transport processes and landscape-level controls on channel form and behavior. The data acquired in 2011 also provide a basis for planning future remote sensing missions, with additional flights scheduled for August 2012. This project thus involved a combination of geospatial data analysis and field work; these two components are described in the following sections.

**Remotely sensed data and image processing**

In 2010, the first year of this ongoing study, we focused on compiling existing remotely sensed data sets and acquiring digital aerial photography along the Snake River corridor; these data sets are described in detail in our previous report. Our attention has now turned to satellite images acquired by the WorldView2 sensor on 13 September 2011. This new instrument features a unique combination of spatial and spectral resolution well-suited for river applications. The WorldView2 data set consists of 2 m-pixel size multispectral images with eight bands spanning the visible and near-infrared wavelengths, and panchromatic images that are acquired simultaneously and have the same area of coverage but a smaller pixel size of 0.5 m. Other satellites can provide similar spatial resolution, but not with the same level of spectral detail as WorldView2. We obtained two cloud-free images that cover the Snake River from Jackson Lake dam downstream past the Park boundary at Moose. These data were delivered in a geo-referenced format, and alignment between the images and our field-based surveys was highly accurate. The data provider, Digital Globe, also performed a radiometric calibration and atmospheric correction that served to convert the original, raw digital numbers for each pixel to apparent surface reflectance values. To facilitate data processing and reduce computational requirements, we subdivided the original images into a series of 22 individual tiles extending from Jackson Lake to Moose (Figure 2).
Our analysis of the satellite images has focused on evaluating whether these data might be useful for mapping river bathymetry. Previous studies have shown that, under appropriate conditions (i.e., relatively shallow, clear water), water depth can be estimated from passive optical images. More specifically, because the rate at which light is attenuated by the water column varies as a function of wavelength, as depth increases the amount of reflected solar energy recorded in a spectral band experiencing stronger attenuation decreases more rapidly than does the amount of energy measured in a band for which attenuation is weaker. Calculating the logarithm of the ratio of the pixel values for two spectral bands thus yields an image-derived quantity that is linearly related to water depth. Whereas the attenuation coefficient of pure water increases by an order of magnitude from the visible into the near-infrared, the bottom reflectance of different substrate types varies by only a few percent over this range of wavelengths, so the band ratio is highly sensitive to depth and robust to variations in bottom type. Calibration is achieved by regressing values of this image-derived quantity against depths measured in the field (Legleiter et al. 2009). This relatively simple method of retrieving depth information was appropriate for the WorldView2 images because these data were acquired in late summer, when concentrations of suspended sediment were minimal, water clarity was high, and field data were collected within a few days of image acquisition. This technique was also applied to a mosaic of digital aerial photographs from 2010, which were also collected under low-flow, clear-water conditions. The ratio-based depth retrieval algorithm allowed us to develop bathymetric maps that depict pools, riffles, and shallow submerged bars for both time periods.

To complement these data sets and extend our image time series, we have already made plans to acquire more sophisticated hyperspectral and light detection and ranging (LiDAR) data that will further enhance our capacity to measure the morphology and dynamics of the Snake River. Ultimately, the principal channel attributes we intend to map via remote sensing are flow depth, bed topography, and water surface slope. Several data sets potentially useful for these purposes have been compiled in a GIS, as described in our previous report. Although LiDAR provides highly accurate topographic information from exposed bars and floodplains, LiDAR is of little value within the wetted channel proper due to strong absorption of near-infrared laser pulses by water. To produce a complete topographic representation of the riverine environment, LiDAR topography and spectrally-based bathymetry can be combined into a single digital terrain model. The LiDAR provides elevations for exposed areas, and bed elevations within the channel can be determined by subtracting image-derived depth estimates from water surface elevations recorded for LiDAR points along the edge of the water (Legleiter, forthcoming 2012b). Some adjustment might be necessary to account for differences in flow level if the LiDAR and optical data were not acquired simultaneously, but this offset can be determined from gage heights recorded at Jackson Lake and Moose on each date. This analysis will be completed after we obtain LiDAR coverage in August 2012.
Field data collection

In addition to the geospatial data analysis described above, our study also involved extensive field work intended to validate remotely sensed river information and to support our geomorphic research agenda. As part of our overall effort to advance the remote sensing of rivers, the development of which has been hindered by a lack of in situ observations, we made direct field measurements of several optical characteristics of the Snake River. Reflectance spectra were recorded above the water surface using an Analytical Spectral Devices (ASD) FieldSpec3 spectroradiometer. A 100% reflectant Spectralon calibration panel was used to establish a white reference prior to each round of measurements. The spectroradiometer was mounted on a specially designed cataraft and configured to record spectra once each second as we traversed the river on a series of channel-spanning transects (Figure 3a). Flow depths were recorded simultaneously using the survey instrumentation described below. This protocol thus provided paired observations of depth and reflectance needed to develop and refine bathymetric mapping algorithms. Moreover, these data extended the range of river conditions under which spectra have been measured from shallow, wadable streams (Legleiter et al., 2009) to a deeper, larger channel with more diverse bottom types. For example, our Swallow and Rusty Bend study sites were up to 3 m deep and featured submerged aquatic vegetation and bright-colored clay bedrock substrates, respectively (Figure 3b).

In addition to bathymetry, the composition of the streambed also might be mapped via remote sensing. To explore this possibility and begin the process of building a spectral library of different substrate types, we attached the ASD to a submersible cable and waterproof fore-optic to make direct measurements of the bottom reflectance of various bottom types. As for the above-water measurements, raw spectra were converted to reflectance using digital counts from a white reference panel adjacent to the target. Data were collected from side channels of the Snake River and included the following features: submerged aquatic vegetation (Figure 4a); fine-grained sediment; clean gravel; and periphyton (algae attached to the bed; Figure 4b).

An important constraint on remote mapping of bathymetry and/or bottom type is the optical properties of the water column, and we collected field data on several characteristics of the Snake River water itself. For example, connecting the spectroradiometer to a waterproof, upward-facing detector allowed us to measure the amount of downwelling radiant energy propagating to various depths within the water column (Figure 5a). These data were used to calculate a diffuse attenuation coefficient at each wavelength following the procedure outlined by Mishra et al. (2005). In addition, we used a WetLabs ac-9 to directly measure two key inherent optical properties of the water column, the absorption and attenuation coefficients, $a$ and $c$ (Figure 5b). These optical data were collected on several dates at sites along the Snake River. Ancillary data in support of these measurements included water samples analyzed for suspended sediment concentration and in situ turbidity readings with a Eureka Environmental Manta 2 multi-probe.

Figure 3. (a) Field measurements of flow depth and spectral reflectance were obtained from a cataraft; the spectroradiometer extends out over the water from the rear of the raft (right in this photo). (b) Blocks of light-colored material present along Rusty Bend.
A second key component of our field effort was a survey of channel bed topography. These data were collected using a high-precision (sub-centimeter) real-time kinematic GPS receiver that was attached to a survey rod for measuring terrestrial surface elevations. Survey points were arranged along cross-sections traversing exposed bars and shallow areas of the active channel and selected so as to emphasize important breaks in slope, such as the top and base of stream banks. For areas that were too deep to wade safely, the GPS receiver was mounted on the cataraft and configured to record water surface elevations while communicating with an echo sounder that measures flow depths; subtracting the depth from the water surface elevation yielded measurements of the bed elevation. Over 22 km of the Snake River was surveyed in this manner. Measurements were obtained along a series of transects in our detailed study sites as well as longitudinal profiles recorded as we progressed downstream each day. In total, 73,686 point measurements were obtained in this manner, and an example from Rusty Bend is shown in Figure 6. These field measurements allowed us to relate depths to WorldView2 image-derived quantities.
In an effort to better characterize and understand the fluvial processes driving the channel changes observed in our image time series, we measured flow conditions within the Snake River using an acoustic Doppler current profiler (ADCP). This instrument was deployed from a kayak outfitted with a specialized mounting system (Figure 7a) and recorded flow velocities in a series of cells distributed vertically throughout the water column. The ADCP measured streamwise, cross-stream, and vertical velocity components at a frequency of once per second and thus provided a very detailed characterization of the flow field. We also used the ADCP to measure river discharge by integrating the product of depth and velocity as we moved across the channel. In addition to cross-sections located in our two primary study sites (Figure 7b), we also recorded flow velocities along profiles oriented down the river. The ADCP also recorded flow depths and thus provided an additional source of field data for evaluating remotely sensed bathymetry. In addition, data acquired with the ADCP will support future work on the interactions between flow processes, bed material transport, and the evolution of channel form.

**RESULTS**

In 2011, the second year of this ongoing study, we conducted a successful field campaign from 29 August to 16 September. Our field work was delayed until this late summer/early fall time period due to a large snowpack last winter that translated into unusually high flow conditions throughout the spring and summer. Only in late August did the discharge along the Snake River recede to a level at which we could work safely, and even then flows were ~75% higher than during our 2010 field season, which occurred in early August. In any case, we enjoyed favorable weather conditions and took full advantage of our new research cataraft, kayak, and measurement devices. To date, our analysis has focused on characterizing the river’s optical properties, evaluating the feasibility of mapping river bathymetry from satellite image data, summarizing the hydraulic information collected with the ADCP, and documenting channel changes between 2010 and 2011. The following sections report some of our initial findings and discuss our plans for further work along the Snake.

**Optical properties of the Snake River**

An impediment to progress in the remote sensing of rivers has been a paucity of direct, *in situ* measurements of spectral reflectance and water column optical properties; our field data from the Snake River address this void. Although measuring spectra aboard a moving cataraft was a new challenge for our research team, the data we obtained have already yielded some encouraging results. Reflectance spectra measured from above the water surface on transects across Rusty Bend are shown in Figure 7. (a) Flow velocities were measured with an acoustic Doppler current profiler (ADCP) deployed from a kayak. (b) Velocity data from our Rusty Bend study site along the Snake River; the variable depicted in this map is the depth-averaged three-dimensional velocity magnitude.
Figure 8a to illustrate variability in brightness and spectral shape; note that only 10% (95, selected at random) of the measured spectra are included in this plot. Figure 8b is an example spectral/bathymetric cross-section where as depth increased toward the left (outer) bank, the reflectance at a wavelength of 607 nm decreased at a faster rate, due to exponential attenuation by the water column, only to spike near the outside of the bend where bright blocks of exposed bedrock were exposed on the bed (Figure 3b). To evaluate the feasibility of spectrally-based depth retrieval in this environment, the 953 reflectance spectra measured at Rusty Bend were subjected to the Optimal Band Ratio Analysis (OBRA) procedure described by Legleiter et al. (2009). Briefly, this technique: 1) takes as input paired observations of depth and reflectance, 2) computes an image-derived quantity $X$, defined the logarithm of the ratio of two spectral bands, for all possible pairs of wavelengths, 3) performs a regression of depth vs. $X$ for each band combination; and 4) identifies the optimal band ratio as that which yields the highest regression $R^2$ value. OBRA results can be represented as a matrix that highlights spectral variations in the strength of the relationship between depth and $X$. For the Rusty Bend data set, defining $X$ using reflectances measured in green and red wavelengths yielded a strong linear relationship with depth ($R^2 = 0.884$). Applying the OBRA equation to the field spectra produced a spectrally-based depth estimates (dashed blue line in Figure 8b) that agreed closely with the surveyed cross-section (solid blue line). Moreover, the extensive warm tones in the matrix of $R^2$ values shown in Figure 8c indicates that many other band combinations would yield reliable depth information as well.

We also obtained data on the optical properties of the water itself. Vertical profiles of downwelling irradiance were recorded on four different dates along the Snake River. Diffuse attenuation coefficient $K_d$ values calculated from these data are shown in Figure 9a, along with similar data from Soda Butte Creek, a smaller gravel-bed river in nearby Yellowstone National Park (Legleiter et al., 2009).

$K_d$ is an apparent optical property that influences the precision of image-derived depth estimates, as well as their dynamic range; higher $K_d$ values imply less precise depth retrieval and shallower maximum detectable depths. The $K_d$ spectra from each date/site are quite similar, but data acquired under more overcast conditions plot higher than those obtained under clear skies. A $K_d$ spectrum

\[
\begin{align*}
\lambda_1 &= 506 \text{ nm} \\
\lambda_2 &= 607 \text{ nm} \\
d &= 3.68X + 1.38 \\
R^2 &= 0.884; \text{ S.E.} = 0.215 \text{ m}
\end{align*}
\]

![Figure 8](image_url)

Figure 8. (a) Reflectance spectra from Rusty Bend. (b) A single transect of depth and reflectance observations showing the effect of bright failed bank blocks. (c) Optimal band ratio analysis used to establish a relationship between reflectance and water depth; see text for details.
from Platte River, a much more turbid stream where we have examined previously (Legleiter et al., 2011), to highlight the greater clarity of the water in the Snake River and Soda Butte Creek, where optical methods are a more viable means of mapping bathymetry. These results were corroborated by the ac-9 data shown in Figure 9b, in which the inherent optical properties are seen to be quite similar across all sites and dates. This plot also depicts the absorption coefficients of pure water and a small concentration of suspended sediment to show that a simple, two-component optical model might be sufficient to describe these streams, although colored dissolved organic matter should be considered as well to account for the increase at wavelengths shorter than 500 nm. The turbidity values recorded during our field campaign were consistent and low: 2 - 3 NTU. Suspended sediment concentrations were also minimal: 2 mg/L for each of three water samples. These data quantify the exceptional clarity of the Snake River and imply that this stream is amenable to remote sensing techniques.

Also during our 2011 field campaign, we made significant progress toward our goal of establishing a spectral library of different riverbed bottom types, ranging from submerged vegetation and green algae to fine sediment, clean gravel, and blocks of failed bank material. The photo in Figure 10a shows how these features are arranged in complex patterns along a side channel of the Snake River, with considerable fine-scale spatial variability.
The bottom reflectance data in Figure 10b indicate that various substrate types are spectrally distinct from one another, however, implying that this type of information might be used to map various substrates at a sub-pixel scale via spectral mixture analysis or similar techniques. Future work will explore this possibility via radiative transfer modeling and hyperspectral image data to be acquired in 2012.

Mapping flow depth from remotely sensed data

In addition to their more traditional role as a means of recording changes in channel planform, remotely sensed data can be used to quantify spatial variations in flow depth, thus adding a third dimension to the analysis of river dynamics. In this study, we applied the band ratio-based algorithm described above to retrieve depth information from the WorldView2 images acquired in September 2011. Whereas the reflectance spectra measured in the field were essentially continuous, with a 1 nm sampling interval, the multispectral satellite measures reflectance in a set of only eight discrete bands. To assess whether this reduction in spectral resolution might affect depth retrieval performance, we resampled the original field spectra to the band passes of the WorldView2 sensor and repeated the OBRA calculations for the degraded, eight-band spectra. This analysis is summarized in Figure 11a, which is remarkably similar to Figure 8c, with only a slight reduction in the depth vs. \( X \) regression \( R^2 \) for the optimal band ratio: 0.839 for green/yellow. These results imply that mapping the bathymetry of a gravel-bed river from space was not only possible but potentially highly accurate.

More direct evidence to support this contention was obtained by extracting spectra from WorldView2 image pixels at the locations of field-based depth measurements. These data were then used to perform an OBRA of the WorldView2 spectra, and the results depicted in Figure 11b once again imply a strong, linear relationship between the image-derived quantity and flow depth, with an \( R^2 \) value of 0.819 for the ratio of blue and yellow bands.

Applying the corresponding equation to the image produced the continuous bathymetric map in Figure 12. The greatest depths occur along the outer bank, with much shallower flow over the point bar on the right (north) side of the channel through the apex of Rusty Bend. A riffle extends across the channel at the exit to the bend before entering a pool along the right bank where the channel curves to the left. This spatial pattern is hydraulically reasonable and consistent with our field observations.

To assess the accuracy of the image-derived bathymetry, we compared the spectrally-based depth estimates to field measurements obtained via wading in shallow areas or with the echo sounder mounted on the cataraft. Of these field data, half were selected at random for use in calibrating the OBRA relation and the other half set aside for validation. A plot of observed vs. predicted depths is shown in Figure 13a, which indicates a strong agreement with an \( R^2 \) value of 0.83. Moreover, the slope and intercept of the regression line are nearly equal to 1 and 0, respectively, indicating that depth estimates are unbiased on average. A closer inspection, however, reveals that the scatter plot includes some curvature, which is manifested as under-estimation of both the smallest and largest depths. To visualize the spatial distribution of these depth retrieval errors, we produced a continuous
depth map from our field data via ordinary block kriging (OBK), a geostatistical interpolation technique, and subtracted the image-derived bathymetry from this map. The resulting map of residuals, or depth retrieval errors, is shown in Figure 13b. In this representation, positive values occur where depths were under-predicted from the image and negative values where spectrally-based depth estimates were greater than those interpolated from the field data (i.e., over-predicted from the image).

In Rusty Bend, positive residuals along the outer bank suggest that the full depth of the pool on the left side of the channel could not be resolved from the image data. Conversely, the red tones past the bend apex indicate an area where depths were over-predicted from the image. These results are consistent with radiative transfer theory (Legleiter et al., 2004) and imply that some systematic biases in depth retrieval performance might arise solely as a function of the river morphology itself, most notably a tendency to under estimate pool depths. Nevertheless, these errors were relatively small, and the overall depth retrieval performance of the WorldView2 satellite was quite good. In general, our results suggest that spectrally-based bathymetric mapping from space is not only feasible, but potentially sufficiently accurate for many practical applications. At a minimum, a remote sensing approach can provide an informative, qualitative impression of the gross morphology of a channel.

Obtaining precise measurements of bed elevation to serve as topographic input data for hydraulic modeling or for quantifying erosion and deposition might require more sophisticated hyperspectral image data with greater radiometric resolution. We intend to acquire such data in 2012 and will evaluate the extent to which reliable river information needed to support more demanding applications can be obtained via remote sensing. Although the potential for remote mapping of fluvial systems is clearly significant, the inherent limitations of this approach - shadows, reduced water clarity, greater depths, etc. - must be borne in mind as well.

Channel change during the 2011 spring runoff

An unusually large snowpack accumulated in the Snake River watershed during the winter of
2010-2011 and persisted well into the spring. When the snow finally melted, a prolonged period of sustained high flow ensued and lasted throughout August. We hypothesized that this flood event would produce significant channel changes along the Snake River corridor and we used the 2010 digital aerial photography and 2011 satellite images to examine the magnitude, nature, and extent of morphologic adjustments. We have only recently initiated this analysis and the results reported herein are preliminary and might be revised to some extent as we refine our methodology. Also, for the purposes of this report, we focus on a segment of the river upstream from the Deadman’s Bar boat access that we expected to be dynamic based on field observations, the braided morphology of the reach, and geomorphic context.

To identify areas of channel change, we produced land cover classifications from each image date using a decision tree algorithm. This technique assigns a heterogeneous population (i.e., image pixels) into pre-defined groups by creating a set of rules based on training data provided for each class. These rules take the form of simple binary choices based on thresholds for one of the variables (i.e., spectral bands) used to perform the classification. In this study, we sought to distinguish six classes present along the valley floor: water, gravel, riparian vegetation, forest, sage, and shadows. Representative training sites for each of these classes were digitized from both the 2010 air photos and the 2011 satellite image and a separate decision tree developed for each date. Applying the trees to the images produced the land cover maps shown in Figure 14.
red areas along either side of the channel might indicate actual erosion but are largely a consequence of the higher flows at the time the 2011 image was acquired, implying a greater inundated area and not necessarily erosion. Similarly, some areas mapped as recovery could be an artifact of classification errors, as the gravel and sage categories were easily confused with one another. Despite these caveats, we were underwhelmed by the amount of change that occurred during the 2011 flood within a reach that we had expected to exhibit much more dynamic behavior. These results might imply that the channel morphology is adjusted so as to remain relatively stable from a larger-scale, synoptic perspective, despite local reworking of mid-channel bars. Ongoing work will examine other reaches along the river and assess whether the river is, as these preliminary results suggest, dynamically stable.

Field measurements of river hydraulics

In addition to field surveys of channel and floodplain topography, we also used an acoustic Doppler current profiler (ADCP) deployed from a kayak to measure flow velocities on cross-sections and longitudinal profiles distributed throughout our study area along the Snake River. This instrument provided a wealth of hydraulic information, including observations of three-dimensional velocity components in a set of vertical cells distributed throughout the water column, recorded at a frequency of once per second as the kayak moved along and across the river. These data thus yield a detailed depiction of the flow patterns that determine the magnitude and orientation of fluid forces that in turn mobilize and transport sediment and thus dictate the trajectory of channel change. Though not directly relevant to remote sensing, the ADCP data will thus help us to understand the geomorphic processes responsible for the river dynamics observed in our image time series.

We have made significant progress analyzing the ADCP data collected in 2011, but only a couple of examples are presented here to illustrate the kind of information we have obtained. Our efforts to characterize the flow field were focused on a pair of meander bends that have a similar curvature and overall geometry but a very different morphology. The first site, Swallow Bend, is unusual in that a terrace protruding into the channel near the bend entrance has created an obstruction that has modified the flow field such that a large gravel bar has accumulated along the outside of the bend, in addition to a point bar along the inner bank. The second study reach, Rusty Bend, has a more typical configuration, with a single point bar located along the inside of the curve (Figure 7b). Comparing the flow field through these two bends will thus allow us to isolate the influence of a constriction on patterns of velocity, sediment transport, and channel morphology. The ADCP data provide detailed information on three-dimensional flow structure for examining these issues. For example, the transect shown in Figure 16a illustrates the helical flow pattern typical of meander bends, with outward-directed flow (toward the left bank) along the shallow margins of the point bar on the right (inside) of the channel and near the water surface, and inward flow near the bed in the pool and onto the lower slope of the point bar. Similarly, streamwise profiles like that shown in Figure 16b highlight along-channel undulations of the bed topography and their influence on the flow field and will be used to examine the relationship between bar amplitude and form-related flow resistance. The ADCP was also configured to measure river discharge, with typical values of 85-90 m$^3$/s recorded during our field campaign. These discharge readings will be used to develop new algorithms for retrieving depth information from remotely sensed data when direct field measurements are not available for calibration, based on hydraulic relationships that serve to constrain a numerical optimization procedure. Future work also will involve collecting additional ADCP data to help advance our understanding of the manner in which river morphology and hydraulics influence sediment transport and ultimately channel change.

✦ MANAGEMENT IMPLICATIONS

This ongoing study directly contributes to the Park Service's current management priorities and could provide a powerful tool for assessment and
monitoring of riverine resources throughout the region. The 2009 Craig Thomas Snake River Headwaters Act designated the river above Jackson Lake as a Wild River and the segment from Jackson Lake Dam to Moose, along with the Pacific Creek and Buffalo Fork tributaries, as Scenic Rivers in recognition of their ecological, aesthetic, and recreational value. This legislation provides these streams with protected status as part of the National Wild and Scenic Rivers System and ensures the free-flowing condition of these waterways. Along with this designation comes the task of determining how best to preserve this remarkable fluvial system. Accordingly, the Park Service has set out to develop a new river management plan, which will involve documenting these unique natural resources and identifying effective strategies for their protection. Park managers are thus obligated to characterize the form and behavior of the Snake River, along with the associated habitat conditions and recreational opportunities. Our primary objective is to derive such information from remotely sensed data; this continuing project will thus directly inform the Park's river management plan. Moreover, the techniques developed as part of this investigation could be applied to other streams throughout the Snake River headwaters, both those that have already been awarded Wild and Scenic status and others that might merit such consideration in the future. Although remote sensing clearly offers significant potential to facilitate a number of river-related applications, this potential has not been realized in practice, and the capabilities and limitations of a remote sensing-based approach must first be established. By demonstrating the utility of these methods, and also acknowledging their deficiencies, this study of the Snake River could lead to more widespread, effective use of remote sensing in river research and management.

 ACKNOWLEDGEMENTS

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IDENTIFICATION OF INTERFLOW PATHWAYS AND POTENTIAL WETLAND SITES IN THE KELLY HAYFIELDS

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ANIMAL AND RANGE SCIENCES ♦ MONTANA STATE UNIVERSITY ♦ BOZEMAN

ABSTRACT

In support of Grand Teton National Park Service plans to restore the Kelly Hayfields to pre-homesteading conditions an inventory of soils and associated vegetation was conducted over a two year period, 2010 and 2011. Measurements from 37 soil pits and 19 associated vegetation descriptions revealed little evidence for the presence of riparian wetlands anywhere within the historic hayfields. The exception was a small area near the north eastern end of Blacktail Butte. Faint soil redoximorphic features associated with about 5% wetland indicator plant cover implies the existence of riparian wetlands at the time of homesteading. Differences in soil texture across the hayfields indicates that a mosaic of herbaceous and mountain big sagebrush/grass communities existed when agricultural conversion began. Based on these results Grand Teton National Park’s restoration efforts should focus on re-establishment of sagebrush-grassland complexes.

INTRODUCTION

As part of the 2007 Bison–Elk Management Plan Grand Teton National Park (GTNP) undertook a study of the western section of the Antelope Flats area (Kelly Hayfields) to prioritize areas for future restoration efforts. The central focus of the restoration inventory was identification of wetlands that may have existed prior to agricultural conversion and whether or not the hydrologic/soil factors that had been responsible for their creation and maintenance were still in place. Knowing the extent and location of historic wetlands would help Park Service Specialists decide if wetland recovery would be supported by the current hydrologic patterns, or if extensive wetland reclamation should be part of the Park’s restoration plan for the Antelope Flats area. The study began in the spring of 2010 and continued through the fall of 2011. During the study 28 soil pits were excavated and 9 bore holes drilled (mechanical Giddings probe) seeking evidence for a persistent groundwater table which would have supported historic wetlands in the Kelly Hayfield. Following the soil survey an extensive vegetation inventory was conducted in late summer 2011 to identify the present vegetation community structure and diversity associated with the soil pits and bore holes.

STUDY AREA

Prior to the establishment of Grand Teton National Park (GTNP), intensive homesteading and cultivation turned nearly 4,000 acres of native shrub steppe occupying the Antelope Flat area between Blacktail Butte and the Gros Ventre River into non-native irrigated hayfields and pasture. Further impacts to natural processes were created as a network of irrigation ditches were dug across homestead land to distribute water diverted from nearby surface streams to boost hayfield and pastureland production.

The study area was located near Moose, Wyoming north of Jackson Hole, Wyoming. The Kelly Hayfields are bound by the Gros Ventre road to the south and Antelope Flats road to the north (elevation 6528 feet above sea level) (Figure 1). The
landform setting of the Antelope Flats area (Kelly Hayfields) is a shallow-gradient alluvial fan sloping west-southwest from the toe of the Gros Ventre Mountain range towards Blacktail Butte. The depositional setting is a relatively level plain composed of loess and alluvial sediments deposited over glacial outwash.

Figure 1. Generalized location of the Kelly hayfields within Antelope Flats, Grand Teton National Park, Moose, WY.

**METHODS**

Twenty-eight soil pits were excavated to completion depths of ~30-115 cm (Figure 2). The NRCS Field Book for describing and sampling soils, version 2.0 was employed to sample, code and describe the soil samples. Soils were characterized by: color using the Munsell color guide (hue, value, and chroma), structure (visually following NRCS field book) and application of dilute hydrochloric acid (HCl) to identify calcareous matrix cementation in the field. The extent and rate of effervescence created by application of the acid indicates the amount of carbonate and its chemical and physical nature. The samples were collected in situ labeled and transported to Montana State University for laboratory analysis. Particle-size was characterized by the use of mechanical hydrometer analysis (Gee and Bauder 1986), total carbon was characterized by loss on ignition testing (Heri et al. 1999), and pH was recorded using a Hanna HI 98129 multi-parameter meter. The soil pits were excavated in the Tineman and Leavitt soil series (Scoeneberyer 2002). Vegetation communities within the Kelly hayfields and surrounding shrublands are representative of the Timothy-Kentucky Bluegrass-Smooth Brome, Mountain Big Sagebrush, Mountain Snowberry/Needleandthread shrubland, Mountain Big Sagebrush – Mountain Snowberry/Idaho fescue shrubland and Mountain Big Sagebrush – Mountain Snowberry-Bluebunch wheatgrass shrubland plant alliances (Cogan et al., 2005).

Figure 2. An aerial photo of the Kelly Hayfields on the eastern side of Blacktail Butte. Soil pits are denoted by yellow circles and bore holes by orange squares.
Figure 3. A soil pit and profile descriptions representative of the 37 pits and bore holes sampled within the Kelly hayfields during 2010.

Description of the Vegetation Community

Species composition of the vegetation complexes associated with 19 of the 37 soil pits was determined through foliar cover measurements made by following the Daubenmire technique (Daubenmire 1968). Four sampling lines were anchored on each soil pit location and then oriented in north, south, east, west directions. Foliar cover (by species), bare ground and litter were estimated in three 20 x 50 cm quadrat frames spaced at 5, 25 and 50 m intervals along two randomly selected lines and then repeated at 5 and 25 m intervals along the two remaining sampling lines. This approach produced a total of 10 quadrats per soil pit. Cover measures were summarized for each soil pit and then analyzed for similarity with cluster analysis (STATISTICA Academic 2011). Vegetation within similar groups was further categorized as to obligate (OBL), facultative wetland (FACW) and facultative (FAC) wetland indicator status (Lesica and Husby 2001).

Results

Hydric soil analysis

Soil pits were excavated and the Munsell color guide and NRCS Field Guide were employed to describe soil structure and determine the presence or absence of redoxomorphic diagenesis, gleying or other chemical indicators of a persistent groundwater table. Gleying and redoximorphic features would indicate previous patterns of water flux or soil pore saturation for prolonged periods. Field observations found limited evidence of diagenesis or other soil chemical reactions in most of the soil pits (Figure 3). Weak chemical reactions were apparent around root-holes in pits proximal to the toe of Blacktail Butte (T1P1, T1P2, T2P1, T2P2) with pits revealing the most developed redox-features located on the northern-most end of Blacktail Butte proximal to Ditch Creek (T5P1, T5P2, T3P1 and T3P2). Soil features noted in all other pits were non-supportive of a paleo-wetland or riparian relics.

Particle-size Analysis

Results of laboratory particle-size analysis conducted at Montana State University indicate that much of the Kelly Hayfield soils are composed of clay with lenses of loams to sandy loams, likely a function of proximity to the alluvial fan and paleo-climatic events producing vacillating precipitation or snowmelt discharge outflow.

Pit and bore holes excavation reached depths of ~1 meter (hand excavated pits) to 4 meters (boreholes) below the ground-surface. We observed limited amounts of disseminated clastic material (gravel and rock fragments >2 mm) in the central portions of the hayfields. Clastic material observed were primarily lenticular indicative of pulsating discharge events, again suggestive of paleo-climatic events. With many soil pits lacking any clastic material in the upper 72 cm of soil profile the possibility of fluvial transport is unlikely. This coupled with the high concentration of clays suggest most of the soil material resulted from eolian transport. Also, supportive of eolian transport is the thickness of the clay profile; exceeding 4 meter depths (without any clastic material >2 mm) in many places.

Percent Carbon Analysis

Sequential loss on ignition (LOI) is widely used as a method of estimating the organic and carbonate content of soils. We employed LOI on samples collected at the Kelly Hayfields. Following laboratory analyses, we recorded a total organic carbon percent range of 2% to 7%. These values are significantly less than what is specified by the US Army Corps of Engineers for lentic and lotic wetlands (Wetland Delineation Manual 1987).

Vegetation Community Description

The extensive soil survey of the Kelly hayfield coupled with the vegetation inventory indicates that historically wetlands and riparian areas were restricted to the immediate eastern flank of Blacktail Butte and the topographic restriction on the
north-end of the butte. Soils developed in alluvium, buried soil profiles and the presence of wetland indicators reinforces the potential existence of historic wetlands at sites T5P1, T5P2, T3P1 and T3P2 (blue oval, Figure 4). Overall site similarity was driven by the amount of smooth brome cover at each site (Table 1).

Table 1. Vegetation composition of similarity groups identified in Figure 3. Individual species composing greater than 1% of the plant community are listed. NA = introduced species, INV = invasive non-native species, FAC = facultative wetland indicator, OBL = obligate wetland indicator.

<table>
<thead>
<tr>
<th>Cluster</th>
<th>Species</th>
<th>Foliar Cover (%)</th>
<th>Wetland Status</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blue</td>
<td>Bromus inermis</td>
<td>9</td>
<td>Introduced</td>
</tr>
<tr>
<td></td>
<td>Poa pratensis</td>
<td>4.1</td>
<td>Introduced</td>
</tr>
<tr>
<td></td>
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<td>3.1</td>
<td>Upland</td>
</tr>
<tr>
<td></td>
<td>Geranium richardsonii</td>
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<td>Facultative</td>
</tr>
<tr>
<td>Blue</td>
<td>Eriogonum umbellatum</td>
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<td>Upland</td>
</tr>
<tr>
<td></td>
<td>Symphyotrichum campestre</td>
<td>1.6</td>
<td>Facultative</td>
</tr>
<tr>
<td></td>
<td>Taraxacum officinale</td>
<td>1.6</td>
<td>Introduced</td>
</tr>
<tr>
<td></td>
<td>Cerastium arvense</td>
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<td>Upland</td>
</tr>
<tr>
<td></td>
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<tr>
<td>Red</td>
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<td>Invasive</td>
</tr>
<tr>
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<tr>
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<tr>
<td>Orange</td>
<td>Symphyotrichum campestre</td>
<td>2.4</td>
<td>Facultative</td>
</tr>
</tbody>
</table>

In an earlier study at the Elk Ranch the amount of obligate and facultative wetland cover was strongly correlated (P = 0.001; rsq = 0.76) to groundwater depths less than 0.8m. Furthermore, redoximorphic features, principally soil mottles and gleying, were common in the areas of the Elk Ranch with high ground water. In contrast, only 5 of 37 soil pits revealed some form of redoximorphic action in the Kelly hayfields. These features consisted of faint soil mottles and root oxidation associated with a low coverage of wetland vegetation (< 5% cover). The areas represented by the red oval (Figure 4) had soils with structure and calcic response similar to soils associated with grass and shrub dominated communities. Coupled with the lack of redoximorphic features and wetland indicator species this indicates that the majority of the hayfield area was sagebrush grassland at the time of homesteading. It is likely that there was considerable variation in historic shrub cover across the hayfields because the high clay content recorded at many of the soil pits would have promoted depressional storage for short periods following snowmelt and thunderstorms. This would have produced higher grass and forb cover and less sagebrush at these sites. In direct contrast to these conditions, soil structure and texture at pits T3P6 and T3P7 indicate rapid infiltration and early drying. Sagebrush would dominate in such areas even in close proximity to the stream channel.

** MANAGEMENT IMPLICATIONS **

Based on the data collected and analyzed we suggest that the soils and land surface now described as the Kelly Hayfields formed during the rapid retreat of the Bull Lake glaciation. During this retreat a large
A chunk of ice was disconnected and shielded from solar radiation by Blacktail Butte. As this ice melted, sediment from the denuded Gros Ventre Range was carried across an alluvial fan and deposited adjacent to the melting ice. A large depression (the Kelly hayfields) was left when the abandoned ice finally melted. This depression was then filled with eolian loess lifted from the Gros Ventre derived fan. In time rangeland vegetation colonized, stabilizing and ultimately developing the mature grassland soil features observed in this study.

The isolated occurrence of soil and wetland vegetative indicators to one small area of the Kelly hayfields substantiates the argument that the majority of the hayfields were mountain big sagebrush shrublands interspersed with grass dominated herbaceous communities. Consequently, we conclude that the ecological potential for most of the Kelly Hayfields is sagebrush grassland. With this information restoration efforts can be focused on re-establishment of native grass and shrub species in the former hayfields. It should be noted that reseeding efforts will be more successful when soil level conditions are addressed in developing seeding mixtures. For example, grass and forb species should be seeded into sites with high clay content and shrubs into sandy and gravelly loam sites. Any riparian rehabilitation efforts should be confined to a 30 – 50 m boundary along Ditch Creek and landscapes within the topographic restriction at the north-end of Blacktail Butte.

**ACKNOWLEDGMENTS**

In addition to support from the UW-NPS Research Station, this project has received key funding from the Animal and Range Sciences Department, Montana State University. Access and collection permits were facilitated by Dr. Kelly McCloskey, Grand Teton National Park with data collection and analysis help from Neto Garcia and Eric Hester.

**LITERATURE CITED**


INTRODUCTION

The 2006 Transportation Plan for Grand Teton National Park proposed 22.5 miles of multi-use pathways outside the road to enhance safety and mobility for travelers using non-motorized modes of transportation in the most visited and developed areas of the park. (Grand Teton National Park Transportation Plan 2006, 2007). Construction of the Phase I Pathway, a 7.7-mile segment between Dornan’s Junction and South Jenny Lake Junction along Teton Park Road began in June 2008 (Figure 1). This report summarizes research conducted by the Western Transportation Institute at Montana State University before and after this construction occurred. Researchers counted non-motorized travelers, primarily bicyclists and pedestrians, and administered surveys to learn about visitor perceptions regarding the conditions for non-motorized travel in the park. The primary purpose of this research was to compare the conditions before and after Phase I Pathway was constructed. These results also offer a “point-in-time” glimpse of current non-motorized usage of this region of the park.

Non-Motorized Traveler Counts

Researchers conducted counts of non-motorized users over a three-day period (Friday, Saturday and Sunday) during four time-periods (Table 1):

- The first count was conducted from April 27 through 29, 2007, which represented use during the pre-season closure of Teton Park Road to motor vehicles. The annual tradition of biking the road on the last weekend prior to the seasonal road opening resulted in high usage during this data collection period and is not considered typical non-motorized use during the season.

- Researchers returned on August 24 through 26, 2007. The August data are intended to estimate typical non-motorized use during the peak visitation period of May through September.

- After the Phase I Pathway was completed, data were collected again in August 2010 to
compared with the August 2007 data. Counts were made on August 20 through 22, 2010.

- To capture the peak usage, another data collection trip was completed on July 22 through 24, 2011. Although the August data provided a before-after comparison, the July data indicate the highest use of the summer season.

Table 1: Average Daily Directional Counts for Non-Motorized Travel

<table>
<thead>
<tr>
<th>Day of Week</th>
<th>Pre-Construction August 2007</th>
<th>Post-Construction August 2010</th>
<th>Post-Construction July 2011</th>
</tr>
</thead>
<tbody>
<tr>
<td>Friday</td>
<td>10</td>
<td>116</td>
<td>127</td>
</tr>
<tr>
<td>Sat./Sun.</td>
<td>18</td>
<td>113</td>
<td>155</td>
</tr>
</tbody>
</table>

The count data show that non-motorized usage during a typical week in August increased significantly after the pathway was constructed. With the pathway available, there was slightly more usage in July 2011 than August 2010.

Non-Motorized Traveler Survey

Researchers surveyed travelers at the same times and locations where they conducted the traveler counts. A total of 279 surveys were completed in April 2007; 58 surveys were completed in August 2007; 180 surveys were completed in August 2010; and 192 surveys were completed in July 2011. The surveys asked park visitors where they began their non-motorized trip and where they were headed, the purpose of the trip, some general demographic questions, their experience and opinions regarding park facilities, and the nature of any interactions they might have had with wildlife. Non-motorized user survey results collected after the pathway was constructed were compared to results prior to pathway construction. Based on this comparison, the average non-motorized user after pathway construction:

- Felt safer,
- Was more satisfied with non-motorized travel,
- Was older,
- Was less likely to be travelling alone,
- Was more likely to be traveling with children, and
- Was more likely to be non-local.

In addition, non-motorized users had a more even distribution by gender after the pathway was constructed. The presence of the pathway did not have much impact on the trip purpose, whether users entered the park in a motorized vehicle, or their parking satisfaction.

**Summary**

The construction of the Phase I Pathway has increased non-motorized travel nearly ten-fold. The pathway has also improved the visitor experience, as non-motorized travelers feel safer and are more satisfied with non-motorized travel options in the park. The change in user type also indicates that the presence of a separated pathway attracts more types of individuals to use non-motorized modes of travel.

**Literature Cited**


GREATER YELLOWSTONE ECOSYSTEM
A MULTI-REGIONAL ASSESSMENT OF THE AMERICAN PIKA (OCHOTONA PRINCEPS) IN NATIONAL PARKS

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ABSTRACT

American pikas are conspicuous and charismatic inhabitants of mountainous regions of the western United States. Due to their sensitivity to high temperatures, they are considered an important early warning indicator species for detecting the ecological effects of climate change. This study addresses the potential threat of climate change to American pikas by assessing current occupancy patterns, modeling current gene flow patterns, and combining these two components to project habitat-specific models of occupancy and connectivity into the future under various climate change scenarios. The preliminary results presented here reflect field work conducted in Grand Teton National Park during the summer of 2010 and 2011. We conducted occupancy surveys, collected non-invasive genetic samples, and conducted preliminary genetic analyses.

INTRODUCTION

The American pika (Ochotona princeps) is a small lagomorph distributed throughout the mountainous areas of western North America including Canada and the conterminous United States (Figure 1). American pikas are temperature sensitive and rely on talus and other specialized rocky habitats to behaviorally thermoregulate. Climate change has been implicated in recent local extinctions of pika populations, particularly in the Great Basin (Beever et al. 2010, 2011). Research suggests pikas may be an early warning indicator species for detecting ecological effects of climate change (McDonald and Brown 1992, Hafner 1993, 1994, Beever et al. 2003, Krajick 2004, Morrison and Hik 2007, Erb et al. 2011). As a result, pikas are a focal species for climate change research.

The goal of this multi-regional, multidisciplinary study, involving scientists and researchers from the National Park Service and academic institutions, is to assess the vulnerability of this species to climate change in eight National Parks. The eight parks included in this study represent an elevational gradient as well as the various habitat types utilized by pikas. The three objectives of this study are to: 1) document pika occurrence patterns and predict pika distribution, 2) measure gene flow and model connectivity of pika populations, and 3) project climate change effects on the future distribution, connectivity, and vulnerability of pika populations. Objective one will include all eight parks while objectives two and three will include five of the eight parks. Grand Teton National Park is one of the five parks included in objectives two and three.
The results presented here reflect work done in Grand Teton National Park during the summers of 2010 and 2011 and are preliminary. At the completion of this study, we will identify pika populations that may be a priority for monitoring, provide models of occupancy and genetic diversity to facilitate the evaluation and/or restoration of potential pika habitats and habitat networks, and provide maps of current and hypothesized future pika distribution to facilitate best practices in management of pikas in these parks.

**STUDY AREA**

The eight National Parks included in this study are: Crater Lake National Park, Oregon; Lava Beds National Monument, California; Lassen Volcanic National Park, California; Craters of the Moon National Monument, Idaho; Yellowstone National Park, Wyoming, Montana, and Idaho; Grand Teton National Park, Wyoming; Rocky Mountain National Park, Colorado; and Great Sand Dunes National Monument, Colorado (Figure 1). Potential pika habitat varies among the study sites with talus predominating in Grand Teton, Great Sand Dunes, Rocky Mountain, and Yellowstone. Craters of the Moon is characterized by a large series of lava flows, while Lassen and Crater Lake have both talus and lava habitats.

Within Grand Teton National Park, potential pika habitat is restricted to the Teton Range in the western half of the park. Classic talus habitat is typically found on mountain slopes and is composed of creviced rock greater than six inches in diameter that can provide shelter for pikas (Figure 2).

![Figure 2. Field crews searching pika habitat at Grand Teton National Park.](image)

**METHODS**

**OCCUPANCY SURVEYS**

Survey site locations were drawn from GIS-based models of predicted habitat according to a random stratified design following methods described in the peer-reviewed monitoring protocol developed by the Upper Columbia Basin Network (Jeffress et al. forthcoming 2013). The sampling frame excluded inaccessible areas and those that would require traversing dangerous terrain. For Grand Teton National Park, the sampling frame included areas within 1 km of roads and 600 m of maintained trails. Additionally, areas with slope greater than 35°, identified using digital elevation models in a GIS, were designated as hazardous and excluded from the sampling frame. The pika sampling frame was stratified by four elevational quantiles, with spatially-balanced samples distributed equally across each stratum. Each survey consisted of a systematic search for pika sign as well as characterization of habitat variables including vegetation type and cover.

**COLLECTION OF GENETIC SAMPLES**

We obtained genetic material from pika fecal pellets. Non-invasive genetic sampling provides the benefits of enabling collection of a large number of samples without the need to trap individual pikas. Fecal samples were collected according to three sampling schemes: random, from within the occupancy survey plots; opportunistic, while travelling between survey sites; and targeted, while exhaustively searching an area identified as potential habitat. Only the freshest fecal samples available were collected as older, degraded fecal samples will not yield high quality DNA. Fecal samples were handled to avoid contamination with other fecal samples and human DNA. Samples were placed in paper coin envelopes and stored in a cool, dry place.

**LAB TECHNIQUES**

We conducted lab work in the Epps Population Genetics Laboratory and the Center for Genome Research and Biocomputing (CGRB) at Oregon State University. DNA was extracted from fecal pellets according to a modified AquaGenomic Stool and Soil DNA extraction protocol (MultiTarget Pharmaceuticals LLC, Salt Lake City, UT, USA) presented in Wehausen et al. (2004) and optimized for pika fecal pellets. We amplified a total of 24 microsatellite markers in four polymerase chain reactions using a Qiagen Multiplex PCR kit (Qiagen, Valencia, CA, USA) according to the manufacturer’s
specifications. DNA obtained from fecal pellets is relatively low quality and can result in a high rate of genotyping errors, such as allelic dropout, therefore we genotyped each individual a minimum of three times to ensure accuracy of our data.

**Preliminary Results**

**Occupancy Surveys**

Occupancy surveys were carried out if the survey plot, the area within a 12 m radius of the plot center, contained more than 10% target habitat. In 2011, seven people conducted occupancy surveys in Grand Teton National Park from 18 July to 28 September. Sixty-seven new sites were surveyed and 37 sites previously surveyed in 2010 were resurveyed in 2011. Fifty of the 104 survey sites were occupied, 31 had only old sign, and 23 lacked any evidence of pika activity within the plot. Therefore, 48% of the sites surveyed in 2011 were considered currently occupied. Ten of the 37 sites resurveyed changed occupancy status, with three being colonized in 2011 and seven being lost in 2011. This represents 27% observed site turnover. When the 2010 and 2011 results are combined, 89 of 184 sites (48%) were considered occupied.

**Collection of Genetic Samples**

Fecal samples were collected at Grand Teton National Park during the same time period as occupancy surveys. In 2011, a total of 270 fecal samples were collected. Of those, 189 were collected in association with an occupancy survey. A total of 383 fecal samples were collected at Grand Teton National Park between 2010 and 2011 (Figure 3).

**Lab Techniques**

Of the 383 fecal samples collected at Grand Teton National Park, DNA has been extracted from 280. Fecal samples, while relatively easily collected in the field, are more difficult to work with in the lab because prolonged exposure to moisture, variable temperatures, and sunlight degrade the DNA. We have successfully genotyped 228 individuals, representing an 81% success rate of our fecal DNA extractions.

Another common obstacle encountered with fecal DNA is contamination with other pika DNA. There are four main sources of pika to pika DNA contamination. The first two are related to the behavior of American pikas. Like other lagomorphs, pikas are coprophageous and ingest their own feces as well as the feces of other pikas. This behavior could potentially lead to the DNA from one pika ending up in the feces of another pika. A second behavior of pikas that may lead to contamination is the use of latrines. Pikas are highly territorial and territories are re-used by subsequent individuals. Pikas defecate in huge piles, or latrines, that contain the feces of multiple individuals (Figure 4). If fecal pellets from one individual are touching pellets from another individual, then DNA may be transferred from one pellet to another via physical contact. The remaining two sources of contamination are the result of human error either in the field while collecting pellets, or in the laboratory while processing samples. If a sample is contaminated, it is very difficult to determine the specific source of contamination because there are so many potential sources. Regardless, contaminated samples must be excluded from all analyses. Of the 228 individuals successfully genotyped, 20 were contaminated representing less than 9% of the samples processed.

Figure 3. Collection localities of pika fecal samples in Grand Teton National Park for the 2010 and 2011 summer field seasons.

The approximately 200 samples successfully genotyped for all microsatellite markers will be used to characterize genetic diversity and connectivity
within Grand Teton National Park. Additionally we will develop habitat-specific models of gene flow to understand how distance and intervening habitat affect successful dispersal of pikas. Finally, we will conduct a vulnerability assessment for American pikas based on climate projections and information gained through the predictive habitat models and gene flow models. We will compare among National Parks to gain a more comprehensive understanding of the factors affecting pika persistence.

Figure 4. Pika latrine with feces from multiple years and likely multiple individuals.

For additional information on this project, please visit the Pikas in Peril website: http://science.nature.nps.gov/im/units/ucbn/monitor/pika/pika_peril/index.cfm

◆ ACKNOWLEDGEMENTS

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◆ LITERATURE CITED


THE EFFECTS OF A COMPLEX TROPHIC STRUCTURE OF MAMMALIAN HOST SPECIES ON THE ECOLOGY OF EMERGING INFECTIOUS DISEASES

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UNIVERSITY OF MISSOURI-SAINT LOUIS

ABSTRACT

Wildlife-parasite interactions among both ectoparasites and haemoparasites and their hosts are not well known among North American mammals, particularly in the case of relatively intact and complex communities of mammals that include top-level predators, large herbivores and a wide variety of rodent species. Understanding the distribution of haemoparasites among potential mammalian hosts can indicate links between hosts, biological vectors, disease agents, and human disease risk. This study examines the role and effects of a complex community of mammalian host species in maintaining the overall health of the ecosystem. Thereby, it explores the indirect and direct effects of wildlife in preventing the emergence of human infectious diseases depending upon land-use change/vegetation cover and host species richness.

INTRODUCTION

This survey of haemoparasites will provide a first look at the haemoparasite status of mammal populations in western US. This might elucidate possible predator-prey parasitic interactions through a detailed characterization of the trophic network, and form the basis for investigating the community ecology of zoonotic mammalian infectious diseases. Empirically examining the potential protective role of the trophic complexity of mammalian communities is a novel field, which just has been proposed theoretically. However its real effects on the ecosystem and in human health have yet to be documented.
This project combines the fields of disease ecology, epidemiology, and conservation. Exploring how preserving high species diversity in mammal communities, along with a strong complexity in all its trophic levels, can have an intrinsic measurable value to human health, it will be used to address conservation policies. Emerging infectious disease (EID) risk models will directly benefit the human populations, bringing together new land-use management strategies that will benefit humans as well as protect wildlife.

**Project Description**

Grand Teton National Park (GTNP) and Yellowstone National Park (YNP) are the largest protected areas within the Greater Yellowstone Ecosystem (GYE) and, at the same time, they are the largest semi-intact northern temperate zone ecosystem on Earth. In fact, this area has substantially more large carnivores and large ungulates that, although endemic to the area, were reintroduced to YNP after the gradual loss of habitat and deliberate extermination programs that led to their demise throughout most of the United States in the early 1900s. By 1926, when the National Park Service ended its predator control efforts, there were no gray wolf packs left in YNP, no cougars, no wolverines and almost no grizzly bears, etc. In the decades that followed, the importance of gray wolves, for example, as part of a functioning ecosystem came to be better understood (Ripple and Beschta 2004, Schmitz et al 2008.), and the gray wolf was eventually listed as an endangered species throughout its traditional range except Alaska. Research after its devastation, and on the recovery and restitution of the Great Yellowstone area, has shown the value of diversity for the performance and complex trophic structure of this ecosystem (Ripple and Beschta 2004, Schmitz et al 2008.).

However, other aspects of the beneficial value of a complex community of mammals in terms of a healthy ecosystem and therefore lower emerging infectious disease (EID) risk has not been deeply explored yet. Mechanisms of disease transmission are determined by the capabilities of the pathogens, by the immune system of the host, role of vectors, interactions between haemoparasites as well as interactions among the species making up the host network. The diversity and distribution of haemoparasites in any large mammal fauna, including the flagship GYE, are virtually unknown, outside of a few diseases having economic importance for livestock and public health (e.g. brucellosis, tuberculosis, chronic wasting disease). However, many diseases are endemic to North America but are not well understood in terms of transmission factors, prevalence, and contagiousness. Many of these pathogens nowadays are considered to be potential EIDs that could spread to adjacent areas with climate change, land-use shift and the expansion of distributions of the natural vectors of such haemoparasites. This study will be focused in rodent-borne diseases/tick-borne diseases and mosquito-borne malaria that have a high value for human public health as zoonotic diseases as well as for the unknown natural history of the mammalian community network of the GYE. Pathogens from the following genera will be targeted: *Plasmodium, Rickettsia, Babesia, Borrelia, Ehrlichia, Hepatozoon, Anaplasma, Theileria, Francisella* and *Trypanosoma*.

To accomplish this project, small rodent species were captured and screened for blood parasites and ectoparasites in spring and summer of 2011 within the GYE. Sites were chosen by land-use/vegetation cover. Small blood samples from trapped individuals were collected and kept in lysis buffer/FTA cards. All the animals were released unharmed after blood sampling and ectoparasite collection. Collaborative efforts lead to collection of
blood/tick samples from large predators, mesocarnivores and ungulates. Parasite DNA isolated from mammalian blood samples is being analyzed using the polymerase chain reaction (PCR) and reverse line blot (RLB). DNA sequencing, as well as visually examination of blood smears, will be carried out to identify the haemoparasites, mentioned above, in the blood and in ticks/fleas samples.

SCIENTIFIC SIGNIFICANCE

No comprehensive study has been undertaken of the pathogen community in the GYE using PCR, RLB and DNA sequencing to screen for mammalian haemoparasites. To date, studies have been limited to eimerias, coccidias, and general gastrointestinal parasites of small rodents, ungulates and some carnivores. Some viruses, such as distemper, rabies, and canine parvovirus have been detected in wolves (Smith and Almberg 2007) and brucellosis has been studied in ungulates (Treanor et al. 2007). Mammalian haemoparasite status, zoonosis transmission, parasite sharing among hosts, and biological vectors are poorly known among mammals of western North America in general. The influence of predators on haemoparasite diversity and infection levels in large herbivores and small mammals also is poorly understood (Cross et al. 2009). At this point, a crucial step towards understanding the influence of parasites on mammal populations and EID risk is simply to describe the distribution of parasites within the entire mammal community and characterize the interconnections between pathogens, ectoparasite vectors, hosts species and land-use.

Finally, the field work described in this brief report will provide the basis for the second, third and fourth chapters of the graduate student’s dissertation, which will be an integrative study of mammal species that are connected through trophic and parasitic networks. The GYE, which is the last example of a well-conserved temperate ecosystem in the northern hemisphere, will be a first step towards characterizing the haemoparasite community in a mammal community with a full complement of top predators. Hopefully, this work will help to clarify the favorable influence of carnivores and large herbivores and other less known interactions on parasite infections dynamics. Moreover, one of these benefits might be decreasing the risk of human EIDs transmitted by rodents which would be expected to reduce the negative perception of the local community toward these animals.

Materials and Methods

Study area:

The field study was located in the GYE, in Grand Teton National Park (43°44′0″N 110°48′12″W). Field sites were specifically located at: AMK ranch, Two Ocean Lake, Triangle X Ranch, and pastures close by the Moran entrance.

Mammal trapping:

To collect blood samples from small mammals, we used 110 Sherman live traps placed at ~10-meter intervals in 10 transect lines of 100m length.

Traps were located with respect to previous evidence of small rodent trails, feces, or rodent activity. Seven parcels were chosen for this purpose, divided by anthropogenic disturbance and land-use/vegetation cover: 1 grazing plot, 1 horse ranch, and 1 settlement as part of the highly disturbed areas lacking large mammals and 1 pristine wet meadows, 1 pristine meadow, 1 pristine sagebrush plot, and 1 pine/willow forest as part of the undisturbed areas where a complex trophic structure in the mammalian community is expected to occur. This effort was achieved by one doctoral graduate student as project leader, one undergraduate field assistant, and one additional field assistant with vast veterinary technician training. Oats, sunflower seeds and dry raisins were used as bait and occasionally mixed with peanut butter. Traps were baited at sunset and checked the following morning at sunrise. Traps were maintained closed during the day and at night they were provided cotton balls to avoid hypothermia. Trapping was done during 5 consecutive nights on average. All traps were numbered; all sites were marked using colorful flagging and also were GPS georeferenced. All individuals captured were identified with numbered ear tags, weighed, sexed and released unharmed (see appendix for the details on rodents trapped).

Blood sample collection:

When an animal was captured, the Sherman live trap was placed for 3 minutes inside of a chamber composed of a clear plastic box (58x43x35 cm) with a snap-on lid and a petri dish containing 5 cotton balls soaked with 15ml of Isoflurane. Otherwise, Isoflurane was administrated using a nose cone made of a 50 ml falcon tube (30 x 115 mm polypropylene) with 3 cotton balls soaked with 5 ml
of Isoflurane, which induces anesthesia in about 0.5 min.

Mammals easily recovered from the anesthesia in 3-5 min (Parker 2008). From each anesthetized small (<100 g) mammal, we collected blood in a 40-μl capillary tube from the sub-mandibular vein or saphenous vein, and as an alternative a retro-orbital plexus puncture (Table 1). Part of the sample was preserved in Longmire’s lysis buffer/FTA cards and part was used to make a smear. This blood collection protocol was chosen since this method is the least invasive among others described for small size mammals (Van Herck 2001).

Table 1: Rodent blood samples collected at GTNP.

<table>
<thead>
<tr>
<th>Species</th>
<th>Numbers collected</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tamias amoenus</td>
<td>3</td>
</tr>
<tr>
<td>Tamias minimus</td>
<td>18</td>
</tr>
<tr>
<td>Spermophilus beecheyi</td>
<td>20</td>
</tr>
<tr>
<td>Zapus pinax</td>
<td>20</td>
</tr>
<tr>
<td>Sorex vagrans</td>
<td>12</td>
</tr>
<tr>
<td>Zapus olympiae</td>
<td>10</td>
</tr>
<tr>
<td>Eutamias flavipes</td>
<td>1</td>
</tr>
</tbody>
</table>

**Blood sample aliquots:**

Biological samples from large mammals were obtained through collaboration with established research groups that already have collected blood samples from wolves, elks, bison, snowshoe hares, jackrabbits, wolverines, grizzly bears (Appendix 1).

From those blood samples, were taken aliquots of up to 3 drops of either: whole fresh/frozen blood, or the same volume of buffy coat and red blood coagulate; or whole blood with EDTA, into of each cryotube filled with Longmire’s lysis buffer. Then, the mixture was shaken well by inverting, thus the mix was homogenized. The new sample was stored in a -20Cº or -80Cº freezer at UMSL. Information regarding mammal species, date of collection, sex, age, weight, GPS coordinates and blood source type (whole, frozen, EDTA, etc) was recorded.

Collaborative agreements were established during 2011 with the National Park Service—YNP, USGS-NOROCK, US Forest Service, Montana Fish, Wildlife & Parks, and with the Montana State University. The agreements consist solely in sharing blood samples from wolves, elks, bison, snowshoe hares, jackrabbits, wolverines, grizzly bears, and as an alternative a retro-orbital plexus puncture (Table 1). Part of the sample was preserved in Longmire’s lysis buffer/FTA cards and part was used to make a smear. This blood collection protocol was chosen since this method is the least invasive among others described for small size mammals (Van Herck 2001).

**Ectoparasites collection:**

Each trapped mammal was checked through direct visual inspection and ectoparasites were collected with anatomical fine tweezers. Ectoparasites (ticks and flies) were kept in Eppendorf vials for 24 hrs in order to let the blood meals with the host DNA be thoroughly digested (Schall and Smith, 2006). The parasites were then preserved in 1 ml 70% ethanol (Beveridge et al. 1985), frozen and subsequently lyophilized. Hence, it was possible to preserve the ectoparasite DNA until it can be processed in Dr. Ricklefs’ lab.

**Molecular analysis:**

To identify haemoparasitic organisms, DNA extracted from the collected samples (blood and ectoparasites) were subjected first to RLB assay which was carried out to assess in a cost-effective way the identification of bacterial and piroplasma haemoparasites from the collected samples. DNA of the pathogens was amplified by multiplex PCR using biotin-labeled general primers for eubacteria and piroplasma. 5'-end amino-link species-specific probes were blotted in lines using Miniblotter 45 (Immunetic, Cambridge, MA). Results were detected by using a chemiluminiscent substrate in x-ray film (Allan et al. 2010, Pichon et al. 2003). This assay has the advantage of screening 43 samples against 44 different probes, therefore it is an excellent screening tool for the first stage of the molecular analysis. In addition, PCR will be carried out using taxon-specific primers. In the case of positive infections, 18S rDNA, 16S rDNA, mitochondrial cytochrome b, or other...
specific genetic markers will be sequenced for parasite identification. According to objectives established in this project, we will identify Plasmodium, Rickettsia, Babesia, Borrelia, Ehrlichia, Hepatozoon, Anaplasma, Theileria, Francisella, and Trypanosoma haemoparasites. Thus, we will use specific primers to these haemoparasites. DNA sequencing will be done by the Genomics Core Facility- PennState.

**NEW DATA**

The field season proposed for 2012 will provide data from 24 new sampling sites and as a result about 1,300 new rodent samples from the GYE area. These sites will be distributed in a block design, having 4 blocks containing the treatment plots. Accordingly, the same lab analysis will be performed on the new blood and ectoparasite samples. Blood samples obtained in 2012-2013 from collaboration will be analyzed by the same methodology described above.

![Map of proposed 2012 field season](image)

**Figure 2. Map of proposed 2012 field season.**

**PENDING ANALYSIS**

Lab analysis: RLB, PCR and DNA sequencing.

1) Phylogenetic analysis of the pathogen’s DNA sequences obtained. Published pathogen sequences in GenBank will be used as alignment template; MEGA 5 will be used for this purpose. Phylogenetic tree building will be made for each pathogen species found using Geneious. Phylogenetic tree visualization will be corrected with FigTree.

2) Statistical analysis: Logistic regression will be used to find a set of independent variables such as sex and age that might be responsible for haemoparasites species prevalence differences within host species. Student’s t-test will be performed to determine if there are significant differences between the mammalian host parasitemias of highly disturbed areas compared with pristine areas (land-use/vegetation cover).

3) Spatial relationships using GIS will analyze in a visual fashion the risk of EIDs depending upon rodent species abundance and richness, haemoparasites prevalence, plot location in relation with human settlements, individual specific location and geographic characterization.

4) Trophic network modeling will incorporate mammalian host-haemoparasite-vector interactions and disease transmission dynamics in a metanetwork, which will shed light on the relationships between diversity of pathogens (e.g. pathogens aggregation) and the complexity of the mammalian community.

**INTERPRETATION**

1) High richness of haemoparasites, but in low prevalence in the mammalian community, would be interpreted as a proxy for ecosystem healthiness and for low EID risk.

2) Low richness of haemoparasites, but high prevalence of the most pathogenic species, in the host species would be interpreted as low ecosystem healthiness and high EID risk.

3) EIDs would be also studied by location, proximity to human settlement, level of disturbance (land-use) and abundance of rodent species. Therefore, it would be possible to infer the dynamic patterns of disease transmission and risk.
4) Identification of the pathogens present in the rodent mammalian community would provide the possible reservoir of each studied disease.

The data generated with this project will enhance the knowledge of the ecology of infectious diseases of the North American mammalian fauna, uncertain until now. Conclusive data regarding the distribution and dynamics of these pathogens associated with the trophic structure of certain areas can lead to a better understanding of disease risk and spread. This work also will provide a direct insight in the role of carnivores and large herbivores as modulators of disease transmission and hopefully the interpretation of the results will be useful to conservation policy makers and for promoting the study of the ecosystem health/functioning as a cohesive unit.

**Detail of the Broader Impacts of the Proposed Activities**

This project addresses a major gap in current knowledge and understanding of EID dynamic patterns and risk factors through an empirical study of the semi-pristine area of the GYE. This comprehensive in-situ study integrates a diverse array of disciplines such as disease ecology, epidemiology, and conservation, which will lead to increased understanding of the role of a complex trophic structure in disease dynamics.

Exploring how preserving high species diversity of a mammalian community, along with a strong complexity in all its trophic levels, can have an intrinsic measurable value to human health, which will be used to address conservation policies and management. EID risk models will directly benefit the human populations, bringing together new land-use management that will benefit humans as well as protect wildlife.

This project currently promotes, and it will continue to do so throughout its extent, collaboration among several governmental agencies such as YNP-National Park Service, Northern Rocky Mountain Science Center-U.S. Geological Survey, U.S. Forest Service, Montana Fish, Wildlife & Parks and Ecology Department of the Montana State University. In addition, the interdisciplinary nature of this research provides many opportunities for undergraduate students to be involved in hands-on field and lab research as part of an undergraduate mentoring program. In addition, this research project supports the doctoral dissertation research of a graduate student. Outreach will be focused in the local communities, general public and tourists of GYE, as well as through the broad dissemination through scientific publications and presentations in scientific conferences.

**Acknowledgements**

We are grateful to the UW-NPS Research Center, for logistic support; especially to Dr. Henry Harlow who gave the necessary pieces of advice and support concerning this project. The authors thank D. Smith, D. Tyers, P. Cross, C. Schwartz, C. Whitman, M. Haroldson, J. Treanor, R. Wallen, R. Garrott, N. Anderson, and C. Gower for the willingness to provide blood aliquots of large carnivores, mesocarnivores, ungulates and lagomorphs, crucial for this project. L. Andrews for invaluable help with rodent trapping and sampling the animals. R. Thach for assistance and advice in laboratory analysis. Scientific Research Collecting Permits: Grand Teton NP permit #GRTE-2011-SCI-0050, Wyoming Game and Fish Department permit # 33-822, Montana Wildlife Bureau permit # 2011-039, Idaho FG Wildlife Bureau permit # 110308. U.S. Department Of Justice: Drug Enforcement Administration Registration #RG0398621, Schedules 2, 2N, 3 and 3N. This project was conducted under approved University of Missouri-St. Louis Institutional Animal Care and Use Committee, Protocol # 09-11-09.

**Literature Cited**


**APPENDIX**

**Appendix 1**

**COLLABORATIONS**

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<th>Institution</th>
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ALTERED FORAGING BEHAVIOR UNDER VARYING FOOD QUALITY: DOES INCREASED FEEDING EFFICIENCY MEDIATE THE INVASION SUCCESS OF THE SNAIL, Potamopyrgus antipodarum?

BRENDA K. HANSEN • UNIVERSITY OF WYOMING • LARAMIE

ABSTRACT

Resource competition can shape the species composition of an ecosystem. In environments where nutrients are limited in either quantity or quality, the organisms best equipped to exploit these resources may gain a competitive advantage. The New Zealand mudsnail (Potamopyrgus antipodarum), a successful invader of the Greater Yellowstone Ecosystem, may benefit from such an advantage. Potamopyrgus antipodarum is a parthenogenetic snail, with high growth rates, and a high percent of somatic phosphorus (P). Consequently, these snails should have a high demand for P. Because freshwater ecosystems are often limited in P, successful animals like P. antipodarum must be exceptionally efficient at acquiring P from their food, either through effective foraging or digestive efficiency. We conducted experiments comparing the feeding rate and foraging preference of P. antipodarum and the coexisting native snail, Fossaria sp., under two levels of P (low and high). We conducted additional experiments to examine how foraging preference is altered by the presence of conspecific and heterospecific interactors. Both species consumed low P food at a higher rate than high P food. However, only Fossaria preferred high P food when given a choice between patch quality, and only exhibited this preference when they alone. Additional experiments are needed to further explore the foraging behavior of these two species, and to determine if these differences mediate the invasion success of P. antipodarum.

INTRODUCTION

The propagation of genetic material is the evolutionary driver for all species. To successfully pass on its genetic material, an animal must both survive long enough to reproduce, and reach reproductive size (or age), which requires a diet adequate in quantity and quality. As many environments are limited in food quality (Cross et al. 2005), understanding how organisms cope with dietary limitation is essential to construe population and community-level interactions, and ecosystem function. Understanding these coping mechanisms may be important when examining interactions among organisms at different trophic levels, as nutrient ratios are often mismatched between consumers and their resources, which becomes more pronounced with increasing phylogenetic distance (Sterner and Elser 2002). Ecological stoichiometry, the balance of elemental nutrients between organisms and their environment (Sterner and Elser 2002), is a valuable tool to assess the quality of available resources. Ecological stoichiometry focuses on ratios of the elements carbon (C), nitrogen (N) and phosphorus (P), as they are critical to the function of all living organisms and comprise the largest proportion of an animal’s dry mass (Sterner and Elser 2002). Carbon limitation occurs when the available quantity of food is limited. In contrast, N and P limitation occurs when available forage is poor in quality. Nitrogen is the primary component of amino acids and is thus important for protein production, while P is a major component of nucleic acids (DNA and RNA), making both elements critical for organism growth and reproduction (Sterner and Elser
2002). Because both N and P are limiting resources in many ecosystems (Sterner and Elser 2002, Cross et al. 2005), increased competitive interactions within and between species could lead to dominance by species that are better adapted to cope with limitation (Tilman 1982). This potential for a change in species composition due to competitive interactions may be of particular concern in cases where successful invaders colonize and dominate sensitive habitats. Ecological stoichiometry can help evaluate how invasive species may impact a native community by investigating potential changes in nutrient availability and competition for resources.

Growth rate is directly related to somatic ribonucleic acid (RNA) content, because ribosomal RNA is required to make proteins. Consequently, in invertebrates there is a positive relationship between the amount of RNA and somatic P (Elser et al. 1990). This “Growth Rate Hypothesis” states that animals with high growth rates will have relatively low C:P ratios, because of the high levels of RNA required to support rapid growth (Elser et al. 1990, Sterner and Elser, 2002). High growth rates may facilitate invasion success by allowing organisms to reach reproductive maturity at a younger age, thus producing more generations in a given time (Stearns 1992). However, high growth rates come at the cost of an increased demand for dietary P. High P requirements of animals with elevated growth rates can be achieved by physiological and behavioral mechanisms. When faced with limited quantity or quality of nutrients, an animal may preferentially feed on high quality patches, or simply consume more food in lower quality patches (Fink and Von Elert 2006). The ability to select higher quality forage is dependent on the ability of the animal to distinguish between patches varying in quality, which may require specialized sensory structures. An animal’s foraging behavior may also be altered by the presence of potential conspecific or heterospecific interactors (Peckarsky 1996, Cope and Winterbourn 2004, Brenneis et al. 2010). Physiological responses to nutrient limitation include an increase in the retention time of food within the digestive system (which increases exposure to digestive enzymes and time for absorption) and an increase in key digestive enzyme production, thereby increasing digestive efficiency (Darchambeau 2005). For example, in a P-limited environment, several invertebrate species increase levels of alkaline phosphatase (AP), a digestive enzyme that cleaves phosphate molecules (Boavinda and Heath 1984, Bei-ping and Kang-sen 2003, McCarthy et al. 2010). Animals can improve their ability to process low-quality foods by combining more than one of these mechanisms, although physiological constraints prevent the concomitant increase of feeding rate and gut retention time. Superior foraging efficiency may contribute to the success of many invasive species in nutrient limited environments. Understanding how invasive species dominate native ecosystems is particularly important to the protection of sensitive native ecosystems, like those found in the Greater Yellowstone Ecosystem (GYE).

We compared the foraging behavior of an invasive snail (Potamopyrgus antipodarum, the New Zealand mudsnail), and a co-occurring native snail (Fossaria sp.) from streams of the GYE. Because P. antipodarum possesses high growth rates and high somatic P content (Tibbets et al. 2010), we expected that they should have a higher demand for P relative to potentially competing native animals with slower growth rates, like Fossaria (Thon and Krist forthcoming). We examined feeding rate and foraging preference for each species under two levels of dietary P. If P. antipodarum possesses mechanisms to cope more effectively with dietary P limitation, these traits may confer a competitive advantage over native grazers, and consequently may contribute to the invasive success of this snail.

♦ METHODS

Experimental Diet

To establish two levels of dietary P, we cultured the green algae, Scenedesmus acutus, in separate flasks with a nutrient medium containing identical N and either low (C:P ~ 1,119) or high (C:P ~ 203) amounts of P, so that the low P treatment contained a C:P ratio five times greater than the high P treatment (Dubberfuhl and Elser 1999). For each culture, we concentrated all of the harvested algae from one week and pipetted aliquots (0.25 mL for preference and 2 mL for feeding rate) of the solution into aluminum weigh boats. To ensure adhesion of the algae, we scuffed the bottoms of the boats using a Dremel with 120 grit bits prior to adding food. We reserved a portion of the algae for elemental analysis. Although we have not completed this work, we will measure P in each culture using the standard ammonium-molybdate blue ascorbic acid method on a DU-64 Spectrophotometer (APHA 1992). Percent C and N will be measured using a C/N analyzer at the University of Wyoming Stable Isotope Facility.
Study Animals

*Potamopyrgus antipodarum* is a world-wide invasive snail with a high growth rate (Hall et al. 2006, Tibbets et al. 2010). *Potamopyrgus antipodarum* primarily feeds on periphyton (a biofilm growing on submerged substrata that is comprised primarily of algae, with bacteria and fungi) and detritus (Haynes and Taylor 1985). Despite their small size (3-5 mm adults), in one invaded stream where *P. antipodarum* have reached a high population density, they consumed 75% of the gross primary productivity and contributed two-thirds of the ammonium demand via excretion (Hall et al. 2003). *Potamopyrgus antipodarum* was first observed in the Western United States in 1987 (Bowler 1991). In 1994, *P. antipodarum* was identified in the Greater Yellowstone Ecosystem (GYE) (Hall et al. 2003) and can occur at densities exceeding 500,000/m² (Hall et al. 2006). In a field experiment, *P. antipodarum* negatively affected growth rates of the native, rare snail species, *Pyrgulopsis idahoensis* (Riley et al. 2008) and in a laboratory experiment, at high biomass levels that occur in the invaded range, *P. antipodarum* severely reduced growth of the native snail, *Fossaria* (Bakerlymnaeae) bulimoides group (Thon and Krist forthcoming). My experiments compared the foraging behavior of *P. antipodarum* and *Fossaria*.

We collected all of the animals from the GYE during the summer of 2011. All *Potamopyrgus antipodarum* (3.5-5 mm) were collected from lower Polecat Creek, near Flagg Ranch, using aquatic nets. Animals were transported *P. antipodarum* in damp paper towels placed on ice. We collected *Fossaria* sp. (7-10 mm) by hand, from the Snake River and, using aquatic nets, from a tributary of upper Polecat Creek on the Boundary Trail of Grand Teton and Yellowstone National Park. *Fossaria* sp. were transported in five gallon buckets filled with stream water. We froze 100 individuals of each species upon return for C:N:P analysis (see methods in “Experimental Diet). The remaining animals were housed in aquaria located in the UW Zoology and Physiology Animal Facility, under a 12 hour light cycle. We maintained the temperature at 23 °C and changed the stock water every three days. Prior to the experiment, animals were fed an *ad libitum* diet of organic leaf lettuce, goldfish flakes and algae pellets.

Feeding Rate

To determine whether either species compensates for low quality food by increasing feeding rate, we housed thirty replicates of each species in 300 mL chambers and provided a single boat containing a pre-weighed amount of low or high P food. To ensure that a measurable amount of food was consumed, we used multiple animals in each replicate. Because individual *Fossaria* are approximately 15 times larger than individual *P. antipodarum*, we compared species treatments using equal biomass, rather than an equal numbers of individuals. To minimize intraspecific competition in the *P. antipodarum* treatments, we used 60% of the *Fossaria* biomass, so that each *Fossaria* replicate contained three individuals, while each *P. antipodarum* replicate contained 30 individuals. All snails fasted for three days prior to running experimental trials. Following a three-hour feeding period, we removed boats, placed them in a drying oven for 24 hours and re-weighed them to determine how much algae was consumed. We analyzed the data using one-way ANOVAs for each species, with P level as a fixed factor.

Foraging Preference

To determine whether either species preferentially feeds on high quality food, we placed an individual, marked snail (target) in 300 mL chambers and placed a single low P and single high P boat (3.5 mm diameter), evenly spaced in the center of the chamber. To determine whether foraging preference was altered by the presence of an interactor, we had three treatments for each species. In the first treatment, the target was alone, in the second and third treatments the target was with a single conspecific interactor or a single heterospecific interactor respectively. We recorded each eight-hour trial using a high definition video camera. For each trial, we documented the amount of time the target spent on each food type and, when present, the activity of the interactor. We calculated preference as:

\[
\text{Preference} = \frac{\text{Target time on high P}}{\text{Total time spent on high P and low P}}
\]

We compared preference results to the null (arcsin√0.5) using a t-test. To determine whether foraging is altered by the presence of an interactor, we conducted a one-way ANOVA for each species with treatment as a fixed factor.
RESULTS

Feeding Rate

Both Potamopyrgus antipodarum and Fossaria sp. consumed low phosphorus food at a greater rate than high P food during a three hour time period (P. antipodarum: \( F_{1, 58} = 181.5492; P < 0.0001 \); Fossaria sp.: \( F_{1, 48} = 12.8993; P = 0.0008 \); Figure 1). In both treatments, P. antipodarum consumed more food, per unit mass than Fossaria.

Feeding Preference

Preliminary results from the feeding preference experiments were only conclusive for Fossaria sp. because only three replicates of P. antipodarum (two from the conspecific treatment and one from the heterospecific treatment) fed during the trials. When alone, Fossaria sp. exhibited a significant foraging preference for high P food (\( T_{21, 1} = 2.1254; P = 0.0228 \); Figure 2), however Fossaria sp. showed no preference when a conspecific or heterospecific snail was present (\( T_{15, 1} = -0.7401; P = 0.7659 \) and \( T_{17, 1} = 0.950; P = 0.1777 \) respectively). In addition to displaying preference for high P food, when alone, Fossaria spent significantly more time foraging than they did in the presence of a conspecific (\( F_{2, 65} = 3.6791; P = 0.0306 \); Figure 3).

DISCUSSION

Understanding the relationship between nutrient needs and the complex interactions occurring among species and their environments is especially important as we witness dramatic decreases in global biodiversity. Invasive species are among the leading threats to biodiversity (Sala et al. 2000), and ecosystems in the GYE are not immune to this threat.
The increased feeding rate of nutrient limited resources has been shown in several studies (Suzuki-Ohono et al. 2012). In nitrogen deficient environments the grasshopper, *Omocestus viridulus*, partially compensates by increasing feeding rate (Berner et al. 2005). In another study, the snail, *Radix ovata*, also responded to N and P limited food by increasing food consumption (Fink and von Elert 2006). In our experiments, both the invasive, *P. antipodarum*, and the native snail, *Fossaria* sp., also responded to low quality food by increasing their feeding rate. However, neither species was able to fully compensate for the difference in the low P diet by increasing feeding rate alone. To approximate the total amount of P intake possible in the high P treatment, each species would have needed to increase their rate of low P consumption by a factor of five. However, *Fossaria* only compensated for 50% of the difference in the low P treatment, while *P. antipodarum* did only slightly better by compensating for 66% of the difference in P. We will be able to provide a more accurate estimate of compensation when we complete the C:N:P analyses of both animal species. The higher total amount eaten by *P. antipodarum* relative to *Fossaria* under both food types is likely an artifact of an increased mass-specific metabolic rate in the much smaller (~15 times) *P. antipodarum* (Karasov and Martinez del Río 2007).

In addition to compensatory feeding, some organisms are able to increase their feeding efficiency by preferentially consuming higher quality resources. Along with increased consumption of poor quality resources, when N-rich forage is available, *O. viridulus* will preferentially consume the higher quality food over the low quality food (Berner et al. 2005). Similar results have been found for zooplankters and caddisflies (Fulton 1988, Butler et al. 1989, Hart 1981). Consistent with these studies, my results suggest that *Fossaria* is able to distinguish between the quality of food patches (with respect to P), which may enable it to compensate more fully in variable environments. While too few *P. antipodarum* fed in these experiments to make any conclusion about feeding preference, experiments that we conducted using a different algal species, the invasive snail displayed no apparent preference for high P over low P algae (Hansen, forthcoming). If *P. antipodarum* is unable to distinguish between the quality of food patches, they would need to employ additional physiological mechanisms to fully compensate for P limitation.

The presence of interactors may positively or negatively affect the foraging behavior of organisms (Brenneis et al. 2010). For instance, the presence of the aggressive blackfly larvae, *Simulium virgatum*, decreases the foraging activity of the midge, *Blepharicer a micheneri* (Dudley et al. 1990). Our experiments suggest that *Fossaria* reduce feeding when a conspecific is present. In our experiments, pairs of *Fossaria* in individual chambers were very active and often followed each other. At the end of the trial, we found egg masses in several chambers, suggesting that the presence of conspecific interactors changed the focus of activity from foraging to breeding, and hence the decrease in feeding was not due to competition for resources. Also, the lack of preference in the *Fossaria* conspecific and heterospecific treatments may be an artifact of small sample sizes, rather than an actual change in feeding preference (15 and 17 respectively).

In additional experiments with another algae species as the food source, *P. antipodarum* increased their feeding time considerably in the presence of a conspecific (Hansen, forthcoming). It is possible that rather than experiencing increased competition, *P. antipodarum* is facilitated by certain densities of conspecific interactors. To address this possibility of facilitation, we will conduct additional experiments with varying levels of both conspecific and heterospecific interactors. We will also repeat the Feeding Preference experiment to confirm that *P. antipodarum* does not exhibit preference for high P food, and to assess the effects of interactors and density on the foraging behavior of both species.
CONCLUSIONS

In our experiments, both the native snail, Fossaria sp., and the invasive snail, Potamopyrgus antipodarum partially compensate for phosphorus-deficient food by increasing their feeding rate. Additional experiments are needed to determine whether this behavior is similar when other nutrients are limited, and if either species is also employing other compensatory mechanisms, such as increased digestive enzyme production. As both species increase their feeding rate of low P food, it is unlikely that increased gut retention time is a factor. In addition to the compensatory feeding of low P food, Fossaria is also able to locate higher quality patches and preferentially feed on these higher quality resources, while P. antipodarum may to lack this ability.

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LITERATURE CITED


BEHAVIORAL SYNDROMES IN THE SAGEBRUSH CRICKET: A PILOT STUDY TO QUANTIFY INDIVIDUAL VARIATION IN MALE CALLING BEHAVIOR

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ABSTRACT

The field of behavioral ecology has recently been reinvigorated by the addition of the notion of behavioral syndromes (a.k.a. animal personality). Behavioral syndromes imply the existence of individual variation in behavioral expression that is consistent across distinct functional contexts (e.g. foraging, mating, anti-predator). The syndromes paradigm suggests that the behavioral phenotype is best viewed as an integrated phenomenon wherein any given behavior can only be fully understood by studying selection pressures in all contexts. Here we report on a pilot study on behavioral syndromes in the Sagebrush cricket (Cyphoderris strepitans), an acoustic Orthopteran insect that inhabits high altitude sagebrush meadows of Grand Teton National Park. The results of our preliminary analysis suggest very little consistent repeatability in the mating behavior of C. strepitans. In addition, we make note of the synergistic collaboration in our group between faculty researchers and graduate, undergraduate and high school research collaborators.

INTRODUCTION

The traditional adaptive paradigm suggests that, over time, natural selection acts to drive phenotypes towards an optimal expression (Figure 1). While the evolutionary power of natural selection is not in question, most evolutionary ecologists work from the underlying assumption that many forces constrain adaptation. For example, available sources of genetic variation limit the types of traits that can be favored by natural selection.

In contrast to this the notion of unbridled plasticity, the field of behavioral ecology has recently been reinvigorated by the notion of behavioral syndromes (i.e. animal personalities; reviewed in Sih et al. 2004, 2010; Figure 2). A behavioral syndrome is individual variation that is consistent across distinct functional contexts. For example, Riechert and colleagues studied behavioral syndromes in the funnel web spider, Agelenopsis aperta. Funnel web spiders demonstrate positive correlations among aggression toward prey, including superfluous killing, boldness toward predators, aggression toward conspecifics, and the size of territory defended. Controlled crosses revealed a genetic basis (probably pleiotropy) to these behavioral correlations (see references in Maupin and Riechert 2001 Riechert and Maupin, 2008). In addition to being correlated at the individual level, these behaviors are also correlated at the population level. Riparian populations of A. aperta enjoy six times higher prey availability but

![Figure 1. The traditional adaptive paradigm suggesting extensive adaptive plasticity.](image-url)
suffer significantly higher predation risk relative to their counterparts from grassland populations. As one might predict then from a traditional adaptive paradigm, spiders from riparian populations are significantly shyer toward predation risk, less voracious toward prey, less agonistic toward conspecifics, and defend smaller territories than grassland spiders. However, what is most interesting is that within the adaptive modulation going on across populations, we continue to see correlations at the individual level. In other words, although riparian spiders are, on average, shy toward predation risk, some individuals from riparian populations continue to show high levels of boldness toward predators, and this individual variation can be explained by the fact that these bolder individuals are also more voracious toward prey. Conversely, grassland populations are, on average, more voracious toward prey, but some individuals continue to show low voracity toward prey, and this can be explained, at least in part, by the fact that these individuals are also exceedingly shy toward predators (Riechert and Hedrick 1993). This work provides a beautiful illustration of the tug-of-war occurring between adaptation to one’s environment at the population level and potential constraints arising from behavioral correlations occurring at the level of individuals.

More recently, Johnson and Sih (2005, 2007), working with the semiaquatic fishing spider *Dolomedes triton*, investigated a connection between behavioral syndromes and precopulatory cannibalism by females on courting males. Precopulatory sexual cannibalism can be puzzling from an evolutionary point of view particularly when it results in females not mating enough to fertilize their eggs (Arnqvist and Henriksson 1997). The adaptive foraging hypothesis (Johnson and Sih 2005) explains precopulatory sexual cannibalism by positing that females that had poor foraging success on other prey (e.g., crickets) might be willing to risk the cost of lost reproduction in favor of the benefits of food. Contrary to this hypothesis, Johnson and Sih found that females that most readily attack males are the voracious females that had the highest levels of recent foraging success on other prey. That is, female spiders exhibited positive behavioral correlations between voracity toward heterospecific prey, boldness toward predation, and tendency to attack males. These data are consistent with the hypothesis that precopulatory sexual cannibalism reflects a carryover of voraciousness toward prey, in general, onto voraciousness toward potential mates.

Subsequent studies showed that this carryover is not absolute: if a female grew up experiencing low availability of males, then she is less likely to engage in sexual cannibalism (Johnson and Sih 2005).

Thus, the extent to which animal behavior is driven by adaptive plasticity versus constraint is a pressing question in the current field of behavioral ecology. To address this issue, more studies on more taxa need to follow individuals through their lifetime: 1) documenting the repeatability of an individual’s behavioral expression within a context, and 2) looking for the across-context correlations that are the hallmark of a behavioral syndrome. Here we approach the mating behavior of the sagebrush cricket, *Cyphoderris strepitans*, with the behavioral syndromes approach.

**STUDY SYSTEM**

*Cyphoderris strepitans* is an acoustic Orthopteran insect from the family Haglidae. Sagebrush crickets emerge soon after snowmelt in high-altitude sagebrush meadows. Several populations residing within and around Grand Teton National Park have received considerable attention (e.g. Sakaluk 1991, Sakaluk and Sneddon 1990, Sakaluk et al. 1987, 1995, 2004).

Of particular interest is the mating system of *C. strepitans*. Male sagebrush crickets stridulate (call) to attract females for mating. Calling song is produced by a file and scraper mechanism found on opposing edges of the male’s calling wings, the tegmina (Figure 3). However, upon mounting a male, females begin to chew on a pair of fleshy hind wings located underneath the tegmina (Figure 3). These
fleshy hind wings then produce hemolymph which the female consumes while the male is busy transferring an external spermatophore to the female. Thus, the mating system of sagebrush crickets is characterized by a non-lethal form of sexual cannibalism—females consume irreplaceable male body parts, but males are not prevented from mating again in the future (Figure 4).

Sexual cannibalism has been argued to be an ideal target behavior in the study of behavioral syndromes as it so naturally combines the distinct functional contexts of foraging and mating behavior into an integrated context (Johnson, 2001). For example, the fishing spider case study discussed above nicely illustrates a case where sexual cannibalism integrates foraging, mating and anti-predator behavior. Here we present preliminary data designed to measure the repeatability of male calling behavior in the field. As per the behavioral syndromes hypothesis we predicted we would find repeatable individual variation (behavioral types) in calling behavior.

**STUDY AREA**

We focused study on a small sub-population of Sagebrush crickets from the Lower Dead Man’s bar population (Figure 5). Our study site was bounded to the North by a steep drop from the meadow to the Snake River, to the South by a dirt road, to the East by forest, and to the West by a small hill below which were more sagebrush bushes. Thus, while this was a reasonably-sized discrete area with an abundance of sagebrush and crickets, the habitat continued to the

**METHODS**

Our 2011 field season ran from June 1 through June 11. Much of our time in Wyoming was limited by rain, which combined with cold temperatures can limit calling behavior for the entire night. Nevertheless, we measured the calling behavior of 18 different males in the field. After this initial field measurement we collected all males and transported them to the laboratory where they were weighed to the nearest milligram and given a unique I.D. tag secured to the pronotum. Marked males were then returned the next day to the base of the bush they were found calling from. On subsequent nights we recorded repeated measures of the calling behavior of these males (N=15 males scored twice; N=9 males scored three times; N=6 males scored 6 times).

**PRELIMINARY RESULTS**

We found no significant differences across repeated measures in calling behavior. Figure 6 shows that the number of calling bouts across repeated measures did not vary ($F_{3,15} = 0.452$, $p=0.72$). Figure 7 shows that calling duration did not differ across repeated measures ($F_{3,15} = 0.937$, 0.376, 0.299, 0.176)
p=0.45). Figure 8 shows that average calling bout length did not vary across repeated measures (F_{3,15} = 1.23, p=0.33). Thus, across time, we found no evidence that crickets changed their calling behavior.

Despite the above analysis suggesting that crickets are calling similarly between repeated measures, we found no evidence of consistent individual variation across repeated measures. In other words, we found no evidence of behavioral calling types in the Sagebrush cricket as crickets did not display consistency in number of calling bouts (Intra—class correlation coefficient = -0.259, F=0.180, p=0.97), calling duration (Intra—class correlation coefficient = -0.553, F=0.288, p=0.99), or average bout length (Intra—class correlation coefficient = -0.078, F=0.711, p=0.63). Lastly, a male’s calling behavior (bout number and calling duration) was not positively correlated with his foraging behavior (measured in the laboratory as mass after a night of laboratory feeding – mass at collection) as would be predicted by the behavioral syndromes hypothesis. However, we did find a marginal, but significant, trend for males that had longer average bout lengths to also gain more weight in lab feedings (r= 0.410, p=0.045; see Figure 9).

While our preliminary analyses do not seem to support a behavioral syndromes hypothesis, they are also surprisingly inconsistent with the more traditional adaptive notion that a male’s calling behavior should be dependent on his current condition—allowing high-condition males the plasticity to call a great deal. Instead, we found no relationship whatsoever between a male’s calling behavior (bout number, average bout length and calling duration) on the night of first capture and his body condition (mass/body length) measured later that night (Pearson correlation, all p>0.05).
Figure 9. A marginal but significant positive correlation between mass change after a night of lab feeding and average bout length.

**DISCUSSION**

We were disappointed to find no evidence of a behavioral syndrome, and shocked to find no relationship between male body condition and calling behavior. These results leave us wondering what is, in fact, driving male calling behavior. We do know that male calling is severely compromised after mating behavior (Sakaluk et al., 1987, Sakaluk and Sneddon, 1990). This, however, could not explain the results of this study as we focused our efforts in the first few days of the mating season and each of our males were virgins at their first capture as evidenced by their intact hindwings. One possible confound could be the lack of power in our dataset from the compromised sample size we were able to secure in a brief field season fraught with rain and cold. Indeed, male calling behavior from night to night was very clearly enhanced by warmer temperatures in the absence of precipitation. These abiotic factors, especially early in the breeding season may drown out any smaller effects of behavioral syndromes and/or condition-dependent adaptive plasticity.

One way to remedy this problem would be to collect virgin males and conduct calling assays in a controlled laboratory setting. While this may be worth consideration, it must be noted that calling behavior in ideal lab settings will not allow us to gain an understanding of the behavioral phenotype of Sagebrush crickets experiencing field conditions. One compromise approach would involve the construction of field mesocosms where a sagebrush bush is surrounded by metal flashing to isolate and contain a focal male cricket, and some type of shelter over the bush is constructed. Thus, by removing precipitation, we suggest male calling behavior could be more readily quantified in the field without losing all of the complexities that field measurements include.

Behavioral syndromes remain an exciting area of research, and while our preliminary results do not support this notion, it is worth noting that we have only addressed one behavioral context so far—male calling behavior. It may be that male calling behavior is too heavily influenced by abiotic factors to be predicted by a behavioral syndrome. As suggested above, foraging behavior and anti-predator behavior are also frequent foci of syndromes research. In particular, we were intrigued last Spring at the extent to which the activity of Robins (*Turdus migratorius*) and the onset of male calling behavior overlapped at dusk. Thus, it is our hope to run preliminary trials this year to see whether Robins do prey upon sagebrush crickets despite the wealth of anti-predator behaviors they employ. Once a realistic anti-predator assay is designed, we could then look for correlations between anti-predator behavior, foraging behavior, and mating behavior.

**BROADER IMPACTS**

Despite a bit of a disappointing dataset in 2011, we left the station more excited than ever about our future involvement in this system. This is, in large part, due to the outstanding level of interaction we were able to have with Chuck Collis and his team of high school researchers. Chuck’s group carried out an impressive mark/recapture study in collaboration with Scott Sakaluk's research group, but at the same time made time to help us with the work detailed above. This collaboration was so successful that Scott, Chuck and our group have teamed up to return this Spring for a more formal collaboration. Scott has successfully secured NSF supplemental funds to help fund this collaboration, and we believe it will be become a model for engaging students across multiple levels in field research.

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LITERATURE CITED


DOES WILDFIRE INCREASE THE RISK OF MOUNTAIN PINE BEETLES OUTBREAKS IN LODGEPOLE PINE FORESTS OF THE GREATER YELLOWSTONE ECOSYSTEM?

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**ABSTRACT**

We examined whether wildfire injury increased lodgepole pine, *Pinus contorta*, susceptibility to mountain pine beetle, *Dendroctonus ponderosae*, how it affects beetle reproduction, whether this interaction differs between endemic and epidemic populations, and how wildfire influences tree defense physiology. Wildfire predisposed trees to mountain pine beetle attack. In particular, fire-injured trees had a lower ability in synthesized monoterpenes in response to simulated attacks than did non-injured trees. However, beetles responded in a non-linear fashion; moderately-injured trees were most preferred. This interaction was influenced by beetle population size. Healthy and fire-injured trees were attacked when populations were high, but no healthy trees and no severely-injured trees were killed when populations were low. Beetle brood production per female was also curvilinear being highest in moderately-injured trees. This reflected a trade-off between high intraspecific competition arising from the large number of beetles needed to overcome defenses in healthy trees, and high interspecific competition and low substrate quality in severely injured trees.

These results suggest that fire-injured trees can provide a resource for mountain pine beetles during the extended periods when populations are not high enough to overcome defenses of vigorous trees. But the likelihood that populations could transition from endemic to epidemic levels due to increased tree susceptibility from wildfire is constrained by the opposing factors of lower nutritional quality and more competition load in severely-injured trees, and the relatively low incidence of moderately-injured trees. Wildfire may cause some reproductive increases in populations that are already in outbreak mode.

**INTRODUCTION**

Conifer forests in western North America are strongly affected by wildfire and bark beetle outbreaks (Romme and Knight 1981, Veblen et al. 1994). These disturbance agents can have interacting effects, but they are not well understood. For example, wildfire injury to trees can sometimes lead to increased rates of attack by bark beetles, but this varies with beetle and tree species, and environmental conditions. (Rasmussen et al. 1996, Ryan and Anman, 1996, Wallin et al. 2003, Hood and Bentz 2007, Six and Skov 2009).

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is of major concern throughout the western United States and Canada. It has recently caused extensive mortality throughout all of western North America (Hicke and Jenkins 2008, Hicke et al. 2006, Kurz et al. 2008, Safranyik et al. 2010). The primary host of the mountain pine beetle is lodgepole pine.

Mountain pine beetle adults emerge from their brood trees, fly, and select new host trees based on chemical cues. They enter the bark, mate, oviposit, and the larvae feed in the phloem. The resulting destruction of transport tissues kills the tree. Trees can defend against attack by employing constitutive and induced defenses, including rapid accumulation of toxic monoterpenes (Zulak and Bohlmann 2010). Bark beetle aggregation attract more beetles, and these mass attacks can overwhelm tree defenses (Raffa and Berryman 1983).

The question of whether burn injury increases susceptibility to mountain pine beetles has important policy implications, with regard to both formulating responses to wildfire and prescribing controlled burns. The population dynamics of tree-killing bark beetles are characterized by lengthy endemic periods, during which beetles occur at very low densities and attack only a few severely stressed trees, followed by large-scale outbreak (Boone et al. 2011). We do not know whether wildfires cause beetle populations to cross the critical threshold between these phases (Raffa et al. 2008).

**METHODS**

We sampled 16 lodgepole pine sites conducted in the Greater Yellowstone Ecosystem. Eight experienced wildfire, and eight were unburned. Four of the burned sites were within areas where mountain pine beetle was in outbreak, and four were in nonoutbreak areas. There were a total of 2056 trees. We measured attack, brood production and competitors within subsampled trees, and in pheromone-baited flight traps.

During 2010-2012, we mapped the spatial extent and intensity of bark beetle infestation (both new activity and older infestations) and the proximity of damage to fires. We partnered with the USGS and NPS to acquire SPOT 10m and 5m satellite imagery over most of the Greater Yellowstone Ecosystem. These images are currently being processed for two sets of analyses: 1) mapping of bark beetle damage with respect to fire locations and 2) mapping of forest vertical structure associated with long-term disturbance history and forest regeneration. The remote sensing efforts were linked to field data collected in 2010-2011.

We evaluated the defense chemistry of lodgepole pines that were uninjured or injured by wildfire. We analyzed monoterpenes by gas liquid chromatography. These measurements include both constitutive chemistry and induced chemistry in response to simulated attack.

**RESULTS**

**Responses of Mountain Pine Beetle to Wildfire**

Wildfire injury strongly influenced mountain pine beetle attack on lodgepole (Powell et al. 2012). Moderately injured trees experienced the highest rates of attack. Brood production per females was also highest on moderately injured trees. Attack densities were highest on uninjured trees, which generated high intraspecific competition and lower brood production per attack. Interspecific competition was highest on severely injured trees. The major competitors were Ips, Monochamus, and Pityogenes. Populations of predators, buprestids, and turpentine beetles were low (Powell et al. 2012).

Background populations had a strong effect on mountain pine beetle attack dynamics (Powell et al. 2012). When mountain pine beetle was already in outbreak mode, uninjured trees were attacked. We did not see this at low populations.

**Spatial Extent and Intensity of Bark Beetle Infestation Relative to Proximity and Extent of Wildfires.**

Field data included plot-based samples of mortality, red trees, newly infested trees and unattacked trees. Because accessibility to large numbers of plots in remote areas was not feasible, we additionally developed a new method in which we used infrared and visible camera with telephoto lenses to take pictures of distant slopes. Using GPS locations, bearings and camera tilt, we precisely located the photos using Google Earth to place the actual camera shot locations on SPOT images. From 47 sets of photos, we co-located 97 positions.

**Lodgepole Pine Defense Chemistry**

Total concentrations of volatiles (including thirteen monoterpenic hydrocarbons four allylic monoterpenic alcohols, one ester and one phenyl propanoid) within constitutive phloem tissue did not vary with fire injury (Powell and Raffa 2011). But the concentrations of induced volatiles decreased by nearly half with wildfire injury. These results illustrate the importance of actively induced biochemical responses in tree defense against mountain pine beetle.

Fire injury also influenced the proportions of some volatiles in both constitutive and induced phloem tissue (Powell and Raffa 2011). Some of these alterations may relate to the behavioral mechanisms by which bark beetles detect weakened trees and communicate during mass attacks.
**Management Implications**

The results of our study have implications for mountain pine beetle population dynamics, disturbance interactions, and natural resource management. Fire-injured trees appear to serve as a reservoir for bark beetles during their extended nonoutbreak population phase, when they cannot overcome the defenses of vigorous trees (Wallin et al. 2003, Powell et al. 2012).

The likelihood that population increases in fire-injured trees could trigger outbreaks, however, is reduced by increased competition and reduced substrate quality in severely-injured trees, and the lack of moderately-injured trees at the stand level (Powell et al. 2012). If an increase in population density following wildfire were to be accompanied by additional predisposing factors such as warm temperatures or drought, however, their combined effects would be more likely to favor transition to outbreaks. Wildfire could also potentially increase total beetle reproduction in stands already experiencing outbreaks.

**Current Work**

Beginning in 2009, we have been comparing the defense chemistry and physiology of whitebark versus lodgepole pines, mountain pine beetle's relative preference for each species in the field and laboratory assays, and how predators and competitors respond to mountain pine beetles in each environment. Results to date indicate that both coevolutionary history and spatial context affect these relationships. Continuing work is extending these studies to the landscape scale, to improve our ability to incorporate chemical ecology, host selection behavior, and forest structure into management strategies.

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SONG, DANCE, AND SMELL ROUTINE? INTERPRETING THE CONTENT AND FUNCTION OF MULTIMODAL SIGNALS IN A SONGBIRD, THE DARK-EYED JUNCO (JUNCO HYEMALIS)

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ABSTRACT

The study of animal communication has been dominated by a focus on signal types that are easily recognized and quantified by human observers. This approach has inevitably limited our ability to identify cryptic signals such as low-amplitude vocalizations and signals that transmit beyond the range of our sensory system, such as most olfactory signals. Only recently with the development of new technologies and less biased sampling techniques have we begun to unravel the importance and function of these non-traditional signal types. Here we report the results of two experiments focusing on poorly studied signals using a common songbird, the dark-eyed junco. We investigated the effect of low-amplitude song on male physiology and the occurrence of bill-wiping behavior during courtship and aggressive interactions. Preliminary results suggest that males do not alter their plasma testosterone or corticosterone levels in response to a song playback of high-amplitude or low-amplitude song, indicating that a stronger stimulus may be necessary to affect circulating hormones. Males that received intrusions of a live male or female conspecific performed significantly more bill-wiping in response to the female conspecific, suggesting that bill-wiping may be an important and overlooked courtship signal in this species.

INTRODUCTION

Animal communication is dependent on a variety of acoustic, visual, and olfactory signals for the successful transmission of information, such as the signaler’s behavioral intent or potentially the inherent qualities of the signaler (McGregor 2005, Searcy and Nowicki 2005). Owing to the abundance of signal types available, receivers of both sexes are often presented with multiple signals of varying types or “multimodal signals” that must be interpreted in order to gain the maximum amount of information about the signaler. These signals may be redundant and all contain the same or similar information, or they may be unique and each relate to different aspects of the signaler. For example, one signal may function primarily to identify the species of the sender, while another may transmit information about that individual’s quality (Hebets and Papaj 2005). Alternatively, one signal alone may be used deceptively (e.g., suggesting the sender is of a high quality) while the integration of multiple signals may give the receiver more accurate information (Ward and Mehner 2010). Understanding the function and information content of all potential signal types is critical for deciphering the full content of a multimodal display, such as courtship behavior.

Male Dark-eyed Juncos (Junco hyemalis), a common North American songbird, produce two distinct classes of song: (1) high amplitude (loud), long-range song (LRS) that functions in mate
attraction and territoriality, and 2) low-amplitude (soft), short-range song (SRS) that is substantially more complex than LRS and functions predominantly in courtship (Titus 1998, Reichard et al., 2011). Previous work has shown that male juncos respond significantly more aggressively to a territorial intrusion containing SRS than to an intrusion of LRS or soft LRS (Reichard et al., 2011). The striking difference in aggression towards SRS raises the question of whether males also experience a distinct physiological response to SRS. Males of many species, including juncos (McGlothlin et al., 2007), are known to elevate their circulating testosterone (T) in response to a territorial challenge containing LRS, while males of other species experience a similar surge in corticosterone (a hormone typically associated with the stress response) rather than T (reviewed in Goymann 2009). To investigate the hormonal response of male juncos to each song class, we performed territorial intrusions with LRS or SRS, quantified aggressive behavior during the intrusion, and captured males post-intrusion to take a blood sample for later hormone analyses. Additionally, to better understand the importance and function of LRS and SRS we attached microphone-transmitters (see below) to free-living male juncos to allow us to observe their natural singing behavior under unmanipulated conditions.

Another objective of this study was to investigate behavior related to chemical communication in juncos. Birds perform a “bill-wiping” behavior during courtship and aggressive interactions, in which they wipe their bills on the perch/branch/other substrate. This same motion is used to clean the bill after eating, but is considered “irrelevant” or displacement behavior in social contexts (Clark, 1970). We have observed in the lab that this motion seems to leave preen oil on perches, and we hypothesize that this is actually a scent-marking behavior.

Additionally, we have found that in two-way choice tests, female juncos prefer the scent of smaller males over that of larger males, and that odor does show a relationship with body size in male juncos (Whittaker et al., 2011). We predicted that smaller males, who are typically less visually attractive to females (Hill et al., 1999), would invest more in chemical communication during courtship, either by producing larger quantities of preen oil (and thus having a larger preen gland) or behaviorally by increasing the frequency of bill-wiping. Similar effects have been observed in insects (Thomas & Simmons, 2011) and sticklebacks (Candolin, 2000).

We tested the following hypotheses: 1) bill-wiping is a form of scent-marking important in competitive interactions and courtship and 2) smaller males invest more effort in chemical signaling to attract females.

**METHODS**

**Song Study**

**Hormonal response to song playback**

We conducted song playbacks with 40 male dark-eyed juncos near the AMK Ranch, the Grand View Point Trail, and south of the Death Canyon trailhead in Grand Teton National Park. 20 males received a song playback of low-amplitude, short-range song (SRS) and 20 males received playback of high-amplitude long-range song (LRS). All playbacks were created using methods previously reported by Reichard et al. (2011). For this study, all song playbacks were 10 min in duration. We quantified male behavior during playback and for an additional 10 min post-playback.

At the completion of the playback and 10 min post-playback observation period, we unfurled a mist net and revealed a live, male conspecific and attempted to capture the focal male. Immediately following capture we rapidly collected 50-200 ul of blood from the alar vein using a micro-hematocrit tube. Birds were then placed in a bag to simulate restraint-induced stress for 15 min. We then took a second blood sample of approximately 50 ul from the opposite wing to examine stress-induced hormone levels. Birds were then banded, measured, and released.

Control males were caught rapidly (> 5 min of playback) and bled rapidly using the same protocol as described above to allow for an estimated of baseline hormone levels. Control males did not receive the handling stress treatment and were released immediately after blood sampling and banding.

All blood samples were stored on ice before being centrifuged. Hormone-containing plasma was then drawn off with a Hamilton syringe and frozen at -20º C for transport to Indiana University. We calculated testosterone and corticosterone concentrations in our plasma samples using commercially available Enzyme Immune Assay (EIA) kits from Cayman Chemical.
Radiotelemetry

We monitored vocalizations and movements of male dark-eyed juncos using a newly developed type of radiotransmitter, the microphone-transmitter (Sparrow Systems, Inc., Fisher, Illinois). Microphone-transmitters are different from traditional radiotransmitters in that they contain a tiny condenser microphone that records and transmits every vocalization produced by the subject as well as the traditional pulse of tones important in locating the subject. Transmitters were attached by first gluing the transmitter to a small piece of cloth and then gluing the cloth+transmitter to the back of the bird after trimming a small patch of feathers. We recaptured males and removed transmitters after the battery died.

After each mic-transmitter was attached we tracked the individual for a minimum of two hours each day typically divided between early morning (0500-0700) and afternoon (1300-1700). During active tracking we took copious observations of the individual’s behavior, location, and social interactions. A stationary antenna continued to record vocalizations independently of our behavioral observations for the entire life of the transmitter.

Olfaction Study

Preen Gland Size

We measured the uropygial gland of all captured juncos following Moreno-Rueda (2010): after carefully wiping the feathers away from the gland using an alcohol wipe, we used digital calipers to measure the length, width, and height from the base of the gland to the base of the papilla. We estimated preen gland volume by multiplying the three measurements.

Bill-wiping in response to a male or female intruder

We conducted playback trials using a very similar method as the song study. Thirty male subjects who were naive to playback received two trials, at least 45 minutes apart, in random order. One trial consisted of a male lure paired with a playback of male LRS, and the other trial used a female lure paired with playback of a female trill (a sound often given by females who are interested in mating). Playback protocol was as follows:

1. Attraction playback (LRS or female trill) to alert the subjects to our presence – up to 10 minutes, until the subject has reached the playback arena;
2. Five minutes of the treatment playback, during which we recorded the subject’s behavior;
3. Five minutes of silence during which we continued to record the subject’s behavior.

Trials were video-recorded, and a shotgun microphone was also used to record any vocalizations made by the subjects. At the end of the trials, we captured the subject with a mistnet, banded it (if not already banded) and took morphological measurements. We also took a preen oil sample for later chemical analyses, stored at -20ºC until transported to Indiana University, and a small blood sample (~200µl) from the alar vein for later genetic analyses, stored at 4ºC until transported to IU.

Data analysis

Videos were scored for the following behaviors: latency to approach lure within 5 meters and within 1 meter, time spent within 5 meters and 1 meter, latency to song, number of LRS, seconds of SRS, and number of bill-wipes, tail-spreads, and flights over the cage. All data were analyzed in SPSS 20.

.Upload Preliminary Results

Song Study

Hormonal response to song playback

Males spent significantly more time within 5 m ($t$-test; $t(1,38) = -4.26$, $P < 0.001$) and 1 m ($t(1,38) = -5.01$, $P <0.001$) of the speaker when responding to SRS than to LRS (Figure 1). Males performed significantly more flights when responding to LRS ($t(1,38) = 4.00$, $P <0.001$), but did not differ in the number of songs produced in response to each playback type ($t(1,38) = -0.79$, $P = 0.437$).

![Figure 1. Mean total time spent within 5 m and 1 m of the speaker during a 10 min playback of long-range song (LRS) or short-range song (SRS).](image-url)
Plasma testosterone did not differ statistically between treatment groups (Figure 2; One-way ANOVA; F(2,57) = 0.587, P = 0.559).

**Figure 2.** Mean plasma testosterone (T) measured following a rapid capture (control) or 10-min playback with LRS or SRS.

Plasma corticosterone did not differ statistically between treatment groups (Figure 3; One-way ANOVA; F(2,55) = 1.039, P = 0.360). Males had significantly higher levels of corticosterone post-handling stress (Repeated Measures t-test; \(t(1,35) = -19.75, P < 0.001\)) than post-STI. Males did not differ in the change in corticosterone between the post-STI sample and post-handling stress sample when compared between LRS and SRS treatments (\(t (1,34) = -0.249, P = 0.805\)).

**Figure 3.** Mean plasma corticosterone (CORT) measured following a rapid capture (control) or 10-min playback with LRS or SRS.

**Radiotelemetry**

We attached mic-transmitters to 9 free-living male juncos located at or near the AMK Ranch. Data from the transmitters are still being analyzed, but we were able to record numerous examples of low-amplitude vocalizations from mated and unmated individuals in a variety of social contexts.

**Olfaction Study**

We conducted trials at 30 territories. One of these trials was deleted from the analysis because the responding subject was a female, leaving a sample size of 29 males. We also measured preen glands for 18 females and 59 males.

**Bill-wiping**

Males bill-wiped significantly more in response to female intruders (per 10 minute trial: mean 6.0 ± 1.6) than in response to male intruders (1.66 ± 0.33, one-way ANOVA, \(p = 0.015\)). When courting females, males showed a strong positive correlation between frequency of bill-wiping and frequency of tail-spread, a behavior observed during courtship in which a male spreads his tail feathers to display his tail-white (Figure 4, Pearson correlation = 0.657, \(p < 0.001\)). Males in their first adult year bill-wiped more frequently in response to females (mean bill-wipes, 13.0 ± 2.98) than older males did (3.0 ± 1.06, one-way ANOVA, \(p = 0.03\)). Wing length was negatively correlated with bill-wiping frequency in response to females (Figure 5, Pearson correlation = -0.603, \(p = 0.01\)). No correlations between bill-wiping in response to male intruders and any other behavioral or morphological characteristic was observed. Bill-wiping in response to males was not correlated with bill-wiping in response to females (Figure 6, Pearson correlation = -1.20, \(p = 0.534\)).

**Figure 4.** Positive relationship between bill-wiping frequency and tail-spread frequency.
Figure 5. Smaller males tend to bill-wipe more frequently in response to females than larger males.

Figure 6. Individual variation in bill-wiping was not consistent across contexts.

Preen gland size

Female preen gland volume was larger than that of males (females: 171 ± 46 ml; males: 145 ± 42 ml; one-way ANOVA, p = 0.03). In females, preen gland volume increased with Julian date (Pearson correlation = 0.629, p = 0.005). In males, volume did not correlate with Julian date; the only individual preen gland measurement that correlated with date in males was height (Pearson correlation = 0.351, p = 0.006). Male preen gland size was not correlated with body size or any other morphological measure; nor did it correlate with any behavioral measure. Thus, if smaller males do invest more in an attractive chemical signal, it is through behavior, not through production of preen oil.

Discussion

Our results highlight the importance of inconspicuous and poorly studied signal classes in mediating social interactions between songbirds and all animal taxa. Although male juncos did not differ in their hormonal response to LRS or SRS, males did respond significantly more strongly to SRS than LRS. Thus, SRS is actually a more potent elictor of aggressive behavior than the more thoroughly studied LRS, which is the song of choice for the vast majority of studies focusing on aggressive behavior in songbirds. In the case of SRS, males may be responding more aggressively because SRS is signaling a courtship event on their territory, which could result in the territory owner being cuckolded by an intruding male (Reichard et al., 2011). The lack of increase in plasma testosterone or corticosterone is surprising given the robust behavioral responses to the song stimuli. Previous studies investigating the hormonal response to song playback have also included a visual stimulus such as a live conspecific or taxidermy mount, which suggests that simply hearing male song, regardless of the level of threat, does not result in changes in physiology (McGlothlin et al. 2007, Goymann 2009).

Acknowledgements

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LITERATURE CITED


AN EXAMINATION OF INTERANNUAL POPULATION VARIATION IN *PARNASSIUS CLODIUS* BUTTERFLIES

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**ABSTRACT**

Examining how population size and structure vary over time is an important part of understanding how environmental factors influence a particular species. Organisms in which multiple generations can be studied in a short period of time are useful when attempting to predict the consequences of such changes. Insects, and in particular butterflies, have a short generation time, which makes them ideal for studying the effects of environmental change on demographics.

In this study, we examine the population dynamics of a butterfly common in the Teton area, Clodius Parnassian (*Parnassius clodius*). This area was initially studied starting in 1998-2000 (Auckland et al. 2004) and surveys were continued in 2009 – 2011. Emergence date varied between years by as much as three weeks. In addition, peak flight and end of flight dates also varied. Preliminary examination of the population data reveals similar patterns across years, where male emergence occurred prior to female emergence. In addition, sex ratios were also fairly consistent between years. Variation among years is observed primarily in the total number of butterflies marked and recaptured. Further data analyses comparing demographic parameters such as survival and population size need to be performed before any additional conclusions can be made. This study will add additional data to an ongoing study of the population dynamics of *Parnassius clodius*.

**INTRODUCTION**

Populations fluctuate both spatially and temporally because of direct and indirect factors that influence their survival and reproduction. It is important to study populations and quantify these fluctuations in order to more thoroughly understand how the organisms respond to certain environmental parameters. Butterflies are particularly useful organisms for such studies because multiple generations can be studied in short period of time. Therefore, the population dynamics of butterflies could be useful indicators of the effects of environmental change on population dynamics.

Clodius Parnassian (*Parnassius clodius*) butterflies are univoltine, meaning that they have one generation per year. Butterflies overwinter as first star instar larvae and emerge in the spring shortly after snowmelt (Scott 1986). Larval development continues through May into June. Adults usually emerge close to the end of June/early July. The adult flight period averages 2 – 3 weeks in length. Males typically emerge first and are followed by females. The success of these butterfly populations is influenced by multiple factors including the timing of the snow melt, the exposure to frosts, the emergence of food plants important to the butterflies, and the timing of male/female emergence. A disturbance to any of these factors or a change in the timing of emergence of butterflies could lead to fluctuations in population size. We studied a population of *Parnassius clodius* butterflies to quantify interannual variation in population size using a mark-release-recapture survey in Grand Teton National Park during 2009-2011. Data from previous studies (Auckland et al. 2004) were combined with the more recent data to study population variation among years. The objectives of this research included surveying the adult population to determine population size, examining and comparing the emergence times between male and female *P. clodius*.
butterflies, and determining the number of unmated females at the end of the flight season.

**METHODS**

A mark-recapture study on a population of *P. clodius* butterflies in Grand Teton National Park, Wyoming was performed from 2009–2011. Six 50 x 50-meter plots were randomly sampled daily in 2009–2011 in a relatively flat sagebrush meadow located in Grand Teton National Park. The plots were located approximately 200 meters apart at an elevation of 2100 m. Surveys began shortly after the first butterflies emerged and were terminated when no butterflies were seen in the plots. During a survey, two people continuously walked around within a plot to survey butterflies for a total of 20 minutes. Surveys were limited to times between 10:00 and 17:00 hours and when the temperature was above 21°C, wind was <16 kmh⁻¹, and the sun was not obscured by clouds.

Butterflies were captured using butterfly nets and placed in glassine envelopes until the end of the survey time. Unmarked individuals were marked individually on the ventral side of each hindwing with unique numbers using a black permanent felt-tipped pen. Unique numbers were recorded for all previously marked individuals. Day, time of capture, and plot location were recorded for each individual. Individual characteristics for each butterfly were also recorded, including the sex, mating status (for females), and wing wear. Sex was determined using external morphological differences present in *P. clodius* butterflies. Female mating status was noted based on the presence or absence of a sphragus (a waxy structure deposited by the male during mating that prevents future matings) (Scott 1986). Wing wear, based on three categories (new, intermediate, and old), was used as an additional measure of age of individual butterflies. Butterflies were then released in the center of the experimental plot in which they were captured. Daily results were recorded as number of individuals captured per day, including recaptures, and number of males, unmated females, and mated females captured per day.

**RESULTS AND DISCUSSION**

Table 1 lists the number of plots surveyed each year, the plot size, time, emergence dates, peak flight dates, and end of flight dates for all of the years. Annual flight periods varied among years with the earliest date of male butterfly emergence being June 17th and the latest July 6th. Female emergence occurred 1 – 3 days after males. Peak flight times and end of season flight also varied with emergence. In addition, peak flight for females was usually 2-4 days later than that of males. End of flight for both females and males was close to the same time. Total annual flight period varied from 11 days to 18 days.

<table>
<thead>
<tr>
<th>Year</th>
<th>Plots</th>
<th>Number of (m²)</th>
<th>Plot Size</th>
<th>Time (min)</th>
<th>Emerged Date</th>
<th>Peak Flight Date</th>
<th>End of Flight Date</th>
</tr>
</thead>
<tbody>
<tr>
<td>1998</td>
<td>3</td>
<td>75</td>
<td>35</td>
<td>30-Jun</td>
<td>7-Jul</td>
<td>10-Jul</td>
<td></td>
</tr>
<tr>
<td>1999</td>
<td>8</td>
<td>50</td>
<td>20</td>
<td>28-Jun</td>
<td>3-Jul</td>
<td>15-Jul</td>
<td></td>
</tr>
<tr>
<td>2000</td>
<td>6</td>
<td>50</td>
<td>20</td>
<td>17-Jun</td>
<td>22-Jun</td>
<td>2-Jul</td>
<td></td>
</tr>
<tr>
<td>2009</td>
<td>6</td>
<td>50</td>
<td>20</td>
<td>24-Jun</td>
<td>2-Jul</td>
<td>12-Jul</td>
<td></td>
</tr>
<tr>
<td>2010</td>
<td>6</td>
<td>50</td>
<td>20</td>
<td>4-Jul</td>
<td>7-Jul</td>
<td>15-Jul</td>
<td></td>
</tr>
<tr>
<td>2011</td>
<td>6</td>
<td>50</td>
<td>20</td>
<td>6-Jul</td>
<td>11-Jul</td>
<td>18-Jul</td>
<td></td>
</tr>
</tbody>
</table>

The total number of butterflies captured varied among the years. Table 2 gives a summary of the number of male and females captured, the total number captured and recaptured, and the recapture rate. The lowest number of males (143) captured occurred in 2011 while the greatest number were caught in 2009 (651). 2011 and 2009 also had the lowest (55) and highest (187) number of females captured, as well. The same number of females was captured in 2010 and 2011 (55).

Recapture rates for males varied from 10% to 60% for males and 3% to 16% for females. In years with lower population numbers, recapture rates were usually higher. In addition, the sex ratio captured favored males in each year. The proportion of male to female captures fluctuated year to year with ranges from 4.2:1 to 2.4:1 with new captures, and approximately 9:1 in the number recaptured. The ratio of individuals captured was always male-biased, potentially due to the differences in behavior between males and females. Males patrol for females and nectar while females stay closer to ground searching for oviposition sites or nectaring on flower. As the flight period progressed, the percentage of mated females increased consistently across the years.

**DISCUSSION**

several differences in emergence date, peak numbers captured, end of flight dates, total number of \textit{P. clodius} captured, recapture rates overall and recapture rate by sex. It is important to note that there were some differences in plot size and number of plots among years, so this will need to be taken into consideration to fully assess differences in population size estimates. Further analysis on population size and survivability between years will add to the knowledge gained from these studies. Once these data are analyzed, we can use the results to tease out factors that might be affecting populations over time, such as environmental changes. Snow cover, snow melt date, growing degree days, and frost days are a few important environmental elements that could add to the understanding of why populations vary from year to year.

<table>
<thead>
<tr>
<th>Year</th>
<th>Males</th>
<th>Females</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1998</td>
<td>Captured</td>
<td>404</td>
<td>96</td>
</tr>
<tr>
<td></td>
<td>Recaptured</td>
<td>107</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>%Recaptured</td>
<td>26</td>
<td>13</td>
</tr>
<tr>
<td>1999</td>
<td>Captured</td>
<td>552</td>
<td>223</td>
</tr>
<tr>
<td></td>
<td>Recaptured</td>
<td>55</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>%Recaptured</td>
<td>10</td>
<td>3</td>
</tr>
<tr>
<td>2000</td>
<td>Captured</td>
<td>343</td>
<td>145</td>
</tr>
<tr>
<td></td>
<td>Recaptured</td>
<td>77</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>%Recaptured</td>
<td>22</td>
<td>6</td>
</tr>
<tr>
<td>2009</td>
<td>Captured</td>
<td>651</td>
<td>187</td>
</tr>
<tr>
<td></td>
<td>Recaptured</td>
<td>187</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>%Recaptured</td>
<td>29</td>
<td>12</td>
</tr>
<tr>
<td>2010</td>
<td>Captured</td>
<td>154</td>
<td>55</td>
</tr>
<tr>
<td></td>
<td>Recaptured</td>
<td>72</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>%Recaptured</td>
<td>47</td>
<td>16</td>
</tr>
<tr>
<td>2011</td>
<td>Captured</td>
<td>143</td>
<td>55</td>
</tr>
<tr>
<td></td>
<td>Recaptured</td>
<td>86</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>%Recaptured</td>
<td>60</td>
<td>16</td>
</tr>
</tbody>
</table>

**ACKNOWLEDGEMENTS**

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**LITERATURE CITED**


ATMOSPHERIC DEPOSITION OF INORGANIC NITROGEN IN GRAND TETON NATIONAL PARK:
DETERMINING BIOLOGICAL EFFECTS ON ALGAL COMMUNITIES IN ALPINE LAKES

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† † ABSTRACT

Sediment records from several high alpine lakes in the Grand Teton National Park (GRTE), Wyoming were examined for stable isotopic signatures $\delta^{15}$N and diatom community composition because atmospheric deposition of reactive nitrogen (Nr) is known to be altering ecosystem functioning in other lakes of the Rocky Mountain Range. Alpine lakes exposed to greater Nr impacts in Colorado have higher N:P ratios in the water column, indicating an excess of N, thus GRTE sites were selected across a range of N:P values, spanning measures indicative of nitrogen to phosphorus limitation. Sediment cores were analyzed for diatom relative abundances, concentrations of carbon, nitrogen and phosphorus, and stable isotopic signatures of $\delta^{13}$C and $\delta^{15}$N. Every sediment record showed progressive $\delta^{15}$N depletion, evidence of increasing Nr deposition during the past forty years. In the GRTE, benthic flora dominated the community composition without changes to the fossil diatom taxonomy, a response atypical of other Nr impacted sites in the Rocky Mountain Range that have exhibited a marked shift towards nitrophilous planktonic diatoms Asterionella formosa and Fragilaria crotonensis. The suite of GRTE lacustrine sediment records exhibited a continuum of increasing nutrient enrichment from low to high N:P ratios, suggesting that lakes sensitive to Nr enrichment exhibit elevated ratios of N:P. The long-term impact of Nr deposition has not reached a critical threshold, but monitoring of the GRTE lakes needs to incorporate assessment of the N:P ratios in advance of greater ecological impacts.

† † INTRODUCTION

In western North America, the atmospheric deposition of reactive nitrogen (Nr), primarily as nitrate and ammonium, results in specific changes in surface water chemistry that shift the species composition of aquatic biota (Burns 2003, Fenn et al. 2003, Porter and Johnson 2007). The northern hemisphere is known to receive from 4 to 16 times more Nr through snow, rain and dry deposition than pre-industrial measures (Holland et al. 2000). In nutrient poor lakes of the northern hemisphere, including the Rocky Mountains, algae have historically been limited by nitrogen (N) and respond to increases in concentration with community and ecosystem level change (Baron et al. 2000, Lafrancois et al. 2004, Nydick et al. 2004, Saros et al. 2003, Bergstrom 2010). Recent work indicates that persistent atmospheric deposition of Nr, resulting in N saturation, has shifted the overall lake nutrient status to phosphorus (P) limitation in Colorado high elevation lakes (Elser et al. 2009). The eutrophication of lakes by deposition of atmospheric Nr is of great concern in the west, particularly in regard to the higher degree of N limitation in high elevation lakes. We lack, however, an understanding of both the degree of impact and the chronology of atmospheric deposition in the majority of the most sensitive areas of western North America.
High elevation lakes in western North America are particularly vulnerable to acidification and eutrophication from inputs of nitrogen through atmospheric deposition (Seastedt et al. 2004, Baron et al. forthcoming). High elevation lakes are typically positioned within watersheds of resistant bedrock and poorly developed soils. As a result, the lakes are low in alkalinity and sensitive to acidification during the spring pulse of ions. Mountains receive large amounts of precipitation as snow, and when the snow melts in the spring it delivers an accumulated pulse of atmospheric pollutants (Williams et al. 1997, Williams and Tonnessen 2000). Ion concentrations in precipitation at high elevation sites deserve further examination (Nanus 2003) because nitrogen loads in the Rocky Mountains of Colorado and southern Wyoming have increased since the 1980s (Burns 2003). Lakes in the Grand Teton National Park (GRTE) were characterized and ranked based on sensitivity to acidification due to atmospheric deposition (Nanus 2005). In that study, thirty six percent of lakes in the park were predicted to be sensitive to acidification from atmospheric deposition of nitrogen and sulfur.

A coherent signal of depleted $\delta^{15}N$ values in precipitation is evident across western North America (Wolfe et al. forthcoming) and across much of the northern hemisphere (Wolfe et al. forthcoming). Stable isotopic signatures of $\delta^{15}O$ and $\delta^{15}N$ in snowfall were depleted in four western parks, particularly in the most northerly GRTE site (Nanus et al. 2008). In the nearby Wind River Mountains, an ice core from the Upper Freemont Glacier showed a pattern of $\delta^{15}N_{N_{no}}$ depletion (-5.9 to -3.2 ‰) and increased $NO_3^-$ concentrations, following the NADP data trend (Naftz et al. 2011). The same trend was seen in the Summit Greenland ice core with rising $NO_3^-$ concentrations and $\delta^{15}N_{N_{no}}$ depletion of up to -12.8 ‰ (Hastings et al. 2009) with 1950-1980 being the greatest rate of change. Today, NADP sites record rising $Nr$ deposition in Wyoming that is composed of one third ammonium (NH$_3$). NADP passive sampling is known to underestimate ammonium concentrations because NH$_3$ can volatilize during snow melt (Nanus 2003) and particulate NH$_3$ formation in the atmosphere with nitrate, sulphate and hydrochloric acids are not captured in wet fall (Clarisse et al. 2009). Remote sensing of NH$_3$ (Clarisse et al. 2009) has recently identified global hot spots, and an area of concern is the Snake River Valley, Idaho, approximately 150 km upwind from GRTE (Clarisse et al. 2009). The need to assess lacustrine sedimentary $\delta^{15}N$ signatures in GRTE is great because of the vulnerability to atmospheric deposition of depleted $\delta^{15}N$ DIN.

Trends in water quality data can also provide a measure of $Nr$ impacts. $Nr$ deposition is known to impact terrestrial catchments, such that $N$ deposition can become in excess of plant and microorganism uptake and lead to soil $N$ saturation, acidification and nitrification (MacDonald et al. 2002, Rogora 2007). The result is export of nitrate to the surface waters, where rates of nitrification and $N$ mineralization are enhanced by increased atmospheric temperatures (Rogora 2007, Baron et al. 2009). Nitrate leaching is strongly dependant on the amount of atmospheric $Nr$ deposition and associated with local sulphate deposition, slope, bedrock geology and latitude (Dise et al. 1998). Changes in lake and precipitation chemistry were measured in several western parks in 1985 and again in 1999 (Clow 2003). Results indicated that sulphate concentrations, like sulphate emissions, had declined from 1985 to 1999, while nitrate concentrations rose with $Nr$ atmospheric loading in lakes across Montana, Wyoming and Colorado. Records from this study, however, included only one site in GRTE and there were no trends for that site. Here we present water chemistry from a suite of eight lakes to establish the current sulphate and nitrate concentrations.

Reactive $N$ impacts a number of autotrophic organisms, although diatoms are the primary marker organism because of their preservation in sediments. Increasingly, diatoms associated with human activities are entering new aquatic systems and resulting in dramatic ecosystem change (Kociolek and Spaulding 2002, Kociolek and Spaulding 2000). Diatoms in lake sediments have been shown to be both responsive to environmental change and to be among the first organisms affected by chemical change (Douglas et al. 1994, Internandi et al. 1999, Ruhland et al. 2008, Pientz and Smol 1993, Hall and Smol 1996, Anderson et al. 1995). In the 14,000 year record from Sky Pond (Rocky Mountain NP), diatom assemblages reflected the pre-industrial period until gradual anthropogenically-induced change during 1950-1970 and a dramatic shift post-1970 towards mesotrophic species (Wolfe et al. 2003, Harper 1990), specifically the diatom Asterionella formosa Hassall. The dominance of this species has been associated with human settlement and lake eutrophication, but is not associated with acidification (Anderson et al. 1995, Harper 1990). Investigation of the physiological responses of A. formosa and Fragilaria crotonensis Kitton has revealed a unique growth response in high elevation western lakes as compared to more temperate lakes (Saros et al. 2005). While these two species are common in fairly nutrient rich temperate lakes, their abundance in low conductivity waters showed
specific nitrogen requirements. In a number of experimental treatments, both A. formosa and F. crotonensis responded strongly to nitrogen enrichment, with no response to phosphorus enrichment alone (Saros et al. 2005, McKnight et al. 1990). Sediment reconstructions from eight lakes surveyed across the Beartooth Absaroka Wilderness and southern Rocky Mountains all showed increases in A. formosa or F. crotonensis, or both, after approximately 1950 due to atmospheric Nr loading (Saros et al. 2003, Saros et al. 2010). The increased deposition of Nr may be causing a nutrient imbalance. Elevated water column total nitrogen to total phosphorus (TN:TP) (Elser et al. 2009, Elser et al. 2009a) or DIN:TP ratios were found to be strongly related to regional Nr deposition trends across the United States, Norway and Sweden. Our research posits the question whether a shift from N- to P-limitation may be a driving force in the dramatic ecological responses seen in A. formosa and F. crotonensis.

Separation of climate change and N deposition impacts can be problematic (Baron et al. 2009) and it is important to use multiple lines of evidence to understand changes in ecosystem processes. Studies in the European Alps have shown that high elevation lakes are sensitive to climate change and that changes in air temperature and pH are linked (Psennonner and Schmidt 1992, Sommaruga-Wograth et al. 1997). Increases in pH with increasing temperature are thought to be the result of greater weathering rates of minerals or greater alkalinity production from microbial decomposition in lakes (Schindler 1986). Such processes might be acting to offset the impacts of acid deposition (Saros et al. 2003), because in some regions increases in atmospheric deposition of inorganic nitrogen have not increased concentrations of N or decreased pH in lake water. Experiments to examine relevant interactions of temperature and nutrient limitation on impacts of ultraviolet radiation in the Beartooth Mountains (Doyle et al. 2005) are informative. For all algal taxa, growth rates were higher at higher temperatures under each nutrient treatment and most growth rates were lower under UVR treatments. Therefore, we might expect that increases in lake temperature resulting from climatic change will amplify the diatom response to Nr deposition. In lakes of Rocky Mountain National Park, climatic changes were insufficient to explain the stratigraphic changes in δ15N and diatom species composition (Wolfe et al. 2003).

Reconstructing historical values of Nr deposition in association with biological change over time allows definition of ecological thresholds at which N induces critical ecosystem impacts known as critical loads (Porter and Johnson 2007, Saros et al. 2010. Information on critical loads is important to federal land managers who are responsible for protection of resources in Class 1 areas. In Colorado, the current deposition of inorganic N is estimated to be an order of magnitude greater than historic values (Baron 2006), a finding that resulted in legislative action to reduce emissions in the state in 2010. Here we assess the paleolimnological record of nitrogen deposition and associated biotic response for the future development of a critical load for the GRTE region.

The purpose of this investigation is to infer the magnitude and history of Nr deposition and resulting impacts on aquatic biota in sensitive, high elevation lakes within the Greater Yellowstone Ecosystem. We analyzed the elemental chemistry of carbon, nitrogen, phosphorus, stable isotopic signature of δ13C and δ15N and the diatom community composition to reconstruct the paleolimnology of seven Grand Teton National Park lakes that span a gradient of N:P ratios. A central focus of our work is to determine the interaction of nitrogen deposition and climate change in these sites. In this study we will evaluate the range alternative explanations for observed changes in the paleolimnological record.

**STUDY AREA**

Grand Teton National Park is located in northwest Wyoming and is a designated Class I protected area, as part of the Greater Yellowstone Ecosystem. The Teton Mountain Range covers nearly half of the 310,000 acres of the national park, with many of the peaks over 3,000 m in elevation. Most of the high elevation lakes formed in glacially scoured basins. The underlying geology is predominately granite, gneiss and schist with veins of volcanic intrusions. Moraine deposits date from the Pinedale glaciation (Love 2007). We sampled eight lakes (Table 1) within three adjacent watersheds (Jenny Lake, Leigh Lake and Bradley Lake watersheds).

High elevation lakes were selected based on an evaluation of the geomorphology and bathymetry for favorable preservation of lacustrine deposition. Study lakes include Grizzly, Holly, Whitebark Moraine Pond (unnamed on USGS maps), Ramshead, Lake of the Crags, Delta, Amphitheater and Surprise. Water chemistry and sediment cores were sampled at a central location of each basin from an inflatable raft in July and August, 2010. Each lake was surveyed with a depth finder along three
transects to assess the deepest point. Maximum lake depth ranged from 3.7 to 19.1 m. Water samples were collected from three depths: surface (0.3 m), mid-depth (2-3 m) and deep (1 m from bottom) for a suite of water chemistry.

**METHODS**

Water samples were collected in DI-rinsed 125 mL and 250 mL Nalgene bottles and glass amber bottles (for dissolved organic carbon, DOC). Samples for dissolved constituents were filtered on site through a 0.7 µm Whatman® GF/F filter. Samples were kept refrigerated or frozen before transport to the Kiowa Environmental Chemistry Lab (INSTAAR, University of Colorado Boulder). Cations were measured with a flame atomic absorption spectrometer (Perkin Elmer AAnalyst 200) ammonium with a fluorescence detection plate reader (BioTek Synergy™ 2) nitrate and silica with an automated chemical analyzer using continuous flow analyses (OI Analytical Flow Solution® IV) anions with ion chromatography using a Metrohm 761 Compact IC, total dissolved phosphorus and ortho-phosphate with colorimetric analyses using the flow injection analyzer (Lachat QC 8000 FIA) and organic carbon and total dissolved nitrogen using combustion catalytic oxidation with a non-dispersive infrared gas analyzer (Shimadzu TOC-VCSN).

**Coring and sediment chronology**

Sediments were collected from the deepest point in each basin with a modified Kajak-Brinkhurst coring device (Glew 1989), fitted with a 3” diameter clear polycarbonate core tube. Short sediment cores were successfully recovered from all lakes, but Lake of the Crags. Upon examination of the visual stratigraphy and confirmation of clear sediment-water interface, cores were extruded on site at increments of 0.25 cm from surface sediments to 10 cm, 0.5 cm increments from 10 to 20 cm and 1 cm increments from 20 to core end. Core sections were bagged in labeled Whirlpak bags and refrigerated until delivery to the Sediment Processing Lab (INSTAAR, University of Colorado Boulder). In the lab, sediment samples were weighed, freeze dried and archived in glass vials.

Radiometric dating of the $^{210}$Pb isotope from the uranium decay series in sediments was conducted using the granddaughter of $^{210}$Pb, $^{210}$Po. $^{210}$Pb activity was measured from a subsample of 0.1 to 5 g that had been sieved with a 100 µm mesh screen, pre-weighed into plastic 50 mL centrifuge vials and analyzed for $^{210}$Pb at the MyCore Scientific lab using alpha spectrometry (Appleby and Oldfield 1978). In samples that were not analyzed for $^{210}$Pb activity, a linear interpolation was used in order to calculate sedimentation rates and chronology.

Sedimentation rates (g m$^{-2}$ yr$^{-1}$) were calculated from the cumulative dry mass (g m$^{-2}$) multiplied by the decay constant ($\lambda$, yr$^{-1}$) divided by the measured background activity $^{210}$Pb (Bq g$^{-1}$). Chronology was established using the constant rate of supply (CRS) model of $^{210}$Pb accumulation where $^{210}$Pb activity is allowed to vary with respect to decay over time and with changes in sediment accumulation rate (Appleby and Oldfield 1978).

**Diatom analysis**

Diatom slide preparation was conducted using 5 mg dry sediment digested in 30% hydrogen peroxide solution and placed in a hot water bath for 2 days. Sediments were rinsed with de-ionized water and centrifuged, repeating until the solution measured neutral pH (Battarbee et al. 2001). A 0.4 to 1 mL aliquot of Polybead® 4.5 µm polystyrene microspheres at concentration 2.5 x 10$^6$ spheres mL$^{-1}$ was added to each diatom digestion. These diatom slurries were pipetted onto glass cover slips, dried overnight and mounted using Zrax mounting medium. Alternate sediment sections were chosen for enumeration with a minimum of 300 diatoms counted along a transect, using an Olympus Vanox microscope equipped with differential interference contrast optics and a 1.3 NA 100X oil-immersion objective. Diatom concentrations were calculated based on the ratio of microspheres to diatom valves in each 300 valve count (Battarbee 1973). Diatom species identifications were based on taxonomic literature that included several volumes (Patrick and Reimer 1966, 1975, Antonaides et al. 2009, Krammer and Lange-Bertalot, 1985, 1986, 1988, 1991, 2000, 2004) and primary literature. Several of the taxa encountered are presented in detail with light and scanning electron micrographs (Spaulding et al. 2011).

**Sediment biogeochemistry**

Sediment stable isotopic composition was measured on bulk matter, weighed into tin capsules and submitted to the University of California Davis Stable Isotope Facility. Stable isotopes $^{13}$C and $^{15}$N were analyzed with a PDZ Europa ANCA-GSL elemental analyzer interfaced with a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). The $\delta^{13}$C values in each sediment
core were corrected for the Suess effect, which is the modeled depletion of atmospheric $\delta^{13}$C values due to accelerated rates of fossil fuel burning during industrialization (Verburg 2006).

**Preliminary Results**

Lake water was circumneutral and oligotrophic with low conductivity, ion and nutrient concentrations. Transparency in most lakes was very high, except for Delta Lake, which was turbid from suspended glacial flour. Both Grizzly and Holly lakes support fish (Stephen 2007) and are known to have been stocked with Yellowstone cutthroat trout, *Oncorhynchus clarkia bovieri*, in the early 20th century (Hazzard 1933). The other lakes are considered to lack fish (Stephens 2007), although three brook trout, *Salvelinus fontinalis*, were captured during a gill net survey of Ramshead Lake in 1994. Since that time, however, fish have not been reported.

A latitudinal gradient in conductivity (linear regression $r^2=0.79$) and ANC ($r^2=0.89$) is present from Grizzly Lake to the north to Surprise Lake to the south (15.6 - 6.4 $\mu$S cm$^{-1}$ and 119 - 50 $\mu$eq L$^{-1}$, respectively). The same N-S gradient exists in calcium ($r^2=0.81$) and sulphate ($r^2=0.64$) concentrations from Grizzly to Surprise Lake (48.4 - 15.2 $\mu$mol L$^{-1}$ and 10.6 - 3.3 $\mu$mol L$^{-1}$, respectively). Silica concentrations have a weaker N-S trend ($r^2=0.46$), with concentrations measuring 13.9 - 43 $\mu$mol L$^{-1}$.

Essential growth nutrients, N and P lacked a latitudinal trend, but showed other patterns. The total N concentrations (mean 7.6 ± 3.2 $\mu$mol L$^{-1}$) amongst lakes varied more than the total P concentrations (0.11 ± 0.025 $\mu$mol L$^{-1}$). The relative proportion of N constituents (NH$_4^+$, NO$_3^-$, particulate N and dissolved organic nitrogen DON) showed a range of speciation Figure 1). The highest TN values were in glacial-fed Delta Lake, with over 95% in the form of NO$_3^-$. In contrast, 85 % of the TN in Whitebark Moraine Pond was in the form of DON. There is a trend with DOC and TP showing a positive linear relationship with the catchment area to surface area ratio at $r^2=0.76$ and 0.63 respectively. The highest TP concentrations were in Whitebark Moraine Pond, largely composed of DOP. The lowest TP concentrations were in Amphitheater Lake, composed predominantly of particulate, bound P.

TN:TP (molar) ratios can be used to characterize the relative availability of N to P in the basin (Figure 1). When N availability is high, phytoplankton productivity in freshwater bodies can become P limited. In North America, TN:TP values above 50 (molar) (Elser et al. 2009, Guildford and Hecky 2000) were found to be P limited systems. Based on those findings, nearly all lakes in GRTE are P-limited, except Holly Lake. Bergstrom (2010) found that DIN:TP (mass) ratios had better predictability than TN:TP ratios with values above 3.4 having a 75% probability of predicting P limitation during fertilization experiments. Since DON is the dominant species of N in White Bark Moraine Pond and Surprise Lake, the DIN:TP values are low ( 3.4, Figure 1) and potentially N-limited during the post-snowmelt season in July and August.

**Figure 1.** Total nitrogen speciation for each of the eight sampling sites in the Grand Teton National Park, WY. (a) Total nitrogen on the outside left vertical axis is represented as a proportion of the N species (from the top down) ammonia (NH$_4^+$), nitrate (NO$_3^-$), particulate N (PN) and dissolved organic N (DON). (b) Total nitrogen (TN) to total phosphorus (TP) molar ratios for each of the GRTE lakes, the long dashed line at 20 denotes the threshold below which phytoplankton were not found to be P deficient and the short dashed line at 50 denotes phytoplankton above which P deficiency was found in freshwater lakes (Guildford and Hecky 2000). (c) Dissolved inorganic nitrogen (DIN) to TP mass ratios are presented on a log scale with log 2.2 denoting 50% probability of P limitation and log 3.4 denoting 75% probability of P limitation (Bergström 2010).

**Chronology**

Sediment records could not be recovered from Lake of the Crags, and thus paleolimnological reconstructions were carried out on the seven remaining lakes. Sediment chronology was based on
the CRS model applied to the $^{210}$Pb activity profiles (Figure 2). Overall, the background $^{210}$Pb activities from the GRTE lakes were considerably high (mean 0.18 Bq g$^{-1}$), ten times what may be expected of an oligotrophic lake (Larder per. com.). Grizzly Lake had the highest $^{210}$Pb activity at 0.57 Bq g$^{-1}$. High background levels were likely the result of $^{226}$Ra and $^{238}$U in the rock and soils within the catchment or from high $^{222}$Rn in groundwater (Norton et al. 1985). The background measures were also more variable between sites, but this is to be expected if the radium is very high (Norton et al. 1985). In Holly Lake, sediment $^{210}$Pb did not measure background levels, so background values from Whitebark Moraine Pond were used as both lakes share similar levels of $^{210}$Pb activity.

Sedimentation rates (Figure 2) were all very low and consistent with similar studies of high alpine lakes (Norton et al. 1985, Brenner et al. 2004). Sedimentation rates in Whitebark Moraine Pond and Surprise Lakes remained relatively unchanged as compared to the large sedimentation events that occurred in Ramshead and Holly Lakes or the trend in rising sedimentation rates in Grizzly (since ~1994) and Delta (~1993) Lakes.

Diatom community structure

All diatom assemblages from GRTE lakes were dominated by benthic taxa with varying relative abundances that were sorted along the range of N:P values from lake water chemistry from Whitbark Moraine Pond to Ramshead Lake (Figure 3). Delta Lake did not have an enumerable preserved diatom fossil record. Whitebark Moraine Pond contained a very high abundance of Staurosirella pinnata (Ehrenberg) Williams et Round, Staurosira construens var. venter (Ehrenberg) Hamilton, and to a lesser extent Pseudoehrenbergiella brevistriata (Grunow in Van Heurck) Williams et Round. Amphitheatre and Surprise Lakes share a similar diatom assemblage likely because of the hydrological connection from the outlet at Amphitheater Lake, which feeds into Surprise Lake downstream. Both lakes have a high number of diatom taxa represented because percent abundances are <10% that include Stauroforma exiguiformis (Lange-Bertalot) Flower et al. Aulacoseira nivalis (W. Smith) English et Potapova and a diversity of monoraphid Psammothidium species.

Aulacoseira nivalis (W. Smith) English et Potapova and Discostella stelligera (Cleve et Grunow) Houk et Klee were one of a few planktonic taxa that were present in greater relative abundances. Aulacoseira nivalis was only present in Amphitheatre and Surprise Lakes at 6.8 to 8.7 % abundance and <1% at all other sites. Discostella stelligera (Cleve et Grunow) Houk et Klee, was represented at 15 to 40 % relative abundance in Holly, Grizzly, and Ramshead Lakes.

Fragilaria crotonensis and Asterionella formosa are mesotrophic planktonic diatoms found in many anthropogenically eutrophied lakes. Fragilaria crotonensis was present in Surprise, Amphitheater and Grizzly Lakes at <1% and in Ramshead Lake at 6.8 % total core abundance. Fragilaria crotonensis was found in sediments dating before 1850 with no discernable population trend. Asterionella formosa was present only in sediment samples from Holly Lake during ~1985 to 2010, however relative abundance does not exceed 3%. Overall, diatom community composition does not indicate a shift towards planktonic mesotrophic taxa, but rather a relatively unaltered benthic diatom community composition during the past 150 years and earlier.

Sediment geochemistry and stable isotopes

Comparison amongst the concentrations of phosphorus, nitrogen and carbon and the C:N (molar), $\delta^{13}$C and $\delta^{15}$N stable isotopic composition of each sediment core (Figures 3 and 4) showed that in all sediment cores C:N (except Delta Lake) and $\delta^{15}$N decline. $\delta^{15}$N plots followed a trend in depletion in all lakes, from pre-industrial values of up 2.7 ‰ to surface sediments of -2.2 ‰, an average $\delta^{15}$N
Figure 3. Diatom stratigraphies and biogeochemistry from A) Whitebark Moraine, B) Surprise and C) Amphitheater Lakes from Grand Teton National Park, WY. Diatom relative abundances from preserved sediment samples (bar charts), sedimentation rates(•), diatom concentrations (grey area plot), % cyst abundance (•), carbon concentrations, (area)  δ^{13}C (•) nitrogen concentrations (area) δ^{15}N (•) phosphorus concentrations (area) and C:N molar ratios(•).
Figure 4. Diatom stratigraphies and biogeochemistry from A) Holly, B) Grizzly and C) Ramshead Lakes from Grand Teton National Park, WY. Diatom relative abundances from preserved sediment samples (bar charts), sedimentation rates (•), diatom concentrations (grey area plot), % cyst abundance (•), carbon concentrations, (area) δ^{13}C (•) nitrogen concentrations (area) δ^{15}N (•) phosphorus concentrations (area) and C:N molar ratios (•).
depletion 2.2 \% during the past 150 years. At the same time, there was also a coincident decline in C:N ratios from an average of 13.0 to 10.5 starting around ~1960 until present. C:N ratios in Delta lake were not discernable. The large fluctuations in inorganic deposition in Ramshead Lake that increased sedimentation rates during ~1942-1951 appear to have impacted the biogeochemical trends.

Sedimentary concentrations of P, C and N varied considerably amongst GRTE lakes, whereas nutrient stoichiometry was consistent. Concentrations of P increased in most lakes but Amphitheater and Grizzly Lakes, while concentrations of C and N have gradually increased in Holly, Amphitheater, Grizzly, Ramshead and Delta Lakes over time. Sedimentary molar ratios of C:P and N:P were on average 7.3 ± 1.0 and 0.58 ± 0.09 respectively for all GRTE lake sediments except Delta Lake (1.6 ± 0.5 and 0.18 ± 0.05). Sedimentary ratios were an order of magnitude lower than water column measures and do not suggest P limitation.


**MANAGEMENT IMPLICATIONS**

The impact of this regional Nr deposition does not appear to affect each lake similarly, but sediment records follow a series of ecological impacts along a continuum of nutrient enrichment. This response continuum starts from a shift in the relative availability of growth limiting nutrients (N and P) to greater primary production, accelerated rates of primary production and increased sedimentation rates. In many other alpine lakes, benthic communities were replaced by planktonic mesotrophic taxa, such as *Asterionella formosa*, as nutrient enrichment can result in benthic habitat loss due to reduced light penetration and self-shading that shift the ecological functioning of an aquatic system (Anderson 1995, Nanus et al. 2009, Hobbs et al. 2010, Steward, Lamoureux and Finnery 2008).

All seven GRTE lakes show coherent influence of anthropogenic N, based on δ^{15}N signatures, despite differential speciation of N in the water chemistry of each lake. This declining δ^{15}N sediment signature is pervasive and evidence strongly suggests Nr deposition is the primary environmental threat to these remote high alpine lakes. This coherent δ^{15}N trend also supports that alpine lakes from the GRTE are an excellent source of long-term atmospheric loading records and could be useful in reconstructing other atmospheric pollutants, such as Pb, Hg and persistent organic pollutants.

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*Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government.*

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THE ROLE OF RED SQUIRRELS (*TAMIASCIURUS HUDSONICUS*) IN SHAPING SPATIAL PATTERNS OF SEROTINITY IN LODGEPOLE PINE (*PINUS CONTORTA*) FORESTS

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**ABSTRACT**

Understanding the effects of individual species on community- and ecosystem-level processes is of critical importance in ecology. Recent work has demonstrated that variation in genetically controlled traits within foundation species can have large implications for ecosystem processes. Identifying these traits and the selective pressures on them is crucial in understanding how ecosystems are structured and how the systems will respond to disturbance. Serotiny, the long-term storage of seeds in the canopy, is thought to be an adaptation to stand replacing fire. Seeds from serotinous plants are released following a fire, and the proportion of serotinous trees determines sapling density following a fire. The effects of serotiny are not limited to the serotinous species, as sapling density is an important determinant of plant community structure and ecosystem processes (including primary productivity and nutrient cycling). Seed predation may select against serotiny, however, no studies have addressed how the relative strengths of selection from fire and seed predation combine to produce the spatial pattern of serotiny on the landscape. Here, we report on an ongoing study of the effects of selection from seed predation in lodgepole pine (*Pinus contorta*), a serotinous North American conifer. Red squirrels are negatively associated with serotiny at broad geographic scales, and may select against the serotinous trait. This project examined the correlation between red squirrel density and the frequency of serotiny in lodgepole pine forests and the mechanisms underlying potential selection against serotiny by red squirrels. Specifically, we tested whether this correlation was present at landscape scales, whether the fitness of serotinous trees was reduced in the presence of red squirrels, and what factors controlled the density of red squirrels. Preliminary results indicate that serotiny and squirrel density is negatively correlated, but only at low elevations. In the presence of squirrels, we observed significantly lower cone survival in serotinous trees, suggesting reduced fitness. Squirrel density was strongly affected by several measures of forest structure, including species composition, overhead canopy cover, and tree size (mean DBH).

**INTRODUCTION**

It is well known that single species can have profound effects on the structure and function of communities and ecosystems. Examples include keystone species (Power et al. 1996), ecosystem engineers (Jones et al. 1994), and foundation species (Ellison et al. 2005) that affect species richness, habitat structure, and nutrient cycling (Crooks 2002, Ellison et al. 2005, Benkman et al. 2008). More recently, interest has grown in how within-species genetic variation can structure communities and ecosystems (Whitham et al. 2008, Johnson et al. 2009). By tying communities and ecosystems to heritable genetic variation within foundation species, this approach has the potential to produce quantitative predictions regarding community and ecosystem properties based on knowledge of a small number of important species (Wymore et al. 2011).

An important question is whether we can identify key traits in foundation species that have community- and ecosystem-level consequences, and
whether we can isolate potential selective agents driving variation in these traits. If abiotic changes are superimposed on existing geographic patterns of selection due to species interactions (Thompson 2005), the result may be novel spatial patterns of selection that cascade to complex and shifting geographic mosaics in which community and ecosystem properties depend on the balance of selective forces within each patch.

Predicted future increases in fire regimes are likely to impact lodgepole pine forests (Pinus contorta) (Liu et al. 2010, Westerling et al. 2011). Furthermore, these effects will be widespread because lodgepole pine is a foundation species that dominates much of the Rocky Mountains, (Critchfield 1980). However, no studies have investigated how changes in disturbance regimes will interact with seed predation from red squirrels (Tamiasciurus hudsonicus), a seed predator that greatly reduces the canopy seed bank in lodgepole pine and may select against canopy seed storage (serotiny; see below) (Benkman and Siepielski 2004, Steele et al. 2005). Reduced canopy seed bank has been linked to lower postfire sapling densities (Tinker and Romme 1994, Schoennagel et al. 2003) and corresponding community (Turner et al. 1997) and ecosystem (Turner et al. 2004) effects. Here, we report on a study of the interactions between red squirrels and lodgepole pine, focusing on the potential for these interactions to produce complex spatial patterns in community and ecosystem structure. Specifically, we attempted to detect correlation between the abundance of red squirrels and the frequency of serotiny, to determine what factors influence red squirrel abundance on the landscape, to measure the strength of selection on serotiny exerted by red squirrels.

Serotiny is an adaptation to stand-replacing fire (Keeley and Zedler 1998); therefore, the spatial and temporal patterns of fire have important consequences for lodgepole pine. Moreover, serotiny is a good candidate for a trait linking the genetics of a foundation species to landscape-scale mosaics in community and ecosystem function. First, serotiny is a heritable characteristic (Critchfield 1980, Parchman et al. 2011), and % serotiny varies, both within continuous forest patches (Tinker and Romme 1994), and among mountain ranges (Benkman and Siepielski 2004). Finally, serotiny has predictable effects on community and ecosystem properties in lodgepole pine forests. In the Greater Yellowstone Ecosystem (GYE), % serotiny prior to widespread fires in 1988 predicted postfire seedling density (Tinker and Romme 1994, Schoennagel et al. 2003), resulting in postfire differences in community composition (Turner et al. 1997) and ecosystem processes (annual net primary productivity and leaf area index, Turner et al. 2004).

A number of studies have addressed patterns of serotiny in relation to hypothesized selective agents. Fire frequency is positively correlated with % serotiny, and models and empirical work have suggested that increased fire frequency can select for serotiny (Perry and Lotan 1979, Gauthier et al. 1996, Enright et al. 1998, Schoennagel et al. 2003, Radeloff et al. 2004). Less attention has been given to the potential of biotic interactions to influence spatial patterns in serotiny. Seed predation could potentially have a large selective effect on serotiny, as seed storage extends a plant’s vulnerability to pre-dispersal seed predation, providing a selective advantage to plants that can either escape predation (i.e., by not being serotinous) or defend the stored seed (Janzen 1969).

In lodgepole pine, recent work has indicated that T. hudsonicus may select against serotiny (Benkman and Siepielski, 2004), suggesting that escape from predation by dispersing seeds quickly and reducing the period of vulnerability (with non-serotinous cones) may be favored in some situations. This pattern also occurs in a geographic mosaic; mountain ranges that have historically lacked red squirrels had very high frequencies of serotiny and demonstrated poor defense against seed predation. Thus, spatial patterns in serotiny are likely produced by the interplay of opposing directional selective forces from fire, favoring increased frequencies of serotiny, and from squirrels, favoring decreased frequencies of serotiny. The interaction of these two factors may therefore have considerable influence in determining community and ecosystem structure in lodgepole pine forests during postfire recovery.

We used a field study of red squirrels and lodgepole pines in Yellowstone National Park to address the general hypothesis that predation from red squirrels selects against serotiny in lodgepole pine. We focused on the following specific hypotheses: 1) There is a broad-scale negative correlation between the abundance of red squirrels and the frequency of serotiny, 2) Variation in red squirrel abundance is determined by factors other than serotiny (in other words, any correlation in hypothesis 1 is not due to red squirrels preferentially selecting low-serotiny sites), and 3) Cones on serotinous trees experience greater mortality rates than those on nonserotinous trees in the presence of predation from red squirrels.
STUDY AREA

Our study area included mature lodgepole pine forests throughout Yellowstone National Park, focusing on the central plateau and adjacent areas. A map of plot locations is provided in Figure 1.

Figure 1. Location of study sites within Yellowstone National Park, along with the extent of mature lodgepole pine used for site selection.

METHODS

Plot Selection

We randomly located 26 plots in mature lodgepole pine forest in Yellowstone National Park. Plots were approximately 25 ha (exact dimensions varied depending on the presence of barriers to sampling necessitating slightly smaller plots). We stratified the plots into equal numbers of high (≥ 2456 m) and low (< 2456 m) elevation plots based on previous work in the region showing an elevational threshold above which serotiny is uncommon, likely due to a decrease in the frequency of stand-replacing fires at higher elevations (Schoennagel et al. 2003). Due to a GIS error, one of the low-elevation plots was excluded from the study, for a final sample size of 12 low- and 13 high-elevation plots. We sampled 14 plots in 2010 and an additional 11 plots in 2011.

Within each plot, we established 6 (2011 plots) or 8 (2010 plots) north-south oriented strip transects (200 × 20 m), arranged in two rows with 150 m separating transect centerlines in each direction. We also established two 400-m² subplots along each transect. Subplots were located 50 m from the end of each transect. When transects intersected barriers (e.g., standing water, wide trails, topographic barriers) or patches dominated by species other than lodgepole pine, the transect was interrupted and continued on the other side of the barrier. If barriers intersected >25% of a transect’s total length, that transect was dropped from the plot.

Red Squirrel Density

Red squirrels are central place foragers that produce a single large midden (Smith 1968). Because each squirrel produces only one midden, we used active midden density as a proxy for squirrel density. We counted the number of middens per 0.4 ha strip transect, and converted this count into individuals/ha at the plot level.

Single observers spotted middens while walking the transect centerline, and the right angle distance from the transect centerline to the center point of each midden was measured with 5-cm precision. Identification of active central middens was based on size (>1 m in diameter) and the presence of recently chewed cone cores and scales on the top of the midden. When satellite middens were identified without an accompanying central midden, we left the transect line and attempted to locate the central midden. When estimating squirrel density, we only counted active middens that were within 20 m of the transect centerline.

Frequency of Serotiny

To estimate % serotiny, we recorded the number of serotinous and non-serotinous trees within each 400-m² subplot. If a subplot contained fewer than 20 trees, we counted the closest 20 trees to the subplot center. We classified trees into four categories based on the number of mature, non-weathered (i.e., brown in color) closed cones: strongly serotinous (95–100% closed cones), weakly serotinous (50–95% closed cones), weakly non-serotinous (5–50% closed cones), and strongly non-serotinous (0–5% closed cones). In practice, most trees were strongly serotinous or strongly non-serotinous; therefore, for analysis, we considered both weakly and strongly serotinous trees as serotinous, and all other trees as non-serotinous.
Forest Structure

To determine what aspects of forest structure influenced squirrel density, we measured several aspects of forest structure within each 400- m² subplot. We measured overhead canopy cover at five points spaced 5 m apart using a Forestry Suppliers Model A Spherical Crown Densiometer. We made a single measurement of basal area at the plot center using a 2.0 BAF basal area prism. Finally, we recorded the species and diameter at breast height (DBH) for the 20 trees closest to the plot center that exceeded 10 cm DBH. In addition to these field measurements, we included GIS-based data for mean annual precipitation, slope and aspect in our analysis of squirrel habitat.

Differential Cone Mortality

To determine whether squirrels exert selection on serotiny, we measured individual cone survival for serotinous and nonserotinous trees at a single site. During August 2010, when green cones were large enough to be easily spotted but not yet ripe enough to be removed by squirrels, we marked 187 trees within 43 m of active squirrel middens in an area with moderate squirrel density and moderate serotiny. We photographed branches with green cones from each tree. Because predation rates for serotinous trees vary with cone age (Smith 1970), we also photographed branches with young (i.e., brown) and older (i.e., gray) serotinous cones. In July 2011, we returned to these trees and used the photographs to determine the proportion of cones lost due to squirrel mortality.

Data Analysis

For all analyses that compared multiple models, we calculated Akaike’s Information Criterion, adjusted for small samples sizes (AICc) as well as ΔAICc values and the associated model weights. These model weights can be interpreted as the probability that a given model in a set is the best model in the set (Burnham and Anderson 2002). We considered a single model in a set to be superior when ΔAICc > 10 for all other models in the set. In this case, we interpreted the best model and ignored all others. All analyses were performed using the R software package (R Development Core Team 2012).

To describe the correlation between red squirrel density and % serotiny, we used generalized linear models (GLMs) with binomial errors and logit link functions. Previous studies have analyzed the effects of physical factors (e.g., soils, topography) on % serotiny and found no clear relationships (except for elevation, see below) (Tinker and Romme 1994), therefore we excluded these factors from our analysis and focused only on the relationship between squirrel density and serotiny. Preliminary analyses of data obtained in 2010 suggested that this relationship might differ at high and low elevations, so we also included elevation as a factor with two levels (low and high) in our analysis. We compared a total of four models: squirrel density only, elevation only, squirrel density + elevation (additive model), and squirrel density * elevation (interaction model).

For the analysis of squirrel habitat, we used principal components analysis (PCA) to reduce the number of variables and eliminate correlations among predictor variables. We included 7 variables describing habitat structure as well as local climate and topography in the PCA (northern exposure, eastern exposure, precipitation, overhead canopy cover, mean DBH, % CV of DBH, % cover of lodgepole pine, and % cover of Pinus albicaulis whitebark pine), and retained for analysis all axes with eigenvalues >1. We then included the retained PCA axes in GLMs with squirrel density as the response.

Because serotiny was uncommon at high elevations, we initially used the high elevation data (n = 12) to construct a model describing squirrel density in the absence of variation in % serotiny. To test whether squirrel density varies independently of serotiny, we then built two models using the low-elevation data: one containing the same predictors as the most supported high-elevation model, and a second model that included those predictors as well as % serotiny. We then used analysis of variance (ANOVA) to test the hypothesis that the more complex model was not an improvement over the simpler model.

To compare cone mortality between serotinous and non-serotinous trees, we compared cone mortality across cone types. Because cone mortality in serotinous cones varies with cone age (Smith 1970), we categorized cone type based on the degree of weathering, evident by the color of the scale. Cones were categorized as either non-serotinous, serotinous-green (< 1 year old), serotinous-brown (1-approx 5 years), and serotinous-grey (> 5 years old). We then used a χ² goodness of fit test on the hypothesis that cone mortality rates were equal among groups.
RESULTS

We observed a strong negative relationship between squirrel density and percent serotiny, but only at low elevations (Figure 2). The model including both squirrel density, elevation (as a categorical variable), and their interaction was the most strongly supported model ($\Delta AIC_c = 0$, weight = 1), and the next closest model had essentially no support ($\Delta AIC_c = 36.8$, weight = 0).

For the analysis of factors controlling squirrel density, we retained the first four principal components, which explained a total of 82% of the variance in the original dataset. PC3 and PC4 did not explain any of the variance in squirrel density in any of our models, so we focus further discussion solely on PC1 and PC2, which together explained 54% of the variance in the original dataset.

PC1 primarily described species composition, with a positive correlation with % lodgepole pine cover and a negative correlation with % whitebark pine cover. PC1 was also negatively correlated with mean annual precipitation, which is unsurprising given the tendency for whitebark pine to occur on drier high-elevation slopes. PC2 described canopy and understory structure, and was negatively correlated with overhead canopy cover, mean DBH of all trees, and the %CV in DBH of all trees. This axis was also positively correlated with northern and western exposure.

A model with PC1 and PC2 as predictors explained 78% of the variance in squirrel density at high elevations, and had greater support (i.e., minimum AICc) than any other models in the model set. Using the same model at low elevations, PC1 was not significant (likely due to a lack of whitebark pine at low elevations), but a model including only PC2 as a predictor explained 33% of the variation in squirrel density. Furthermore, the parameter estimates in both the high- and low-elevation models were similar, suggesting that similar processes control squirrel density regardless of elevation. Finally, adding % serotiny as a predictor to the low elevation model did not significantly improve the fit of the model ($F = 2.14, P = 0.18$), indicating that serotiny does not control squirrel density.

We found that annual survival of first-year serotinous cones was significantly lower than that of non-serotinous cones (serotinous survival = 0.23, non-serotinous survival = 0.44, $\chi^2$ test $P < 0.001$), demonstrating that squirrels can greatly reduce seed survival, and that predation has a larger impact on serotinous trees. Survival was higher in older serotinous cones (brown cone survival = 0.63, gray cone survival = 0.78). However, because predation is cumulative, the probability of a serotinous cone surviving long enough to disperse its seeds is relatively low.

Figure 2. The relationship between squirrel density and the frequency of serotiny at low and high elevations.
MANAGEMENT IMPLICATIONS

The frequency of serotiny has a large effect on postfire recovery in lodgepole pine forests; previous research has shown that seedling densities following a stand replacing fires are several orders of magnitude higher in highly serotinous stands (Turner et al. 2003). Thus, serotiny is a keystone trait, in that its frequency determines seedling density, which cascades to a number of ecosystem- and community-level processes (Turner et al. 2004). If the intensity of predation from red squirrels affects the frequency of serotiny at relatively local (i.e., < 100 ha) scales, then understanding how squirrels affect serotiny and what factors determine predation intensity can yield important predictive information about how forests will respond to fire. This information can be used to construct a model predicting the frequency of serotiny that incorporates input from both fire frequency and squirrel predation intensity. Furthermore, if climate change is expected to drive changes in fire frequency or in the distribution of red squirrels, such changes can be incorporated into the model to investigate future expected changes to the distribution of serotiny on the landscape and thus to the expected outcome of stand-replacing fires.

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LITERATURE CITED


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ABSTRACT

Invasive species are one of the top two threats to native biodiversity worldwide (Mack et al. 2000). A primary goal of invasion biology is to predict which introduced species become invasive, or reach pest status, and which systems are susceptible to invasion (Heger and Trepl 2003). In order to complete this goal, it is vital to understand long-term dynamics of invasive species populations and their interactions with native communities in their introduced range. Most studies of invasions by non-native species are not extensive enough to determine long-term effects on the native systems (Strayer 2010). The first objective of this study is to determine the long-term abundance and biomass of the New Zealand mud snail, (*Potamopyrgus antipodarum*), in the Greater Yellowstone Area (GYA). The second objective is to analyze the long-term effects of *P. antipodarum* on the biomass, abundance, and taxon diversity of native benthic invertebrate assemblages in the GYA. The ten-year span of data available for *P. antipodarum* and the native macroinvertebrate communities at Lower Polecat Creek in Grand Teton National Park and the Gibbon and Firehole Rivers in Yellowstone National Park provide a unique opportunity to study the macroinvertebrate community succession over time. Data from the proposed macroinvertebrate community survey in the summer of 2011 will be compiled with previous surveys from 2001-2009 to evaluate the long-term changes in the macroinvertebrate community at Polecat Creek and the Gibbon and Firehole Rivers.

INTRODUCTION

The New Zealand mud snail (*Potamopyrgus antipodarum*), a herbivorous gastropod native to New Zealand, has spread throughout Europe, Australia, and North America (Zaranko et al. 1997), frequently reaching pest densities. *P. antipodarum* is currently found in all western states in the United States except for New Mexico and is predicted to continue expansion into the Midwest states to the east coast (Loo et al. 2007). Introduced populations of *P. antipodarum* in Europe and North America are made up of 3 genetic clones of parthenogenic, ovoviviparous females (Dybdahl and Kane 2005) that can rapidly produce large populations in introduced freshwater habitats (Schreiber et al. 2003, Hall et al. 2006). While prevention of its initial invasion is a major management goal, there is still a question about how ecosystems that are already invaded will be affected in the long-term. There has been a recent increase in criticism that most studies of invasions by non-native species are not extensive enough to determine long-term effects on the native systems (Strayer 2010). There is much to be learned by following the ecological effects of non-native species over time since we know very little about long-term changes at the population, community, and ecosystem levels. Therefore, there is an urgent need to understand the long-term outcome in systems where introduction has already occurred.

Since *P. antipodarum* was first detected in the Greater Yellowstone Area in 1994, it has since spread across the region, reaching high densities in
stable, geothermally influenced rivers in the area (Kerans et al. 2005, Hall et al. 2006). High rates of growth and secondary production have been documented for P. antipodarum in its introduced range in the GYA (Hall et al. 2003, Kerans et al. 2005, Hall et al. 2006), as have evidence of negative interactions between P. antipodarum and native macroinvertebrates (Kerans et al. 2005, Riley et al. 2008). Another example of the potential effect of high P. antipodarum biomass is its control of ecosystem-scale fluxes of carbon and nitrogen, as observed in Polecat Creek (Hall et al. 2003).

Results from Hall et al. (2003 and 2006) indicate that P. antipodarum can achieve high densities in rivers within the GYA and have a large effect on primary productivity and other ecosystem processes. Recent studies indicate at least five groups of native macroinvertebrates are affected by P. antipodarum. In experimental conditions, two species of native snails, Pyrgulopsis robusta (like P. antipodarum, a member of the Hydrobiidae), and Fossaria sp. (Lymnaeidae) exhibit reduced growth in the presence of P. antipodarum (Riley et al. 2008). Inter-specific competition is also suggested by negative associations between the density of P. antipodarum and several families of insects in a river basin of the GYA (Kerans et al. 2005).

However, P. antipodarum has not reached uniformly high densities through its new range in the GYA (personal observation, Kerans et al. 2005). In addition, observations over the past few years indicate a potential decline in the abundance of P. antipodarum in Lower Polecats Creek (A. Kriv and T. Tibbets personal communication). During field work in July 2007 and 2008, many thousands of individuals of P. antipodarum could be collected in an hour at Polecats Creek. Currently, the same effort yields a few hundred at most. Does this observation indicate a real decline in mud snail population? Is this decline unique to Polecats Creek, or at a regional scale? I intend to answer these questions within rivers of the GYA. My first objective is to determine if changes have occurred in the abundance and biomass of P. antipodarum during the past ten years in rivers of the GYA. The second objective is to analyze the long-term effects of P. antipodarum on the biomass, abundance, and taxon diversity of native benthic invertebrate assemblages.

STUDY AREA

The first sample site is located in Lower Polecats Creek approximately 300 km upstream of Huckleberry Hot Springs outlet in the John D. Rockefeller National Parkway, within the permit jurisdiction of Grand Teton National Park (UTM 12 525010E, 4883960N). The two study sites in Yellowstone National Park are the Gibbon and Firehole Rivers. The sample site on the Gibbon River is approximately 200m upstream from the bridge at Madison Junction (UTM 12 511173E, 4943166N). The sample site for the Firehole River is approximately 100-300m downstream of the Fountain freight bridge near Ojo Caliente spring at the downstream end of Geyser Basin. The specific study sites were chosen based on sites used in Hall et al. 2006.

METHODS

Benthic invertebrate biomass and abundance was quantified for three sampling dates in the months of June, July, and September 2011 in Lower Polecats Creek. The Gibbon and Firehole Rivers were sampled in late September 2011. I used methods from previous sampling efforts identical to those described in Hall et al. 2003 and 2006.

Each month, six quantitative samples of benthic invertebrates were collected using a 15.2 cm diameter stovepipe corer (Figure 1). For each sample, fine sediments (< 5 cm) and macrophytes were removed before samples were elutriated and collected on a 250 μm sieve or Hess sampler. All biomass from primary producers was sorted and analyzed for ash-free dry mass. Subsamples of tissue from primary producers will be analyzed for Carbon and Nitrogen elemental composition using a Carlo-Erba CN analyzer at the University of Wyoming Stable Isotope Laboratory. Each macroinvertebrate sample was preserved in 95% ethanol immediately. Samples were stained with Phloxine B and sorted in the laboratory into 250 μm – 1 μm and > 1 μm size classes before identification to genus. I estimated invertebrate biomass by measuring the length of each individual and using published length-mass regressions to estimate ash-free dry mass for each taxon (see Benke et al. 1999, Hall et al. 2006).

Robert Hall (University of Wyoming) and Mark Dybdahl (Washington State University) have agreed to share published and unpublished data from 2000-2001 with me for the purpose of this historical study. Amy Krist and Heather Thon (University of Wyoming) will contribute invertebrate data from 2007 and 2009. The collaborators noted above will be co-authors on any publications resulting from these analyses. I will use the long-term data outlined above to determine relative changes of P.
antipodarum and native invertebrate community abundance and biomass over the past ten years at each study location by comparing mean values across months and sample years. I will compare the mean numerical and biomass proportions of each invertebrate taxon for each sampling data set to determine whether these proportions could be used to investigate community structure over time. Bootstrap analyses will be used to test for differences between confidence intervals between years within re-sampled populations.

Figure 1. Stovepipe sampling device used to estimate macroinvertebrate biomass and abundance.

**PRELIMINARY RESULTS**

All samples in the >1-mm size fraction have been picked from debris and separated into two subsample categories for measurement and identification: 1) mud snails and 2) all other invertebrates. Mud snails have been counted and measured in the samples for June and July at Polecat Creek. Mud snails have been counted and measured in three of the six samples at the Firehole River and all samples in the Gibbon River. Macroinvertebrates are in the process of being identified to the level of genus. Cataloging of specimens is in process at this time because all specimens have not been identified. Results are reported for the >1-mm size fractions only.

The mean abundance of mud snails in Polecat Creek for the > 1-mm size fraction was 9540 and 3583 individuals/m², for June and July respectively. In comparison, mean abundance of mud snails in the >1-mm size fraction sampled in June and July 2001 by Hall et al. (2006) were 42,400 and 121,550 individuals/m², respectively. The abundance of mud snails in the Gibbon River for the > 1-mm size fraction ranged from 0 – 100 individuals/m², with three out of the six samples containing no mud snails and very few other macroinvertebrates. The abundance in the Firehole River for mud snails in the >1-mm size fraction ranged from 133 – 313 individuals/m². Mean abundance estimates of mud snails in August 2000 by Hall et al. (2006) were 7235 individuals/m² for the Gibbon River and 80.711 individuals/m² for the Firehole River. Data from recent macroinvertebrate samples indicate a 10 – 100 fold decline in P. antipodarum abundance compared to surveys from 2001. Native macroinvertebrate species not found in 2001 were present in later samples, indicating changes in community assemblages.

These estimates support observational evidence from researchers over the past 5 years that mud snail abundance has decreased from previous levels. However, after preliminary analysis of data collected in 2011, it is clear that another year of study is necessary to better quantify a statistical difference in populations of P. antipodarum between years. The cool, wet summer and high flows may have affected the results of the survey in 2011, therefore the study will be continued in the summer of 2012.

**MANAGEMENT IMPLICATIONS**

The proposed study serves to extend earlier assessments of changes within freshwater invertebrate assemblages that are imperative for understanding the long-term affects of P. antipodarum in the GYA. The results of this study are directly applicable to management of P. antipodarum with the GYA, and have potential consequences for understanding succession of this species in other regions. Considering the ecological and economic impact of invasive species at a global scale, understanding long-term affects of these species is vital for their long-term management.

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**LITERATURE CITED**


THE INFLUENCE OF FOREST MANAGEMENT ON FUTURE FOREST STRUCTURE FOLLOWING A MOUNTAIN PINE BEETLE OUTBREAK IN LODGEPOLE PINE STANDS IN NORTHWESTERN WYOMING

INTRODUCTION

Forest managers in the western U.S. are currently confronted with a bark beetle epidemic that is unprecedented in extent, severity, and duration. Several species of native bark beetle including the mountain pine beetle (MPB), spruce beetle, western balsam bark beetle, and Douglas-fir beetle are simultaneously affecting over 5 million ha of forest in the Intermountain West (Logan et al. 2003, Hicke et al. 2006). Estimates of the total area affected by the current bark beetle outbreak are updated annually, typically using aerial surveillance and manual mapping techniques. However, these estimates are often inaccurate and do not provide quantitative information on stand-level beetle activity and/or tree mortality. More importantly, these annual estimates of “spread” of the epidemic do not provide any information on the abundance of the surviving understory trees, which may be substantial, nor do they provide information on post-disturbance tree seedling establishment. This “advance forest regeneration” represents the future forests in these regions. Therefore, understanding the current structure of the forests is critical for making predictions about future structure and function.

Effects of bark beetle outbreaks on pre-disturbance stand structure (tree density, basal area, and species composition) have been well documented in the Rocky Mountain region for mountain pine beetle in ponderosa and lodgepole pine (Romme et al. 1986, Dordel et al. 2008, Axelson et al. 2009), for spruce beetle and western balsam bark beetle in spruce-fir forests (Kulakowski et al. 2003, McMillan et al. 2003), and for DFB in Douglas-fir forests (Negron et al. 1999, McMillan and Allen 2003). While forest regeneration following fire has been well documented for many types of fire and forests, forest regeneration following bark beetle outbreak is not well understood, and differs from fire in several ways. In contrast to stand-replacing fires, which typically kill all trees in a stand, including small trees, following a bark beetle outbreak the understory and the small trees that grow there are rarely killed. Thus, the release of understory survivors by overstory removal is often the major mechanism of post-beetle outbreak forest regeneration (Nigh et al. 2008, Boggs et al. 2008). Romme et al. (1986) found that understory survival was a critical mechanism for regeneration of lodgepole pine stands following mountain pine beetle outbreaks in Wyoming. More recently, Nigh et al. (2008) documented post-beetle regeneration in lodgepole pine forests in British Columbia. Notably, they found that ALL stands showed at least some level of advance regeneration, and over half of the stands had 1000 or more individual trees per hectare.

As future forests develop, it is important to learn from the past, specifically to investigate the influence of past forest management on overstory mortality from bark beetles and advance regeneration. Unfortunately, little work has been done to understand how previous forest management actions, such as timber harvest, pre-commercial thinning, or fuel reduction projects have influenced the mortality of mature trees in the overstory, or the composition and abundance of advance regeneration. This pilot study investigated how past forest
management treatments may have influenced bark beetle impacts and post-outbreak understory advance regeneration in the Shoshone National Forest (SNF), Wyoming.

Understanding these questions is important for helping natural resource management agencies make informed decisions. Both elected officials and the general public are putting pressure on forest managers to “do something” about the outbreak. There is ongoing controversy over whether hands-off management promotes diversity and resiliency, while others believe commercial timber treatments should be allowed in roadless and wilderness areas because of uncertainty about whether the forests will recover without human-intervention. Previous research on forest responses to beetle-killed trees in other regions has shown that trees grow back naturally to adequate stocking levels (Collins et al. 2010, Boggs et al. 2008). For this pilot study, we focused on one primary question: How do pre-canopy tree density and species composition differ from post-outbreak advance regeneration density and species composition?

**METHODS**

During the summer of 2011, we sampled a total of 12 stands in the Shoshone National Forest in northwest Wyoming. All of these stands were dominated by lodgepole pine (Pinus contorta var. latifolia). Ten of the plots had been previously managed by the USFS, and had been subjected to some level of pre-commercial thinning, and two of the plots had not received any appreciable management treatments. Historical records were provided by the USFS to identify specific past treatments of the managed plots and the local USFS staff also provided welcome assistance in the selection of the plots. All study plots were selected to have similar site characteristics with respect to soil type and topography. The two unmanaged stands were located in USFS roadless areas and we used caution to avoid stands that had experienced fire suppression or tie-hacking activities.

Sampling occurred in a 0.25-hectare plot in each stand to measure overstory and advance regeneration density and composition. Three, 50x4 m belt transects were established in each plot and were used to record tree species, condition (live/dead and beetle activity), diameter at breast height, tree height and sapling basal diameter and height within each plot. We also collected tree increment cores from the ten largest trees in the stand to determine stand age.

**RESULTS**

**Managed stands**

In the ten managed stands, pre-outbreak canopy density averaged 908 stems/ha, and ranged from 400-2216 stems/ha. Approximately 92% of the pre-outbreak canopy was composed of lodgepole pine, with whitebark pine, subalpine fir, and Engelmann spruce comprising the remaining 8% (Figure 1). Advance regeneration, composed of both saplings and seedlings of all species, averaged 1326 stems/ha, and ranged from a low of 317 stems/ha to 2682 stems/ha in the most dense stand. In contrast to the pre-outbreak canopy, only ~44% of the advance regeneration was lodgepole pine, with whitebark pine representing 35% of all advance regeneration. The remaining 21% was mostly aspen and subalpine fir, with a small amount of Engelmann spruce (Figure 1).

![Figure 1. Comparison of proportions of tree species in Pre-outbreak and Post-outbreak (Advance Regeneration) in MANAGED stands in the SNF (POTR – Populus tremuloides; PIEN – Picea engelmannii; ABLA – Abies lasiocarpa; PIAL – Pinus albicaulis; PICO – Pinus contorta).](image-url)

**Unmanaged stands**

In the two unmanaged stands, pre-outbreak canopy density averaged 758 stems/ha, and ranged from 633-883 stems/ha. Lodgepole pine and Engelmann spruce represented nearly 98% of the pre-outbreak canopy, in nearly equal proportions (53% and 45%, respectively; Figure 2). Aspen was the only other tree species represented in the pre-outbreak canopy of unmanaged stands sampled. Advance regeneration averaged 1091 stems/ha, and ranged from 783-1399 stems/ha. The proportion of stems represented by lodgepole pine was considerably smaller than in the pre-outbreak canopy; here, lodgepole pine represented only 18% of the total...
advance regeneration. Both Engelmann spruce and aspen exhibited an increase in proportion in the advance regeneration, with Engelmann spruce representing nearly 50% and aspen comprising 28% of total advance regeneration (Figure 2). The only other tree species represented in the advance regeneration was subalpine fir, and comprised slightly more than 3% of total advance regeneration.

Figure 2. Comparison of proportions of tree species in Pre-outbreak and Post-outbreak (Advance Regeneration) in UNMANAGED stands in the SNF (POTR – Populus tremuloides; PIEN – Picea engelmannii; ABLA – Abies lasiocarpa; PIAL – Pinus albicaulis; PICO – Pinus contorta).

Comparison of Managed and Unmanaged Stands

Average pre-outbreak canopy stem density differed slightly between managed and unmanaged stands, but not substantially (908 vs. 758, respectively). However, lodgepole pine dominated the canopy of managed stands, yet was a co-dominant with Engelmann spruce in the unmanaged stands (Figures 1 and 2). Similarly, advance regeneration was not substantially different between managed and unmanaged stands, although range of stem densities was much larger in the managed stands. Advance regeneration in managed stands was dominated by lodgepole pine, but Engelmann spruce and aspen dominated advance regeneration in the unmanaged stands.

DISCUSSION

Pre-commercial thinning apparently does little to impact advance regeneration in post-outbreak forest stands in SNF. While the range of seedling/sapling densities was broader in the managed stands, the average stem densities were quite similar between managed and unmanaged stands. These results cannot be directly compared to previous studies investigating the effects of more intensive timber harvesting in lodgepole pine forests. For example, Collins et al. (2011) found that new seedling recruitments were four times higher in post-harvest stands than in unharvested stands in Colorado. However, their study involved removal of most of the entire pre-outbreak canopy, which would favor new seedling establishment compared to unharvested stands, especially for shade-intolerant species such as lodgepole pine. However, our findings do agree with a separate study by Collins, et al. (2010), who suggested that post-outbreak regeneration is similar to unharvested (unmanaged) stands.

Our study only provides data from two unmanaged stands, so clearly additional field sampling will be necessary to further clarify trends identified by the current pilot study. Nevertheless, based on these initial findings, and those of other related studies, it appears that post-outbreak forests will be of similar densities to that of pre-outbreak stands, although some changes in the relative proportions of some species may occur. Notably, lodgepole pine will not necessarily be the dominant tree species in post-outbreak forests, but will certainly remain an important component of these forests.

ACKNOWLEDGEMENTS

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LITERATURE CITED


Investigation of Postglacial Sediment Storage and Transport in Garnet Canyon, Teton Range, Wyoming

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Abstract

The Teton Mountains are shaped by interactions between glacial, fluvial and mass wasting processes. In this study we investigate the influence of process interactions on quantitative estimates of erosion rates based on sediment transport and accumulation. Sediment characteristics were measured on talus fan and stream channel deposits. These observations were used to evaluate weathering and rounding, which can indicate transport history and mixing between the two deposits and processes. Talus fans were studied to quantify the stability of fan surfaces and determine the frequency of material transport. Streams were studied to determine the efficiency of meltwater flow to move sand and coarser materials deposited on talus surfaces. Similarities between sediments in the fluvial and talus deposits support strong coupling between these processes. Streams are capable of moving smaller sized talus materials, however active rockfalls continue to supply new sediment and limit stream incision. The source of recent rockfalls appears to be ridges at high elevations or along north facing walls indicated by the frequency of surface weathering and lichen cover on selected talus fans.

Introduction

Rugged topography in the Teton Range was created by forces uplifting mountains relative to the Jackson Hole valley and eroding canyons and peaks by glacial, stream, and mass wasting (rockfall) processes (Love et al. 2003, Foster et al. 2010). As we investigate surficial processes controlling the landscape, we find that erosional mechanisms are closely linked. Quantifying the impact of a single geomorphic process is complicated by interactions with other processes. To understand the challenges associated with process coupling, sedimentary materials were used to measure spatial and temporal patterns of erosion in a canyon with active mass wasting and stream flow.

The accumulation of sedimentary material on a valley floor over a period of time can indicate the rate of processes creating and transporting the materials. Calculations of rockfall rates depend on estimates of the volume of rock debris collected in talus fans (Olyphant 1983), however there is uncertainty in the thickness of talus formations due to the variable debris sizes and possible transport paths on surfaces and beneath deposits. Post-depositional transport of these sediments by mountain streams may cause underestimation of the total material eroded from valley walls through rockfall events.

Sediments are transported and accumulated in stream systems and are used to measure erosion rates. Methods used to determine erosion rates and patterns include quantifying sediment transport, measuring $^{10}$Be isotopes accumulated in quartz grains, and tracing minerals to source rocks (Schaller et al. 2001, Stock et al. 2006, Siame et al. 2011). The application of detrital stream sediments to understand erosion processes is dependent on how efficiently those sediments travel throughout the canyon. Stream incision can produce sediment and transform landscapes, but is limited by accumulation of sediment on canyon floors. While streams may remove talus materials, challenging the accuracy of
rockfall erosion rates, the same talus fans may also prevent sediment transport if they create barriers to water and sediment flow (Korup 2006). Talus fans will also limit incision into bedrock on valley floors, therefore it is necessary to understand the efficiency of mountain streams to transport a range of sedimentary materials (Burbank et al. 1996, Nash 2005).

To understand erosional processes and their interactions this study focused on Garnet Canyon, where stream channels directly interact with talus deposits. Sediments on talus fans and in the stream channel were observed to measure weathering and abrasion caused by different transport mechanisms (mass wasting or stream bedload) and exposure. Rounding was measured as a possible indicator of the distance sediments traveled from the bedrock source. If sediments were deposited on the toe of the fan via rockfalls and were later incorporated into the stream channel, angularity should be similar to other clasts at the toe of the fan above or outside the channel. If cobbles were transported by water flow in the stream channel, they would be more abraded and rounded downstream. Comparisons between stream and talus sediments provide a better understanding of sediment mixing and interactions between geomorphic processes.

STUDY AREA

Garnet Canyon is a mid-sized canyon (~10 km² drainage area) in the center of the Teton Range (Foster et al. 2010). The canyon was eroded by several episodes of glacial advances, which created steep walls of Precambrian igneous and metamorphic rock. The slope of the valley profile decreases where glacial incision scoured and polished the valley floor. Glaciers transported eroded sediments from the canyon floor to form the Bradley Lake moraine in Jackson Hole valley (Love et al. 2003). Since the last glacial retreat, sediment has accumulated due to rockfall from adjacent, steep slopes and small stream meanders.

Based on the extent of talus deposits in Garnet Canyon, mass wasting processes are significant mechanisms of sediment formation and deposition. Rock falls and avalanches carry boulders and sediments from the steep valley walls to the floor of the canyon where the material has accumulated to form fan-shaped deposits. Rocks falling during mass wasting events are angular. Rough edges form as the boulders break into smaller sizes upon impact with the canyon wall and other rocks on the fan. Some edges may be rounded if cobbles or gravels roll from high elevations on a fan surface to the toe of the fan (Whitehouse and McSaveny 1983). Locally, large boulders and rock debris accumulated within or adjacent to the active stream channel.

Melting snow and ice from winter precipitation and a few remaining glaciers contribute to stream flow and modern sediment transport in Garnet Canyon. The morphology of the stream changes as the water flows over different bedrock surfaces or talus deposits. As the stream drains out of the northern fork of Garnet Canyon and enters the trunk valley, it creates a large waterfall cascading over glacially polished bedrock and onto accumulated glacial and talus debris. Cascades also occur where thick talus deposits accumulated along narrow reaches of the canyon. Where the slope decreases along the valley floor, step-pool morphology was observed alternating with plane-bed morphology along the channel (Montgomery and Buffington 1997).

Methods

Talus surfaces and materials

Approximately 20 hand-sized cobbles were measured from four talus fans in, or adjacent to, Garnet Canyon. Cobbles were sampled from each fan surface to determine relative surface weathering based on lichen cover, surface color, and roundness. The four talus fans were chosen based on positions below ridges around Garnet Canyon where erosion rates were previously measured. One talus fan was sampled beneath walls facing each cardinal direction to evaluate how exposure to sunlight (warmer temperatures) influences rockfalls. The amount of daily sun exposure may influence the freezing and thawing of water in rock fractures and the frequency of rockfalls. Observations on the percentage of surface area covered by lichen provided an indication of how frequently cobbles on the fan have moved. If lichen has grown on the surfaces, it is assumed that the rocks remained in a relatively similar position for a longer period of time. The surface color provided an additional measure of surface exposure and weathering (Whitehouse and McSaveny 1983). Rocks exposed at the surface become discolored over time due to chemical weathering. We assumed that darker colors or more distinct changes in surface color indicated more weathering compared to fresh surfaces within the sample. Krumbein roundness was determined for each of the cobbles on each talus fan to measure abrasion on edges during the rockfall event. The Krumbein method assigns a quantitative
value between 0-1 for the angularity of sedimentary materials. The same scale was used on stream sediments to compare materials from both depositional settings.

**Sediment Transport**

Stream cross-sections and discharges were measured at seven sites along the stream within Garnet Canyon to determine the range of sediment sizes transported during summer discharge. The sites were selected from reaches of the catchment where the valley floor had been glacially scoured (Figure 1) and talus had accumulated. Several segments of the stream were measured to determine the sizes of sediments easily transported during snowmelt discharge. Each segment had a different morphology due to proximity of more or less recent rockfall deposition.

![Garnet Canyon Stream Profile](image)

Figure 2. Longitudinal profile of Garnet Canyon begins at the lower saddle in the north fork. Blue asterisks indicate sample elevations. Samples were collected at the blue asterisks. The very steep surface directly above the asterisks indicates the waterfall from the north fork of the canyon.

Cross sections were surveyed to measure the width and depth across each channel, flow velocity, and the distribution of sediment sizes. One liter of water was also collected from one of the channel cross sections to measure suspended sediment. Surface bedload was observed in each cross section to create a grain size distribution of one hundred randomly selected grains. If a hand was placed on a large boulder that could not be moved, the boulder was measured in place. Grains that could be picked up were measured with a granulometer in the field.

Sediment sizes in the stream channel were used to calculate channel roughness, and determine a range of grain sizes transported through each stream section. Sediment entrainment was measured by calculating the boundary shear stress in the stream based on cross-section measurements. Critical shear stresses were calculated for the distribution of grain sizes observed at each stream location. If the critical shear stress was less than the boundary shear stress, grains could be transported by the discharge observed in the stream.

**Preliminary Results**

**Talus Surfaces**

Qualitative measurements of color, lichen cover, and roundness were completed for 15-20 samples from each of the talus fans (Table 1). Samples ttc61 and ttc71 were both collected below ridges at approximately the same elevation (~3000 m). Sample ttc61 was collected beneath a north-facing wall and sample ttc71 was collected beneath a south-facing wall. The north-facing wall had a higher percentage of unaltered clasts (56% original rock color) compared to the south-facing wall (29% original rock color). Alteration of the rock changed the surface from an original light gray-white color to varieties of orange, pink or brown. The difference in color suggests talus below the south-facing wall is older, has weathered longer, and has had fewer recent rockfalls than the north facing and higher elevation walls. More lichen cover on talus sample ttc61 beneath the north facing wall also indicates lower elevation walls may be more stable than the higher elevation walls. Cooler temperatures at higher elevations may either slow weathering processes on the fan surface or enhance rockfall activity.

<table>
<thead>
<tr>
<th>Talus-ID</th>
<th>No. sampled</th>
<th>Aspect</th>
<th>Average Krumbein Roundness</th>
<th>Most common color</th>
<th>% with lichen</th>
</tr>
</thead>
<tbody>
<tr>
<td>ttc71</td>
<td>15</td>
<td>south</td>
<td>0.3</td>
<td>moderate orange</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>pink</td>
<td></td>
</tr>
<tr>
<td>ttc66</td>
<td>20</td>
<td>west</td>
<td>0.3</td>
<td>light gray</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>light gray</td>
<td></td>
</tr>
<tr>
<td>ttc61</td>
<td>16</td>
<td>north</td>
<td>0.4</td>
<td>very light gray</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>light gray</td>
<td></td>
</tr>
<tr>
<td>ttc64</td>
<td>20</td>
<td>east</td>
<td>0.4</td>
<td>light gray</td>
<td>10</td>
</tr>
</tbody>
</table>

**Stream Transport**

Measurements of stream flow and channel sediments were completed in July 2008 and repeated
in July 2011 to determine if flow changed between the two years as a result of differences in snowfall accumulation. Average discharge calculated from velocity and cross sectional area was ~1.6 cms in both study years; therefore, the efficiency of sediment transport is similar each year. At the discharge observed, the Garnet Canyon stream is capable of transporting sand or smaller sized sediments throughout the canyon. The critical shear stress required to move sand grains (2mm) was greater than the boundary shear stress (Table 2). The sizes that could be moved by snowmelt discharge ranged from fine-course gravels (pebbles-small cobbles; Figure 3). Talus deposits did not appear to slow velocity or limit sediment transport near any of the measured cross-sections.

Figure 3. Stream cross section locations and the sizes of gravel that could be transported during typical snowmelt discharge.

<table>
<thead>
<tr>
<th>Cross Section</th>
<th>Elevation (m)</th>
<th>Average Krumbein Roundness</th>
<th>Boundary Shear Stress</th>
<th>Critical Shear Stress: D50 (mm)</th>
<th>Critical Shear Stress: D50</th>
<th>Grain size moved in snowmelt flow</th>
</tr>
</thead>
<tbody>
<tr>
<td>1a</td>
<td>2731</td>
<td>na</td>
<td>147</td>
<td>44</td>
<td>9</td>
<td>195 fine gravel</td>
</tr>
<tr>
<td>1b</td>
<td>2731</td>
<td>0.4</td>
<td>49</td>
<td>7</td>
<td>16</td>
<td>55 medium gravel</td>
</tr>
<tr>
<td>2</td>
<td>2786</td>
<td>na</td>
<td>74</td>
<td>15</td>
<td>29</td>
<td>208 Fine-medium gravel</td>
</tr>
<tr>
<td>3</td>
<td>2871</td>
<td>0.4</td>
<td>317</td>
<td>44</td>
<td>17</td>
<td>380 coarse gravel</td>
</tr>
<tr>
<td>4</td>
<td>2822</td>
<td>0.4</td>
<td>271</td>
<td>41</td>
<td>16</td>
<td>318 fine gravel</td>
</tr>
<tr>
<td>6</td>
<td>2813</td>
<td>na</td>
<td>254</td>
<td>19</td>
<td>72</td>
<td>691 medium gravel</td>
</tr>
<tr>
<td>7</td>
<td>2755</td>
<td>0.4</td>
<td>180</td>
<td>42</td>
<td>16</td>
<td>329 fine gravel</td>
</tr>
<tr>
<td>8a</td>
<td>2810</td>
<td>na</td>
<td>119</td>
<td>15</td>
<td>24</td>
<td>176 coarse gravel</td>
</tr>
<tr>
<td>8b</td>
<td>2810</td>
<td>0.4</td>
<td>135</td>
<td>35</td>
<td>21</td>
<td>372 very fine gravel</td>
</tr>
</tbody>
</table>

Sediment mixing between talus and streams

Estimates of rounding on the edges of the grains were recorded for both talus and stream deposits (Tables 1 and 2). Grains were angular to subangular in all deposits. Only two talus deposits showed slightly lower Krumbein roundness values (0.3) compared to the other talus and stream sediments (0.4). The similarity between talus and stream sediments indicates that the sediments sampled were not transported far from the talus source. There was no indication that sediment in downstream deposits had traveled greater distances than sediments upstream. Rockfalls have created a transport-limited system for the streams in Garnet Canyon where the accumulation of talus material within the stream channel limits bedrock incision (Nash 2005).

Reduction of sharp edges on talus materials suggests that abrasion occurred by rolling or washing materials down the surface of the talus slopes after initial rockfall deposition. If talus materials remained unmoved after initial deposition, the edges would be very angular with little rounding on the edges. Possible post-depositional transport mechanisms include snow avalanches and rain or meltwater runoff from nearby steep slopes or gullies. As with the stream sediments, roundness of talus materials did not change with elevation or position downstream. Surface weathering can also round angular edges and indicate a relative age of talus deposits. The lack of change between high and low elevation deposits suggests this is not a good indicator of relative ages on these talus surfaces.
SUMMARY

Sediment characteristics in Garnet Canyon reflect the connections between mass wasting and fluvial processes. Mass wasting via rockfalls is a continuing process, which actively contributes sediments to the stream channel in Garnet Canyon. New sediments added to the stream channel after rockfall events limit incision, but do not strongly influence the efficiency of sediment transport. Streams flowing across talus deposits are capable of moving sediments ranging in size from sand to small cobbles, however large cobbles and boulders require higher stream discharges.

Variation in talus deposits may result from position in the canyon, ridge processes or rates of glacial retreat. Cooler temperatures below shaded or higher elevations may enhance rockfall events resulting in younger and less weathered talus deposits on the valley floor. Younger talus surfaces below the east facing wall and higher elevations may result from westerly winds carrying snow and precipitation over mountain peaks. Snow and water in rock fractures freeze and push blocks from their position in steep walls causing rockfalls to occur (Brocklehurst et al. 2011). Talus fans at lower elevations have also experienced longer exposure and accumulation time. Glacial melting and retreat slowly exposed the valley floor and allowed sediment accumulation to begin earlier at lower elevations.

ACKNOWLEDGEMENTS

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LITERATURE CITED


BARK BEETLES, FUELS, AND SHORT-INTERVAL FIRES IN DOUGLAS-FIR AND LODGEPOLE PINE FORESTS OF GREATER YELLOWSTONE

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♦ ABSTRACT

Recent increases in insect and fire activity throughout the western US have presented forest managers with formidable challenges. The extent and severity of bark beetle (Curculionidae: Scolytinae) epidemics have reached unprecedented levels, and the frequency of large, severe fires continues to increase. These trends are expected to continue because climate change—especially warmer temperatures, earlier snowmelt and more severe summer droughts—is implicated for both disturbances. Insects and fire have tremendous ecological and economic effects in western forests, yet surprisingly little is known about how fire hazard may change following bark beetle epidemics, and how changing fire regimes may potentially alter forests of Greater Yellowstone. We are employing a combination of field studies, remote sensing and simulation modeling to understand how bark beetle infestation affects fire hazard in Douglas-fir (Pseudotsuga menziesii) forests. The Douglas-fir type is a key component of Rocky Mountain landscapes, and is experiencing extensive and severe bark beetle outbreaks. However, almost no studies have examined Douglas-fir. We hypothesized that differences in fire regime, stand structure, regeneration potential and decomposition of woody fuels lead to important differences in fuel profiles, fire hazard and, in turn, the effectiveness of alternative mitigation strategies in Douglas-fir. Our studies are being conducted in Grand Teton and Yellowstone National Parks, and the Bridger-Teton and Shoshone National Forests within the Greater Yellowstone Ecosystem (GYE), where we build on >20 years of research and our recent studies of bark beetles and fire in lodgepole pine forests. During the summer of 2011, we conducted a significant portion of the field component of the project, collecting ancillary data in our previously measured chronosequence of Douglas-fir forests of differing time since beetle attack (TSB), and measuring burn severity and forest regeneration following a 2008 fire that burned a recently beetle-attacked Douglas-fir forest on the Shoshone National Forest. We also sampled forest regeneration and dead wood biomass following a short (28-year) interval ‘reburn’ in lodgepole pine forests to test whether reduced seed sources associated with younger trees at the time of burning might reduce postfire regeneration potential. Data analyses are ongoing and results will be forthcoming.

♦ INTRODUCTION

Recent increases in insect and fire activity throughout the western US have presented forest managers with formidable challenges. The extent and severity of bark beetle (Curculionidae: Scolytinae) epidemics have reached unprecedented levels and the frequency of large, severe fires continues to increase (Westerling et al. 2006). These trends are expected to continue because climate change—especially warmer temperatures, earlier snowmelt and more severe summer droughts—is implicated for both disturbances. Insects and fire have tremendous ecological and economic effects in western forests, yet their interaction is poorly understood. Surprisingly little is known about how fire hazard may change following bark beetle epidemics, and how changing fire regimes may potentially alter forests of Greater Yellowstone. Scientists have begun tackling these problems (e.g., Jenkins et al. 2008), but empirical
data are scarce. Research has shown that time since beetle outbreak is critical for understanding the relationship between beetle outbreaks, stand structure, fuel dynamics and fire hazard, but again, empirical data are few. We are employing a powerful combination of field studies, remote sensing and simulation modeling to understand how bark beetle infestation and post-outbreak management affect fire hazard in Douglas-fir (*Pseudotsuga menziesii*) forests; very few studies have examined Douglas-fir. Our studies are being conducted in Grand Teton and Yellowstone National Parks, and the Bridger-Teton and Shoshone National Forests within the Greater Yellowstone Ecosystem (GYE), where we build on >20 years of research and our recent studies of bark beetles and fire in lodgepole pine forests.

A second factor that may affect forest resilience in the next century is increased frequency of wildfire. Shorter intervals between stand-replacing fires may result in lower forest resilience (regeneration potential) if the fire interval is shorter than the time required for a mature seed bank to develop. Further, repeated fires may reduce ecosystem carbon storage by consuming a greater portion of woody biomass, an important legacy structure in young post-fire stands.

Lodgepole pine and Douglas-fir forests are key components of Rocky Mountain landscapes. Both are experiencing extensive and severe bark beetle outbreaks, yet important differences between these forest types (Keane 2008) suggest that post-beetle changes in fuel hazard may be distinct. We hypothesize that differences in fire regime, stand structure and regeneration potential lead to important differences in fuel profiles and fire hazard in lodgepole pine and Douglas-fir. We are focusing on changes in fuel profiles over time and the effects of insect outbreak on fire behavior (both recent and future). Collectively, we are directly addressing key bark beetle research priorities identified by US Forest Service scientists for the western US (Negron et al. 2008).

**Project Objectives and Hypotheses**

**Question 1:** How do bark beetle outbreaks affect fuel profiles and subsequent fire hazard in Douglas-fir forests? Bark beetle outbreaks substantially alter stand structure and live and dead fuel characteristics. We are beginning to understand how fuels and potential fire behavior change over time following mountain pine beetle outbreaks in lodgepole pine forests, based on data from our current research (Simard et al. 2011) and similar studies (Lynch et al. 2006, Page and Jenkins 2007a, 2007b, Jenkins et al. 2008). Major trends include an initial (3-5 yr post-outbreak) reduction in canopy bulk density and continuity, as dead needles fall from beetle-killed trees; and a later (20 yr post-outbreak) increase in large dead woody fuels as dead trees fall. Live herbaceous fuels may increase after the canopy is opened, and surviving trees (mostly understory individuals) may grow into the canopy after 20 yr, increasing ladder fuels. Studies in Utah and Idaho (Page and Jenkins 2007a, 2007b, Jenkins et al. 2008) found increased fine fuel loads that increased flame length early after beetle outbreak. Our data for lodgepole pine in the GYE indicate that the likelihood of active crown fire is reduced following beetle outbreak (Simard et al. 2011). Further, little research has addressed interior Douglas-fir forests, which are extensive in the Rockies and often coincide with locations where residential development is increasing. Given differences in structure and dynamics of lodgepole pine and Douglas-fir forests, we anticipate significant differences in post-beetle fuel dynamics and potential fire behavior, and our studies are underway.

**Question 2:** How was the severity of recent fire in Douglas-fir forests affected by prior bark beetle infestation, and does the combination of beetle infestation and fire compromise forest recovery? The ability to address directly the effects of beetle infestation on fire severity has been limited by a lack of spatially explicit data to characterize the extent and severity of both disturbances and an absence of field studies of fire in beetle-killed forests. Because the likelihood and severity of fire is affected by the timing of beetle infestation and may vary with forest type, there is a need to characterize the landscape heterogeneity of fuels created by bark beetle infestation in both space and time. Recent advances in remote sensing of forest ecosystems has led to the development of methods to accurately map both fire severity (e.g., Miller and Thode 2007) and the extent (e.g., Wulder et al. 2006) and severity (our work in prep) of bark beetle damage at broad scales. These advances provide the opportunity to test whether recent beetle damage has contributed to more severe fires in beetle-damaged areas, and these studies are underway.

**Question 3:** How do short-interval fires in lodgepole pine forests influence forest regeneration and ecosystem carbon storage? We hypothesize that tree regeneration would be much lower in the short-interval fire compared to fires burning through mature forest, because of a reduced seed bank stored in serotinous cones. We also hypothesize a
substantially reduced dead wood carbon pool in areas burned twice within a 28-year time period.

STUDY AREA

Our study is being conducted within the GYE in northwestern Wyoming (Figure 1), including Yellowstone (YNP) and Grand Teton National Parks and the Bridger-Teton (BTNF) and Shoshone (SNF) National Forests. The Douglas-fir beetle (DFB) has been active since 2002, and in addition to the well-known 1988 fires, significant beetle-affected area has also burned recently. Also, the 2009 Bearpaw Fire in Grand Teton National Park burned over the 1981 Mystic Fire, creating an opportunity to study the impact of a 28-year interval between stand-replacing fires, which is roughly an order of magnitude shorter than typical fire intervals in GYE lodgepole forests over the last few millennia. All work is being conducted under permits with both the national parks and national forests.

Figure 1. Study sites are located across much of Greater Yellowstone. Fire severity was sampled in two recent fires, along with remote sensing. The Gunbarrel Fire was sampled in the summer of 2011. A time-since-beetle chronosequence of Douglas-fir stands was augmented with dendrochronological sampling in 2011.

METHODS

To assess fuel profiles and fire hazard in beetle-affected forest (Question 1), a “time-since-beetle” (TSB) chronosequence was sampled in Douglas-fir forests of the GYE to quantify fuel profiles from 0 to 20 yrs since the epidemic. Most of the fuel sampling was completed in 2010, but we augmented these data in the summer of 2011 via tree coring and collection of cross-sections of beetle-killed logs, in order to validate the timing and severity of past outbreaks. Results are being compared to our existing data for lodgepole pine. We are developing remote sensing products to map the variation in canopy, herbaceous and woody fuels in post-beetle stands across the GYE with TSB in both forest types. To determine how the behavior and severity of recent fires (2008) were affected by the bark beetle infestation (Question 2), field studies and remote sensing are being used to determine how actual spatial variation of fire severity across the landscape was related to pre-fire beetle infestation. A portion of the field sampling was completed during summer 2010 and summer 2011. To evaluate the effects of a short-interval fire in lodgepole pine forest (Question 3), we sampled tree regeneration and dead wood biomass in the Bearpaw Fire perimeter, and will be comparing these data to those from other recent fires that burned through mature forests (long-interval fire).

Field Measurements

Question 1. In each 0.25-ha plot, we quantified the tree (DBH or height if <1.4 m tall; live / dead; quantity of red needles; presence / absence beetle galleries and pitch tubes; crown base height) and understory (% cover and height in twenty 1-m² quadrats) layers. Surface fuels were sampled in ten 20-m transects using Brown’s planar intercept method (Brown 1974). In 2011 we used these surface and canopy fuels data to parameterize the FCCS fire model (Ottmar et al. 2007) to estimate potential fire behavior in our plots. We produced vertical profiles of canopy bulk density for each plot, using field-measured crown base height, and crown fuel biomass estimated from DBH and allometric relationships (Brown 1978). We used these profiles to derive effective canopy bulk density and canopy base height following Scott and Reinhardt (2001).

Question 2. Field studies were conducted in the Gunbarrel Fire, which burned ~22,000 ha in beetle-killed Douglas-fir on the SNF in 2008 (Figure 1). Using the maps of beetle kill for the GYE derived from remote sensing (described below) and field
reconnaissance, our approach was to locate areas of heterogeneous pre-fire beetle severity within the fire area. We established 85 points in the Gunbarrel Fire. Fire severity was evaluated at each point using 30-m diameter plots, which were designed specifically for studies incorporating remote sensing. We also measured pre-fire stand density, basal area, severity of bark beetle attack and fire, and regeneration, as we have done in previous post-fire studies (e.g., Turner et al. 1997, 1999).

Question 3. We measured tree regeneration and dead wood biomass in 8 plots within the Bearpaw Fire perimeter. Each plot was 0.25-ha in size, comprising three parallel, 50 x 2 m transects in which all prefire trees were sampled for size class and cone serotiny level. Tree seedlings were tallied by species and herbaceous vegetation quantified by percent cover in each of five 0.25-m² quadrats spaced evenly along each transect. Dead down wood was sampled in ten 20-m transects using Brown’s planar intercept method (Brown 1974).

**PRELIMINARY RESULTS**

Questions 1-3. Analysis of the field data collected during summer 2011 is ongoing. Results will be presented at the summer 2012 annual meeting of the Ecological Society of America.

**ACKNOWLEDGEMENTS**

This research was funded by the Joint Fire Science Program (JFSP) and facilitated by Roy Renkin (Yellowstone National Park) and Diane Abendroth (Grand Teton National Park), as well as the Bridger-Teton and Shoshone National Forests. We appreciate the opportunity to lodging and laboratory facilities at the UW-NPS Research Station for a portion of our 2011 field season.

**LITERATURE CITED**


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LICHEN SPECIES DIVERSITY
YELLOWSTONE NATIONAL PARK GLORIA SITE

BERNADETTE KUHN ✦ JOE STEVENS ✦ COLORADO STATE UNIVERSITY ✦ FT. COLLINS

ABSTRACT

Alpine ecosystems are important monitoring targets for examining climate-induced changes of vegetation cover, species composition, and species migration. In 2011, we installed alpine monitoring sites in Yellowstone National Park for the Rocky Mountain Inventory and Monitoring Network. The site was established using the protocol developed by the Global Observation Research Initiative in Alpine Environments [GLORIA] (Grabher et al. 2000). Here, we present a summary of the lichen species diversity documented within these monitoring plots, as well as the summary of field work completed for the GLORIA project in 2011. We report on the results of 40 numbered collections of lichens collected at four alpine sites in the Absaroka Range, Yellowstone National Park. A total of 21 unique taxa were documented. Of these, 6 are new to the documented lichen flora of Yellowstone (Eversman 1998, Eversman et al. 2002).

INTRODUCTION

Unlike vascular flora, comprehensive works documenting lichen and moss diversity in the Northern Rockies are fairly recent (Eversman 1990, Eversman 1998, Eversman et al. 2002, Flora of North America editors 2007, McCune and Goward 1995). Nascent efforts to document lichen diversity within Yellowstone National Park [YELL] have largely been limited to trail corridors and roadsides (Eversman 1990, Eversman 1998, Eversman et al. 2002). Therefore, alpine lichen diversity is poorly documented (Figure 1). Existing checklists for YELL report 8 out of 54 collection sites in the alpine (Eversman 1990, Eversman et al. 2002). Alpine

Figure 3. Locations of Four Sentinel GLORIA Peak in Yellowstone National Park.
mosses are traditionally under-collected by previous bryologists (personal communication Harpel 2011, Spence 1985, Eckel 2007). However, a comprehensive checklist of the moss flora of the Greater Yellowstone Area is in progress (personal communication Harpel 2011).

In this study, we installed and sampled a long-term alpine monitoring site in YELL to examine the composition and structure of vascular and non-vascular plant species. Most vegetation monitoring conducted in National Parks does not include sampling non-vascular species. Thus, the project provided a unique opportunity to further the existing knowledge of alpine lichen and moss species diversity within YELL.

The long-term monitoring site was established by Colorado Natural Heritage Program [CNHP] biologists through a joint project with the National Park Service’s Rocky Mountain Inventory and Monitoring Network [ROMN]. The primary objective of this project is to examine climate-induced changes of alpine vegetation cover, species composition, and species migration. The site was established using protocol developed by the Global Observation Research Initiative in Alpine Environments [GLORIA]. Here, we present a summary of the lichen species diversity documented within these monitoring plots, as well as the summary of field work completed for the GLORIA project in 2011. Since 2011 was the initial sampling year of the GLORIA site, this report does not focus on analysis of plot data, nor does it examine trends. Full sampling events are scheduled every 5 years for this site. We expect to produce reports and publications with in-depth analysis and interpretation following the second full sample event.

**Methods**

We implemented an alpine monitoring protocol from the Global Observation Research Initiative in Alpine Environments (GLORIA), an international monitoring network established in 2001 to assess and predict biodiversity and temperature changes in alpine communities in response to drivers such as climate (Pauli et al. 2010). Supplemental protocol from ROMN was added regarding human disturbance and soils. The goals of the GLORIA program are to provide a global baseline for vegetation monitoring in alpine environments and to assess the risks of biodiversity loss and ecosystem instability from climate change. The methodology is extended by cooperators, such as the ROMN and CNHP, to create a long-term monitoring network at the global scale. The ROMN Alpine Vegetation Composition, Structure, and Soils protocol follows established GLORIA protocols but adds components for soil condition, treeline movement, and human disturbances (Ashton et al. 2010).

**Sample design**

We followed the GLORIA sampling design (Pauli et al. 2010) which calls for the establishment of four sentinel sites on alpine peaks representing an elevation gradient within a target region (e.g. the Absaroka Range in eastern Yellowstone National Park, WY). One GLORIA region includes four sites. The sites are established on the top of the peaks (summits) and the summits vary from just above treeline to the highest life zones of vegetation. Within one region, all four summits share qualitatively similar geology, climate, disturbance, and land-use history leaving vegetation differences among the summits to be driven primarily by elevation.

In 2011, we established monitoring sites at four summits within Yellowstone National Park (US-YEL; Figure 1; Table 1). We examined topographic maps and photographs, discussed options with park managers, took a reconnaissance flight over the area, and hiked to potential sites to select the best summits. The summits we chose are within close proximity of one another and are located in the Upper Lamar River area, on a ridgeline that runs north of Lamar Mountain. The four peaks have similar geology, similar land-use history and disturbance levels, and a similar climate. We permanently marked the sites to ensure accurate relocation, buried HOBO© Onset pendant temperature loggers (UA-001-64) on the north, east, south and west side of all peaks to acquire hourly temperature data for the winter of 2011-2012, and drafted preliminary species lists for the four sites.

---

### Table 1. Name, location, elevation, and vegetation zone of the four alpine sentinel sites within Yellowstone National Park.

<table>
<thead>
<tr>
<th>GLORIA Summit code</th>
<th>Summit name</th>
<th>Latitude (decimal degrees)</th>
<th>Longitude (decimal degrees)</th>
<th>Elevation (m)</th>
<th>Vegetation zone</th>
</tr>
</thead>
<tbody>
<tr>
<td>BLP</td>
<td>Unnamed</td>
<td>44.700184</td>
<td>-109.826731</td>
<td>3,195</td>
<td>lower alpine</td>
</tr>
<tr>
<td>SCP</td>
<td>Unnamed</td>
<td>44.695765</td>
<td>-109.834566</td>
<td>3,122</td>
<td>lower alpine</td>
</tr>
<tr>
<td>SPP</td>
<td>Unnamed</td>
<td>44.701613</td>
<td>-109.835067</td>
<td>3,169</td>
<td>lower alpine</td>
</tr>
<tr>
<td>WSP</td>
<td>Unnamed</td>
<td>44.694275</td>
<td>-109.837219</td>
<td>3,124</td>
<td>lower alpine</td>
</tr>
</tbody>
</table>
At each peak, we installed one marker (a rebar with a labeled aluminum cap) at the highest point on the summit, and identified and marked 9 m² quadrat clusters in each cardinal direction at exactly 5 m in elevation below the summit (all four corners of the quadrat cluster are marked: one with capped rebar and 3 with nails; Figure 2).

**Plot layout**

Once the summits were selected, we established a long-term monitoring plot at each of the summit sites (Figure 2). For each peak, this entailed placing one marker (a rebar with a labeled aluminum cap) at the highest point on the summit, identifying and marking a 3 x 3 m quadrat cluster (Figure 3) in each cardinal direction at exactly 5 m in elevation below the summit (all four corners of the quadrat cluster are marked: one with capped rebar and 3 with nails; Figure 2), and identifying 4 lower and 4 upper summit area sections that describe each aspect to a distance of 10 m below the summit (e.g., the upper north section was the north side from the summit to 5 m below the summit and the lower was from 5 to 10 m below the summit).

**Vegetation, Soils, Temperature, and Disturbance Monitoring**

The quadrat clusters each contain 9-1 m² quadrats (Figure 2, 3) that are used to measure fine changes in vegetation cover and frequency. In addition, one temperature datalogger is buried at 10 cm depth in the center of each quadrat cluster to measure changes in soil temperature over time and variation in temperature associated with aspect. The 1 m² quadrats are also used to record the presence and frequency of herbivore damage including trampling, scat, and browsing. The summit area sections are used to measure the exact dimensions of the peak (area and slope), the coarse-scale ground cover of the peaks (7 cover classes: solid rock, scree, vascular plants, lichens, bryophytes, bare ground, and litter), and the presence of individual plant species used to estimate species diversity and exotic plant cover (Table 2).

<table>
<thead>
<tr>
<th>Plot type</th>
<th>Size</th>
<th>Number of plots per peak</th>
<th>Number of plots in YELL</th>
<th>Available Data</th>
</tr>
</thead>
<tbody>
<tr>
<td>Summit Variable</td>
<td>Variable from 0 to 10 m below highest point</td>
<td>1</td>
<td>4</td>
<td>Natural and anthropogenic disturbance</td>
</tr>
<tr>
<td>Summit Area</td>
<td>Variable from 0-5 m and 5-10 m below highest point for each direction</td>
<td>8</td>
<td>32</td>
<td>Species presence; Cover class</td>
</tr>
<tr>
<td>Quadrat cluster</td>
<td>9 m²</td>
<td>4</td>
<td>16</td>
<td>Hourly soil temperature; Soil parameters</td>
</tr>
<tr>
<td>Quadrat</td>
<td>1 m²</td>
<td>16</td>
<td>64</td>
<td>Cover class; Species cover; Species frequency; Frequency of herbivore damage</td>
</tr>
</tbody>
</table>

Figure 4. Example of the field plot design used for alpine monitoring, which was replicated on four summits varying in elevation. The design is centered by the highest point on the summit, and extends to 10 m in elevation below the highest point. The 1 m² quadrats used to measure changes in vascular and non-vascular plant frequency are indicated in yellow.
After establishing and photographing the quadrats on all peaks, we installed 4 temperature loggers per peak buried 10 cm in the soil, measured plant cover and frequency in at least eight 1 m$^2$ quadrats per peak, and surveyed all summit area sections to determine changes in species diversity by elevation and aspect. We chose the lower left and upper right quadrats for sampling and priority will be given for sampling this subset in the future. Cover was measured in the quadrat by ocular estimate and frequency was measured as the presence of a species in one hundred 10 x 10 cm grid cells with the quadrat. We installed HOBO Onset pendant temperature loggers (UA-001-64) that are programmed to measure and record temperature every hour. To aid in identification, some plant specimens were collected, identified using regional floras, and compared to herbarium specimens. Lichen specimens were collected outside of the Summit Area Section, and care was taken to obtain specimens of all taxa found within all 1 m$^2$ quadrats.

We also collected a bulk soil sample (an aggregate of 3 cores to 20 cm depth) from each of the quadrat clusters to characterize soil chemistry and texture. The soil samples were air dried and sent to a cooperating laboratory at Colorado State University for analysis. In order to qualitatively describe disturbance, we documented the presence of potential stressors in and around each site. Using applicable metrics from the 2008 Human Disturbance Index developed by the Colorado Natural Heritage Program, (Rocchio 2007) and the California Rapid Assessment Method for Wetlands (Collins et al. 2008) we indicated a condition score for each site that ranges from 0 (pristine) to 100 (highly disturbed).

In total, the field work for 2011 took 17 days, four of which were used for travel and access to and from backcountry campsites. As the peaks were all within a close distance of each other, all four peaks could be accessed from one campsite, cutting down on travel time. Initial set-up and establishment of the four peaks took five people roughly six days to complete. This included the datalogger installation and soil sampling for the four peaks. The remaining 7 days of field work were spent acquiring vegetation data, identifying plant species, photographing the summits and obtaining locational data, and sampling lichens and mosses. In the future, we expect the vascular and non-vascular plant sampling to occur more quickly because we now have established species lists for each summit, but we will also allow for more days of field work to compensate for bad weather and short work days.

**Lichen identification**

Lichen specimens were collected at each of the four peaks at the GLORIA site. Field identification was conducted where possible, and lichen species detected in 1 m$^2$ quadrats were collected outside the sampling area for identification. All vouchers were taken to the University of Kansas Herbarium. Identifications were performed using a variety of techniques: chemical spot tests, Thin Layer Chromatography (TLC), and spore examination. TLC plates are deposited at the Colorado Natural Heritage Program. Lichen specimens are identified and labels have been produced. Vouchers will be stored at the University of Kansas, with a duplicate set provided to the Yellowstone Herbarium.

**RESULTS**

We report on results of 40 numbered collections of lichens collected at four alpine sites in the Absaroka Range, Yellowstone National Park. A total of 21 unique taxa were documented. Of these, 6 are new to the documented lichen flora of Yellowstone (Eversman 1998, Eversman et al. 2002). Moss specimens are pending identification.

**Annotated Checklist**

The checklist is alphabetical by species name. Although most taxa were documented within monitoring plots at all sites, only the collection site for the voucher specimens are indicated here.
Nomenclature follows Nash et al. 2001. The format and abbreviations associated with individual taxa in the checklist is as follows:

**Taxon Authority (Collection numbers TLC number) Site Number(s); substrate or species**

! indicates an addition to the Yellowstone lichen flora.

! Acarospora scabrida Hedl. ex H. Magn. (8054, 8078a, 8085, 8100); Sites 1, 2, 3, 4; rock
! Aspicilia americana B. de Lesd. (8072a); Site 1; rock
! Aspicilia desertorum (Kremp.) Mereschk. (8072b, 8080a, 8086, 8095); Sites 1, 3, 4; rock, soil
Caloplaca tiroliensis Zahlbr. (8091); Site 3; moss
Candelariella rosulans (Mull. Arg.) Zahlbr. (8077b, 8090, 8096); Sites 1, 3, 4, rock
! Cetraria islandica subsp. islandica (L.) Ach. (8093 TLC 1-11); Site 3; soil
Cetraria muricata (Ach.) Eckfeldt (8094 TLC 1-12); Site 3; soil
! Cladonia acuminata (Vain.) Lyng. (8087 TLC 1-14); Site 3; soil
Cladonia cariosa (Ach.) Spreng. (8081 TLC 1-15); Site 1; soil
Lecanora garovaglii (Körb.) Zahlbr. (8088 TLC 1-5); Site 3; rock
Lecanora polytropa (Hoffm.) Raben. (8055); Site 2; rock
Lecidea atrobrunnea (Ramond ex Lam. & DC.) Schaer. (8097); Site 4; rock
Lecidella stigmatea (Ach.) Hertel & Leuckert (8076 TLC 1-6, 8084); Site 3; rock
Physconia muscigena (Ach.) Poelt (8083a); Site 1; soil, Selaginella densa
Physconia squamulosum (Sommerf.) Arnold (8083b); Site 1; soil
Physconia muscigena (Ach.) Poelt (8083a); Site 1; soil, Selaginella densa
Physconia muscigena (Ach.) Poelt (8083a); Site 1; soil, Selaginella densa
Physconia muscigena (Ach.) Poelt (8083a); Site 1; soil, Selaginella densa
Rhizoplaca melanopthalma (DC.) Leuckert & Poelt (8070 TLC 1-9, 8072c, 8073 TLC 1-7, 8077a, 8080b, 8082 TLC 1-3); Site 1, rock
! Rinodina rosicina (Sommerf.) Arnold (8083b); Site 1; soil
Spatula heareoletata (Ach.) Lettau (8089, 8098); Site 3, 4; rock
Thamnolia subuliformis (Ehrh.) W.L. Culb. (8056 TLC 1-8); Site 2; soil
Umbilicaria virginis Schaer. (8071a, 8072d, 8078c); Site 1; rock
Xanthoria elegans (Link) Th. Fr. (8069, 8078d, 8080c); Site 1; rock

**DISCUSSION**

Lichen species diversity was relatively low at the YELL GLORIA site (21), as compared to the Rocky Mountain National Park site (ca. 90) (Egan 1971; Henson 2011 unpublished; Willard 1979). However, a large percentage (6 out of 21) of the species documented in our study are new to the lichen flora of Yellowstone. Overall diversity at the GLORIA site is possibly due to the volcanic (andesite) substrates and poorly developed soils that are present at the YELL site. A thin layer of fine, loose scree covers the bedrock at many of the north-facing aspects of the peak. Snowfields on the north and west aspects of the peaks linger late into the summer, and when melting move the scree downhill. Due to an inadequate amount of material, the following specimens were tentatively identified: Candelariella sp. (8071b), Lecidella aff. stigmatea (8071c), Lecidella aff. patavina (8099). Two species, Placidium squamulosum and Sporastatia testudina, were identified within the plot, but adequate material was not available to collect voucher specimens. Although moss cover was very low at the GLORIA site, all moss specimens will be mailed to Judy Harpel for identification. The GLORIA Network is processing all 2011 field data, and will be returning the completed database to ROMN and CNHP in the spring/summer of 2012.

**ACKNOWLEDGEMENTS**

This project was made possible by the funding from the University of Wyoming-National Park Research Station and the National Park Service Rocky Mountain Inventory and Monitoring Network (ROMN). Special thanks to Hank Harlow and Celeste Havener from UW-NPS for making this project possible. Mike Britten and Isabel Ashton from ROMN for their assistance with the GLORIA project. Ann Henson provided field assistance in lichen identification. Caleb Morse graciously donated his time and expertise to assist with the identification of lichen specimens. Erin Shanahan, Kristen Long, Laura O’Gan, Jennifer Whipple, and Christie Hendrix all provided assistance with the GLORIA project logistics. Special thanks to Meade and Andrea Dominick and the staff of the 7D Ranch for packing field and crew supplies into our remote camp site, and to the members of the Yellowstone National Park Dispatch. CNHP would also like to thank Andrew Pills and Julie Lyon with the Shoshone National Forest for input regarding logistics and for the use of the Sunlight Ranger Cabin as a crew base. Lastly, Lighthawk pilots Richard Spencer and Lisa Robertson kindly donated flights to help our crew evaluate terrain and approach.
LITERATURE CITED


Harpel J. 2011. Personal Communication with B. Kuhn regarding interest in identifying moss collections from GRTE and YELL. Email on February 22, 2011.


Comparing Stream Invertebrate Assemblages Before and After Wildfire in Yellowstone National Park

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University of Wyoming ✷ Laramie

Todd M. Koel ✷ Yellowstone National Park ✷ Mammoth

Abstract

Warmer, dryer climate conditions during the past three decades are thought to have increased severe fires in the western United States. Severe fires may change food webs due to altered light levels, nutrient concentrations, and hydrology in streams. To measure how wildfire changes stream food webs, we collected aquatic invertebrates before and after a fire, and calculated their density and biomass. To investigate the effects of wildfire on streams, we collected aquatic invertebrates from Cub and Little Cub Creeks on the east side of Yellowstone Lake before and after the East Fire. The timing of our study was serendipitous with the fire burning after our first year of collecting samples. Therefore, we collected one year of data prior to the wildfire (2003) and 2 years of data after the fire (2004 and 2005). The East Fire was a crown fire that set ablaze >17,000 acres and burned ≥95% of the watersheds of these streams. Working in Yellowstone National Park is opportune, because few other perturbations exist and the effects of wildfire can be easily studied. We analyzed the samples to understand how wildfire alters stream invertebrates. Our specific questions were: 1) What affect did wildfire have on the density and biomass of aquatic invertebrates? 2) How did the composition of aquatic invertebrates change before and after wildfire? Results from our study will inform managers about how the food base for fish and many birds (i.e., aquatic invertebrates) changes after wildfire.

Introduction

Warmer, dryer climatic conditions during the past 30 years have been attributed to increases in severe, stand-replacing fires in the western US (Westerling et al. 2006). The 1988 fires in Yellowstone National Park are an example of large, severe, stand replacing fires. Severe fires continue to burn in Yellowstone National Park in recent years, where thousands of hectares of forest were consumed. These stand-replacing fires remove the forest canopy and begin new successional trajectories that persist for decades (Turner et al. 2003). In addition, a shift in dominant species, along with the creation of abundant bare mineral soil can often increase the inputs of important nutrients such as nitrogen into adjacent streams and lakes (e.g., Gresswell 1999), similar to Likens et al. (1970) who discovered large pulses of nutrients exported from watersheds after clear-cutting a forest. Turner et al. (2007) studied terrestrial N cycling in Yellowstone and Teton National Parks after fire and noted that N uptake switch from microbes to plants as succession proceeded. Turner et al. (2007) and climate predictions have prompted us to further investigate how fire will alter aquatic invertebrates in burned watersheds.

Stream food webs may change after wildfire due to altered light levels, nutrient concentrations, and hydrology. Forest canopies open after wildfire increasing light levels that reach streams. Higher light levels along with higher nutrient concentrations increase primary production (e.g., algae) in streams (Mihuc 2004). Higher primary production may cause...
bottom-up effects in streams and subsequently change the aquatic invertebrates and fish in these ecosystems. However, changes in hydrology may limit algal, invertebrate, and fish growth (Minshall et al. 2001a). Water levels can change rapidly in burned watersheds, because of the lack of terrestrial vegetation as a buffer. Thus, floods can scour streams in burned watersheds removing algae and invertebrates. Bottom up effects and hydrology may change the energy flux to higher trophic levels, but little is known about the effects of fire on aquatic food webs (Minshall 2003). However, Perry et al. (2003) discovered that wildfire limited the invertebrates available to juvenile Chinook salmon (Oncorhynchus tshawytscha) in streams in Yukon Territory, Canada.

To investigate the effects of wildfire on streams, we collected aquatic invertebrates from Cub and Little Cub Creeks on the east side of Yellowstone Lake before and after the East Fire. Many studies of wildfire compare a burned stream with a reference stream (Minshall et al. 2001b), because collecting samples prior to a wildfire is by chance. Thus, having samples before and after fire will improve our knowledge of the effects of wildfire on stream invertebrates. The timing of our study was serendipitous with the fire burning after our first year of collecting samples. We collected one year of data prior to the wildfire (2003) and 2 years of data after the fire (2004 and 2005). Therefore, our study design is ideal to estimate the effects of wildfire on stream invertebrates. The East Fire was a crown fire that set ablaze >17,000 acres and burned ≥95% of the watersheds of these streams. Working in Yellowstone National Park is opportune, because few other perturbations exist and the effects of wildfire can be easily studied. Our specific questions were: 1) What affect did wildfire have on the density and biomass of aquatic invertebrates? and 2) How did the composition of aquatic invertebrates change before and after wildfire? Results from our study will inform managers about how the food base for fish (i.e., aquatic invertebrates) changes after wildfire.

**METHODS**

We collected samples in Cub and Little Cub Creeks (Figure 1), which are tributaries on the east side of Yellowstone Lake, Yellowstone National Park, Wyoming. Cub Creek is a third order stream that is 11.8 km in length and originates in the Absaroka Range near Jones Pass. The 2180 ha Cub Creek watershed was dominated by lodgepole pine (Pinus contorta), whitebark pine (Pinus albicaulis), and subalpine fire (Abies lasiocarpa) and the bedrock was mostly andesite and rhyolite. Little Cub Creek is a first order stream that is 3.0 km in length. The 458 ha watershed is dominated by lodgepole pine. Lightning ignited the East Fire which was discovered on 11 August 2003. The crown fire burned 9510 hectares including 95% of the Cub Creek watershed and 100% of the Little Cub watershed.

To estimate how the hydrograph compared among years, we measured discharge during each visit to the streams in 2003 to 2005. We measured discharge using the current meter method (Gore 1996). We calculated the average daily discharge by integrating under the curve and dividing by the total number of days in the period.

We collected aquatic invertebrate samples from Cub and Little Cub Creeks located on the east side of Yellowstone Lake, Yellowstone National Park. Six Hess samples (0.086 m²) were collected in each stream every 2-4 weeks during the summers of 2003 to 2005. We preserved invertebrates in 70% ethanol. We identified aquatic invertebrates using a dissecting microscope, (Merritt et al. 2008; Thorp and Covich 2010). We calculated biomass by measuring the first 20 individuals of each taxon and converting lengths to biomass using published regressions (Benke et al. 1999). We calculated the number of taxa in the orders Ephemeroptera, Plecoptera, and Trichoptera (EPT), which is a simple diversity index of taxa that are generally sensitive to water quality. Finally, we calculated the density of functional feeding groups using Merritt et al. (2008). We called insects with more than one main feeding method generalists.

**PRELIMINARY RESULTS**

The hydrograph at Cub Creek was less predictable after the fire. In 2003, discharge at Cub Creek decreased throughout the summer. After the watershed burned, discharge displayed a different pattern. On 18 July 2004, a large flood occurred after a rain storm, which scoured and rearranged the

![Figure 1. Photos of Little Cub Creek before and after the wildfire.](image)
stream. We observed that discharge rose after most rain storms during the summers of 2004 and 2005. Average daily discharge was >2x higher after wildfire (66 and 53 m³/s in 2004 and 2005 respectively) monitored before fire (26 m³/s) when compared in June through October (Figure 2). Unfortunately, we did not measure discharge in Little Cub Creek before the fire; however, mean daily discharge in Little Cub Creek was lower in 2004 (0.046 m³/sec) than 2005 (0.094 m³/sec) between May and July.

In Cub Creek, we collected 34 invertebrate taxa of which 31 were insects from 6 orders (Figure 3). Diptera were the most abundant order of insects in the stream, followed by Ephemeroptera and Plecoptera. On average, we collected 11 (range 1-20) taxa in each sample. Total invertebrate density was similar the summer before (1000 ind/m²) and after wildfire (2600 ind/m²), but total density was over two times higher 2 years after wildfire (2200 ind/m²; ANOVA, P = 0.18, df = 2, F = 1.75, respectively). Total Plecoptera density nearly doubled 2 years after the fire (240 ind/m² in 2003 and 2004 vs. 570 ind/m² 2005; ANOVA, P = 0.069, df = 2, F = 2.75 (Figure 3). The most abundant Plecoptera genera were Sweltsa and Suwallia (family Chloroperlidae). Sweltsa density increased 2 years after the fire (470 ind/m²), but the flood in 2004 probably reduced density (130 ind/m²) compared to pre-fire numbers (250 ind/m²; ANOVA, P = 0.064, df = 2, F = 2.83). Conversely, Suwallia density (45 ind/m²) was lower after the fire in 2004 (30 ind/m²) and 2005 (10 ind/m²; ANOVA, P = 0.091, df = 2, F = 2.46).

Diptera density increased by >3x after wildfire (1450 ind/m²) compared to pre-fire estimates (400 ind/m²; ANOVA, P = 0.0048, df = 2, F = 5.65; Figure 3). Chironomidae were the most abundant family of true flies (Diptera). The density of both non-Tanypodinae (1250 ind/m²) and Tanypodinae (predaceous; 82 ind/m²) Chironomidae increased 3x and 5x respectively compared to pre-fire estimates (350 ind/m²; ANOVA, P = 0.011, df = 2, F = 4.75 and 13 ind/m²; ANOVA, P = 0.18, df = 2, F = 1.75, respectively).

Total Ephemeroptera density was similar among years (ANOVA, P = 0.22, df = 2, F = 1.50; Figure 3). Several taxa of mayflies increased after wildfire, such as Rithrogena (50 v. 250 ind/m²; ANOVA, P = 0.15, df = 2, F = 1.95), Drunella doddsi (13 vs. 83 ind/m²; ANOVA, P = 0.0008, df = 2, F = 7.6), and Serratella (3 vs. 45 ind/m² ANOVA, P = 0.0002, df = 2, F = 9.5). In contrast, the density of Cinygma decreased after wildfire (7.6 vs. 0 ind/m²; ANOVA, P = 0.02, df = 2, F = 4.1). Finally, several genera increased in density immediately after wildfire and then decreased to pre-fire density 2 years after fire, such as Cinygmula, Epeorus, and Plauditus.

Total Trichoptera density decreased after wildfire (30 ind/m² in 2003 vs. 12 ind/m² in 2004 and 2005; ANOVA, P = 0.0007, df = 2, F = 7.81; Figure 3). The density of both Glossosoma (18 vs. 3 ind/m²; ANOVA, P = 0.0001, df = 2, F = 10.1), and Rhyacophila (12 vs. 6 ind/m²; ANOVA, P = 0.23, df = 2, F = 1.5), decreased after wildfire.
The dominant functional feeding groups were the same before and after fire. Generalists were the most abundant group before and after the fire and their density increased after fire (530 ind/m² in 2004 and 1300 ind/m² in 2005) compared to pre-fire conditions (370 ind/m²; ANOVA, P = 0.007, df = 2, F = 5.3; Figure 4). Compared to pre-fire densities (350 ind/m²), predators initially decreased in 2004 (220 ind/m²), but nearly double in density in 2005 (660 ind/m²; ANOVA, P = 0.07, df = 2, F = 2.6). Scrapers, the third most abundant group, had similar densities before and immediately after fire (215 ind/m² in 2003 and 250 ind/m² in 2004), but they increased 2 years after fire (400 ind/m²; ANOVA, P = 0.31, df = 2, F = 1.2). The density of collector-gatherers increased after fire (145 ind/m² in 2004 and 125 ind/m² in 2005) compared to pre-fire (45 ind/m²; ANOVA, P = 0.01, df = 2, F = 4.5). Shredders increased in density (30 ind/m² in 2004 and 100 ind/m² in 2005) compared to pre-fire densities (8 ind/m²; ANOVA, P = 0.01, df = 2, F = 4.6). Finally, filterers, the least abundant group, had similar densities before (1 ind/m²) and after fire (2-3 ind/m²; ANOVA, P = 0.7, df = 2; F = 0.3).

Figure 4. Density of aquatic invertebrates by their functional feeding groups before (2003) and after (2004 and 2005) the wildfire in Cub Creek.

We collected 42 invertebrate taxa in Little Cub Creek of which 37 taxa were insects in 5 orders (Figure 5). Diptera were the most abundant order of insects followed by Coleoptera, Plecoptera, Ephemeroptera, and Trichoptera. On average, we collected 13 taxa per sample (range 5-21). Total invertebrate density was lower before wildfire (5800 ind/m²) compared to 2004 (11,300 ind/m²) and 2005 (10,900 ind/m²; ANOVA, P = 0.04, df = 2, F = 3.1). On average, more taxa were collected in 2003 (14) compared to 2004 (12) and 2005 (13; ANOVA, P = 0.035, df = 2, F = 3.5). The most EPT taxa were collected in 2003 (6.9) compared to 2004 (5.3) and 2005 (6.6; ANOVA, P = 0.038, df = 2, F = 3.39).

Diptera increased nearly 4x one year after fire (8000 ind/m²) and nearly 3x two years after fire (5900 ind/m²) compared to pre-fire densities (2400 ind/m²; ANOVA, P = 0.0001, df = 2, F = 9.94) in Little Cub Creek (Figure 5). Similar to Cub Creek, Chironomidae were the most abundant family of Diptera. Non-Tanypodinae Chironomidae were far more abundant than the predaceous Tanypodinae subfamily. Chironomidae increased >3x and >2x after fire in 2004 and 2005 respectively (ANOVA, P = 0.0002, df = 2, F = 9.5). Other common Diptera were Tipulidae (Hexatoma, Rhabdomastis, Dicranota, and Tipula), Ceratopogonidae (Proezzia), Simulidae (Simulium), and Psychopteridae (Psychoptera).

Figure 5. Density of aquatic insect orders in Little Cub Creek before (2003) and after (2004 and 2005) wildfire.

Coleoptera (830 ind/m²; ANOVA, P = 0.31, df = 2, F = 1.18) and Plecoptera (600 ind/m²; ANOVA, P = 0.32, df = 2, F = 1.17) densities were similar among years in Little Cub Creek (Figure 5). Heterlimnius (Elmidae) were by far the most abundant beetles we collected (98% of individuals collected). Sweltsa (Chloroperlidae) were the most abundant stoneflies that we collected (81% of individuals collected).

Ephemeroptera densities increased 2 years after fire (700 ind/m²) compared to 2003 (325 ind/m²) and 2004 (375 ind/m²; ANOVA, P = 0.045, df = 2, F = 3.2) in Little Cub Creek (Figure 5). Cinygmula (Heptageniidae), Plauidus (Baetidae), Serratella (Ephemerellidae), and Ameletus (Ameletidae) were the most abundant mayfly genera in Little Cub Creek. Cinygmula and Serratella densities were similar among years (ANOVA, P >>0.05). In contrast, Plauidus (ANOVA, P = 0.0015, df = 2, F = 7.0) and Ameletus (ANOVA, P = 0.032, df = 2, F = 3.6) densities increased 2 years post-fire.

Similar to Cub Creek, Trichoptera densities decreased post fire in Little Cub Creek (ANOVA, P < 0.0001, df = 2, F = 11; Figure 5). We collected 2 genera of Trichoptera in Little Cub Creek, Glossosoma (Glossosomatidae) and Rhyacophil (Rhyacophilidae), all of which responded similarly to fire.
Non-insect invertebrates were much more abundant in Little Cub Creek compared to Cub Creek. Non-insect invertebrate densities were similar before and after fire (2000 ind/m²; ANOVA, P = 0.41, df = 2, F = 0.91; Figure 5). Oligochaeta (55% of individuals) and Ostracoda (35% of individuals) were the most numerous.

The functional feeding groups in Little Cub Creek were similar before and after fire (Figure 6). Generalists were the most abundant group, following by filterers, gatherers, predators, scrapers, and shredders in decreasing order. Filterers (ANOVA, P < 0.0001, df = 2, F = 10.5), generalist (ANOVA, P = 0.0005, df = 2, F = 8.3), and shredders (ANOVA, P = 0.015, df = 2, F = 4.4) increased in density after the fire. However, the densities of gatherers, predators, and scrapers were similar before and after wildfire (P > 0.05).

The density of aquatic invertebrates not only changed among years, but density changed through time. In general, the density of aquatic invertebrates increased between May and October each year (Figure 7). In general, we measured the highest densities of invertebrates in October. However, the flood that occurred on July 18th 2004 reduced the densities of invertebrates in Cub Creek, but we did not observe the same decrease in density in Little Cub Creek. In Little Cub Creek, invertebrate densities increased each year after fire; however, the density of invertebrates in Cub Creek was similar in 2003 and 2005.

Similarly, biomass changed among years and throughout the summer (Figure 8). In general, biomass tends to increase between May and October; however, biomass in Cub Creek remained low after the flood in 2004. We did not observe a decrease in insect biomass after the flood in Little Cub Creek.
Interestingly, we measured a decrease in insect biomass immediately after the fire in Little Cub Creek, but biomass was similar immediately before and after fire in Cub Creek. Biomass in both streams was highest in October of 2005.

**Management Implications**

Wildfires can greatly change landscapes, ecosystems, communities and population dynamics, but these natural events are unpredictable and difficult to study. Previous studies have investigated the effects of fire by comparing streams in burned watersheds to unburned reference streams (e.g., Minshall et al. 2001a). In our study, we were able to compare pre- and post-fire conditions in the same stream, because a fire unexpectedly burned ≥95% of the watersheds after our first field season.

Several factors likely determine the extent to which stream processes will be affected after wildfire. For example, more severe fires and fires that burn the majority of a watershed tend to have a greater impact on streams (Minshall 2003). In Cub and Little Cub Creeks, most of the watershed was burned by a crown fire, which likely affected the stream to a greater extent. Smaller streams with higher gradients and vegetation cover are also predicted to be affected to a greater degree after fire (Minshall 2003). Cub Creek is a 3rd order stream that drops 51 m per km of stream length. Little Cub Creek is a 1st order stream in a forested watershed that drops 35 m in elevation per km of stream length. Therefore, the East fire likely had a large effect on processes within Cub and Little Cub Creeks.

Aquatic invertebrates declined immediately after wildfire in Little Cub Creek; however, we did not observe the same trend in Cub Creek. Water has a high specific heat which means that a lot of energy is needed to raise the temperature of the water. Little Cub Creek is a much smaller stream than Cub Creek, thus wildfire probably increased water temperatures to a greater degree in the Little Cub Creek. Biomass of invertebrates declined immediately after wildfire in Little Cub Creek. Conversely, invertebrate densities in Cub Creek were higher compared to before wildfire, which appears to be an annual trend. We did not observe changes to stream invertebrates in Cub Creek until the following summer. Roby and Azuma (1995) found that invertebrate density and richness were lower in burned streams 3 weeks after fire in northern California.

Previous studies reported that aquatic invertebrate densities increased after wildfire (Albin 1979, Roby and Azuma 1995, Gresswell 1999). In Cub Creek, invertebrate densities were initially higher than pre-fire estimates the first summer after wildfire, but a July flood greatly reduced abundance for the rest of the year. However, we estimated that invertebrate densities were higher 2 years after wildfire, similar to other studies. In contrast, Minshall et al. (2001b) noted that density was lower in burned streams compared to reference streams in Idaho. In this stream, densities were likely lower because of scouring and runoff in the stream channel, similar to what we observed in 2004.

Invertebrate richness is reported to decrease in burned compared to reference streams (Gresswell 1999, Roby and Azuma 1995, Minshall et al. 2001b). Roby and Azuma (1995) found that invertebrate richness was lower in burned streams for the 11 years that they collected samples. In contrast, taxa richness was similar in burned and reference streams after 10 years, which may have been caused by lower water levels during drought. We did not detect a change in taxa richness during the 2 years after fire as the other studies did.

Food sources and invertebrate functional feeding groups are predicted to change after wildfire. Prior to fire, invertebrates primarily use allochthonous inputs (e.g., leaf litter); however, after the vegetation burns and the forest canopy opens invertebrates in streams likely switch to autochthonous sources (i.e., stream algae; Mihuc 2004). Because of these changes in resources, invertebrate functional feeding groups may change. Shredders and collector-gatherers in unburned streams are predicted to be replaced by scrapers and filterers (Minshall et al. 1989, Gresswell 1999). In fact, Minshall et al. (2001b) noted that scrapers and filterers became more abundant after fire. Scrapers likely increased to eat the biofilm that became more abundant in response to higher nutrient concentrations and light. Similarly, the concentration of fine particles in the water may have increased after fire, making an abundant food source for filterers. In contrast to these studies, the dominant functional feeding groups in Cub Creek did not change before and after fire. Collector-gatherers and shredders were some of the least abundant functional feeding groups before and after the wildfire in Cub Creek, whereas scrapers and filterers were the third and least abundant groups. Perhaps the food web in Cub Creek never relied too heavily upon fine particulate organic matter, but biofilm appeared to have been an important food source in Cub Creek before the fire.
In Little Cub Creek, gatherers and filterers were common before and after wildfire, but scrapers and shredders were never abundant. Many model streams have headwaters in deciduous forest; however, streams in Yellowstone National Park do not have such abundant leaf litter, which may at least partially explain differences compared to other studies.

Wildfire can alter the composition of stream invertebrates. In burned Idaho streams, disturbance adapted insects, such as Baetis and Chironomidae, increased in abundance after wildfire (Minshall et al. 2001b). Similarly, Chironomidae density increased in Cub and Little Cub Creeks after fire. However, the density of more sensitive taxa can decrease after wildfire. For example, Ephemeroptera (Minshall et al. 2001a) and Trichoptera (Albin 1979) densities were lower in burned compared to unburned streams. The density of EPT in Cub and Little Cub Creeks was similar before and after wildfire, but the response varied by order. Therefore, decreased water quality may not have been responsible for changes in composition. Instead, the ability to withstand floods and increased fine sediments may have been at least partially responsible for changes. In Cub Creek, the density of Ephemeroptera with flattened bodies increased in density after wildfire. The body form of these genera may have allowed them to persist through floods and other scouring events that occurred after the fire while other taxa were swept away. Similar to Albin (1979), Trichoptera densities in Cub and Little Cub Creeks decreased after fire. These filter feeders may have been negatively affected by an increase in fine sediments that often occurs after wildfire (Minshall et al. 2001a).

Two opposite forces affect streams after wildfire. First, more nutrients and light typically increase primary production in streams. Increases in in-stream food resources may cause bottom-up effects that increase stream invertebrates and their consumers (e.g., fish). Second, the loss of vegetation and forest on the landscape can alter the hydrology of a watershed. The lack of primary producers can cause variable discharge, scours, and floods. In unburned watersheds, the primary producers slow the movement of water through the watershed creating a slow and decreased release of water through the growing season. In Cub Creek, hydrology controlled the invertebrate assemblage in 2004 by likely reducing biofilm and removing invertebrates. However, bottom-up effects dominated in 2005 when there were no major floods and invertebrate densities were higher.

Fire may also impact fish in burned streams through food web effects. When bottom-up effects predominate in burned streams, more food (i.e., invertebrates) may be available to fish. However, when hydrology dominates burned streams, less food may be available to fish. Yellowstone cutthroat trout (Oncorhynchus clarkii bouvieri) spawn in Cub and Little Cub Creeks for 2 to 3 months each year. Although the adults do not live in these streams, juvenile cutthroat trout rear here. Aquatic invertebrates are likely the dominant food for these young trout. Juvenile cutthroat trout were likely washed out of the stream in 2004 when Cub Creek was scoured; however, these fish may have enjoyed an abundant food source in 2005. High densities of aquatic invertebrates may translate into higher growth rates and ultimately higher survival rates when these fish migrate downstream to Yellowstone Lake.

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INTERN REPORTS
FROM PERMIT TO NEW KNOWLEDGE: IMPROVING INSTITUTIONAL ACCOUNTABILITY AND USER ACCESS BY TRACKING DOCUMENTATION FROM RESEARCH PROJECTS IN GRAND TETON NATIONAL PARK

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INTRODUCTION

In Summer 2011, the author undertook a number of projects for the Museum & Archives in the Science and Resource Management division of Grand Teton National Park (GRTEN). Alice Hart, Museum Curator and Archivist for the Park, supervised the work, which was part of an internship for graduate credit. The two major project categories were 1) Research Permits and 2) Biological Science Program Files.

Some of the projects were completed, while for others, the scope and parameters of what needs to be done was established and recorded. This article provides a summary of what was accomplished, and a pathway to completion of the projects, and it is based on reports presented in memo form to Alice Hart at the end of the internship (Phalen 2011a), and a final report for the graduate course (Phalen 2011b).

The work was done at National Park Service (NPS) offices at the Colter Bay Visitor Center, about 3 miles from the AMK Ranch, and also at the temporary Park headquarters complex in Moose, in the southern part of the Park.

The goal at the outset of these projects was to improve NPS accountability for specimens and reports, as well as other documents that result from decades of scientific and cultural research conducted under Park permits and to increase access to those assets for Park staff and researchers. When scholarly works can be matched to specific Park permits, NPS has direct evidence of how permits lead to new knowledge. The variety of different projects focusing on this goal reflects the diversity of sources about permit work on file in the Archives.

PROJECT CATEGORY I: RESEARCH PERMITS

This category of projects centers on decades of permits for doing research in the Park, which are mostly within a processed collection, Catalog number GRTEN 55552, series: Research Program Records and Permits (Figures 1 and 2). In the July 2011 draft Finding Aid, the scope note indicates the series permits and other types of documents that relate to the “Grand Teton and Yellowstone National Parks research program between 1958 and 2001” (United States Department of the Interior, National Park Service Intermountain Region Museum Services Program, 2011, p.15). The Finding Aid lists permits by date, title or purpose of research project, and investigator name(s), in addition to its series, subseries, and file unit number.

For a majority of the investigators whose permits are listed in the Finding Aid, the following two categories of documentation are either not on file, or at least not readily accessible: 1) the final reports the Park requires investigators to submit at the conclusion of permit work; and 2) other associated scholarly works that were derived from permit work. These two categories are important because they demonstrate how research authorized by NPS through its permit system leads to new knowledge. It appears that over the decades, final reports may have been separated from permits, or in...
some cases, they may not even have been submitted. Since the Park formalized its Archives program, in 2006, these problems are more avoidable because the organization of such important information now has specific professional oversight.

The full cycle of documentation stemming from research done under permits from NPS could include the following, listed in the order in which they are usually generated: proposal $\Rightarrow$ permit application/permit $\Rightarrow$ annual report(s) $\Rightarrow$ final report $\Rightarrow$ other papers (e.g., thesis/dissertation; journal article; book chapter; conference paper; other report). Although examples of each document type were found, final reports were only rarely encountered.

Figure 3 is an example of an application/permit, for insect specimen collection, submitted in 1964 by Howard Evans of Harvard University. The late Dr. Evans is remembered by The National Academies Press as “one of the twentieth century’s leading entomologists and insect natural historians” (West-Eberhard, 2004). This original permit is but one example from the vast amounts of primary and secondary source material on important research that the GRTE Museum and Archives collects, maintains, and provides access to.

In the proposal for this internship, the majority of the time was projected to be spent contacting researchers whose permits lack follow-up documentation, and/or check repositories that house their research materials to record what specimens they had taken and scholarly works written. However, as the work progressed, it became clear that it would not make sense to start contacting people until the various information sources were documented.
Of the various sources consulted in searching for documentation, perhaps the most intriguing is the *Bibliography on the Ecology of Grand Teton National Park*, a 1982 computer printout, on accordion-folding paper with holes on the sides! That is the only known copy, as no electronic file is known to exist. There were numerous matches from the *Bibliography* (U.S. Department of the Interior 1982) to the lists of permits, which have been processed and organized in a *Finding Aid*.

In the final report to the Archivist on this internship (“permit memo” hereinafter) (Phalen 2011a), the Research Permits category was subdivided into distinct projects, re-worded here for clarity:

1. **Finding Aid Revision (Attempted)**
   
   A number of errors were found in the draft finding aid for the collection of permits, so a draft revision was created, with alterations and additions suggested.

   Unfortunately, the attempted revision failed and there was no time to correct it. Formatting and other problems emerged throughout the draft revision, indicating the file had been corrupted. To facilitate quick reconstruction of the revision to that point, the specific problems were listed in the permit memo, with references to an appendix handwritten record of all changes and additions to the draft finding aid.

   
   The *Bibliography* is a list of resources, published and unpublished, resulting from research in GRTE. Though once saved in electronic format, today there is only one hardcopy version known to exist, and it is an accordion-folded computer printout with holes along each side edge, dated 1982, and housed in a simple binder custom-fit for such printouts (Figure 4). It turned out to be a productive resource for this project. Each bibliographic entry is numbered, making it easy to refer to.

   For this project, all pre-1983 permits listed for each investigator in the 55552 *Finding Aid* were cross-referenced with entries in the *Bibliography* to look for documents that appear to be authored or co-authored by the listed investigator, and on or very close to the topic of the permit in the Finding Aid. Matches, or at least possible matches, were found for an estimated 15 to 20 percent of the permit entries. Cross-references to entry numbers in the *Bibliography* were recorded in pencil across from the research topic and investigator’s name on a photocopy of the *Finding Aid*’s Container List section. This project was completed.

   ![Figure 4. Detail from the first page of the only copy known to exist of GRTE’s Bibliography on the Ecology of Grand Teton National Park (1982). The meaning of the designation “Famulus Version” is not known as of this writing (May 2012).](image)

3. **Master Lists Cross-Referenced with Research Permit and Reporting System (RPRS) Database**
   
   Photocopies were made of several “Master Lists of Collecting Permits” (1997 through 2001, from one of the folders in the 55552 *Finding Aid*) (U.S. Department of the Interior 2001). These simply list the investigator name, topic of research, and permit number. It appears that the original permits listed may not have been retained. The names of the investigators on the lists were checked in the Research Permit & Reporting System (RPRS) Database, at rprs.nps.gov, using “IAR” (Investigator Annual Report) searches, with the “Park” field set to “Grand Teton NP”. Report number and Permit number were recorded for each potential match to a report that could have been written based on work done under the permit listed. This work was about half-way completed.

4. **Finding Aid Container List Cross-Referenced with Uncataloged Theses list**
   
   Electronic “Find and Replace” searches were conducted in the MS Word document of the 55552 finding aid, using author names from the bibliographic entries on the printout from an internal Excel spreadsheet listing theses owned by the GRTE Library (U.S. Department of the Interior 2011). When a match was found, the series and folder
number(s) were listed in pencil to the right on the printout. This work was completed.

5. Finding Aid Container List Cross-Referenced with Materials Transferred list

Electronic “Find and Replace” searches were conducted in the electronic version of the Word document of the 55552 Finding Aid, using author names from the bibliographic entries on the printout from an internal Excel spreadsheet listing literature that the Archives had moved from a prior location.

Some matches were found, and these were recorded by handwriting on the printout. This work was about 20 percent completed.

6. Finding Aid Container List Cross-Referenced with online Greater Yellowstone Bibliography (GYB)

The University of Wyoming Libraries maintains the Greater Yellowstone Bibliography (GYB) (VanArsdale and Hert, 2000). The GYB is an electronic resource accessible via the UW Libraries' website. According to the website, the GYB includes “over 28,900 bibliographic citations to scholarly, popular, professional, and creative literature about the greater Yellowstone region...” (Figure 5).

Cross-referencing these results with permits or other research for Joel Berger in the Finding Aid for Catalog Number GRTE 55552 yields the following possible matches: a) #1 in the above Results list might be based, at least in part, on research done under the permits listed in the finding aid as: “Carnivores - Pyare/Berger, 2000” (Series 001.001, Folder 011), and “Wolves/Coyotes/Antelope - Berger/Pyare/Snow, 1999-2001” (Series 001.004, Folder 186); b) #4 in Results above, highly likely correlates with Finding Aid listing: “Brucellosis in Bison/Bison Ecology - Berger/Cain, 1997-2000” (Series 001.004, Folder 038).

However, using the GYB was generally a frustrating process overall. For example, a GYB author search for “Cole, G.” returned a full 52 results, yet none of them correlates with permits listed in the Finding Aid for Glen Cole, a prolific researcher. In fact, the only entry in the finding aid attributed to Cole is for work with bald eagles, but that work is not in GYB. It is important to consider that many of the GYB listings for Cole stem specifically from research in Yellowstone National Park, not Grand Teton.

For purposes of this project, the most useful search in GYB is by author. Comparison of the GYB, which was completed in 2000 and last updated in 2001, with the 1982 computer printout bibliography (for the pre-1982 period covered by both) showed some overlap in listings between the two, but also numerous unique entries in each resource. Some attempts to cross-reference author search results in GYB with permits or other research in the Finding Aid yielded possible matches. As an example, Figure 6 shows the results from a GYB author search for “Berger, J.” That search returned seven results, of which, two were possible matches to permits listed in the Finding Aid.

Figure 6. GYB search result list for Author search on: “Berger, J”.

Figure 5. University of Wyoming’s “Greater Yellowstone Bibliography” search interface page. Accessible via UW Libraries - www-lib.uwyo.edu - under Research Tools => Articles and Databases. Text at bottom has been highlighted for easier reading. Accessed September 2011.
since there was a limited amount of time that could be spent using it. Also, only the **Finding Aid** container list was checked, and to complete this project, the Master Lists should also be checked for matches.

### PROJECT CATEGORY II.
**GRTE BIOLOGICAL SCIENCE PROGRAM FILES**

**Inventory of the Senior Biologist's files**

A preliminary inventory was completed for approximately 25 linear feet of material, from three four-drawer cabinets in Senior Wildlife Biologist Steve Cain's office in the temporary Science & Resource Management office building in Moose (Figures 7 and 8).

**Figure 7. Senior Biologist Steve Cain, in his office in Moose. Science and Resource Management building, temporary GRTE headquarters complex, Moose, Wyoming.**

The material mostly contained files on various animals in the Park, with major entries for Bison, Elk, Grizzly Bear, and Wolves. For each file cabinet drawer, an Excel spreadsheet file was created, with a concise descriptive line of data for each folder. Contrary to modern spreadsheet data entry conventions, which call for separate columns for each data category, a single field was used for several categories of descriptive data: Transcribed Folder Label; Subject; Format; and Inclusive Date(s) (Figures 9 and 10). This was necessary to maintain consistency in formatting with prior preliminary inventories.

**Figure 8. GRTE Biological Science Program Files. These are the cabinets where Senior Biologist Steve Cain kept the files. Science and Resource Management building, temporary GRTE headquarters complex, Moose, Wyoming.**

**Figure 9. Preliminary Inventory of GRTE Biological Science Program Files: Screen capture showing excerpt of Excel spreadsheet file for File Cabinet 4, 4th drawer from top. Preservation alerts are in red.**
There is a balance that must be maintained when doing this kind of descriptive work on a collection. In a “perfect world,” this preliminary inventory would only be the first descriptive overview of the collection. Subsequent phases of processing of the collection would entail increasingly-detailed description, eventually at the item level. However, the realities of time and money constraints in the realm of archives usually impose limits on the amount of processing that can be done. So it can often be assumed that there will be few phases of processing. Also, the Science and Resource Management division needed to account for these files, especially the older archival material, prior to the impending move into the newly remodeled Park headquarters building. For those reasons, this was an extra thorough preliminary inventory, with some appraisal of the material as well. Red text was used to highlight notes about preservation issues, e.g., for colour photo prints with fading or transferring colours; or for privacy alerts, e.g., when a person’s Social Security Number or personal medical information was found in a file. (Figure 10).

Thus, until recently, the manner and extent of what was kept of the records of each staff member’s files was entirely up to each individual staff member. Through the years, the senior biologists appear to have erred on the side of keeping more than throwing away. While better than the inverse tendency, there is a downside in that there is a great deal of redundancy in the files. It can be time-consuming to sort through, but on the whole, it is corrected fairly easily; whereas the other extreme of being too quick to discard material would have more likely resulted in valuable archival information being lost.

The preliminary inventory was completed, but the task of cross-referencing the dozens, perhaps even hundreds, of reports with the permit files from GRTE 55552 needed to be left for others to complete.

**CONCLUSION**

Searching for matches between lists of documents is sometimes tedious, but has valuable outcomes. Through these projects, with every match of a report or publication to an old permit that authorized scientific or cultural research in the Park, the GRTE Museum and Archives enhances the accountability of the National Park Service for its resources; resources that have been in high demand for use by researchers for many decades now.

Final reports and other scholarly works that are derived from permits document new knowledge in physical and social science areas; and the one-of-a-kind archival files from the Park's Biological Science program document the history of GRTE wildlife management. As a result of these projects, NPS staff, visitors, and researchers will have greatly improved access to that legacy of knowledge and Park history.

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**LITERATURE CITED**


CLASSES
ECOLOGY OF THE GREATER YELLOWSTONE ECOSYSTEM

INSTRUCTOR ♦ SCOTT CARLTON ♦ LARAMIE COUNTY COMMUNITY COLLEGE ♦ LARAMIE

Figure 1. Issues investigated included ungulate grazing (photo by C. Havener).

CLASS OVERVIEW

During June, 2010 six wildlife students from Laramie, WY traveled to Grand Teton and Yellowstone National Parks for a 10 day course on the Ecology of the Greater Yellowstone Ecosystem. The course focused on the vegetation, animals, geology, and management challenges concerning the parks. For each of the components, a student gave a brief introduction to the class on the topic we would be exploring that day. Students learned to identify trees using dichotomous keys and then spent the day in the field performing vegetation transects in recently burned to mature forests within the parks. Students then used their data sets to make inferences into species composition and the process of succession across the landscape. Students learned about individual tree life histories, including the role of serotiny in early forest successional stages following a fire.

The geology of Yellowstone National Park was explored by visiting and talking about the volcanic history of the park, the various geysers and hot springs, and the biota that inhabit these springs. This was an excellent opportunity to introduce the students to survival in extreme environments. Students were able to spend the morning with bison biologists for the park where they had the opportunity to hear about the challenges both ecological and political in managing bison herds. Students then spent the remainder of the day tracking bison using VHF telemetry and performing behavioral observations on large herds.

The fisheries crew in charge of lake trout removal hosted the students for a day on Yellowstone Lake. Students participated in assisting fisheries biologists in pulling nets and removing lake trout captured in the nets. They were able to interact with park biologists and see firsthand one of the challenges with maintaining native fish species by trying to control non-native fish species.

This course exposed wildlife students to many facets of Grand Teton and Yellowstone National Parks and allowed them to interact one on one with park biologists.
Field Research and Conservation

Instructors ✶ Chuck Collis ✶ Katie Storms
Clayton High School ✶ Clayton, MO

Class Overview

Field Research & Conservation emphasizes long-term field research experiences, examines ecosystem processes, and explores the evolution of American perspectives about nature.

A group of four students was selected from numerous applicants to serve as research assistants to Dr. Scott Sakaluk. During our two week stay at the AMK, our primary objective was to perform a mark-recapture study to estimate the sagebrush cricket (Cyphoderris strepitans) population at Dead Man’s Bar. We determined that the male population is 914 +/- 333 individuals (95% confidence interval).

Our secondary research objective was to gather preliminary data pertaining to female receptiveness to male nuptial gift behaviors when the females are held on different diets. Our hypothesis was that females on poor diets (apple only) would be more receptive to calling males than females held on an ad libitum diet consisting of apple, pollen, and cat food. Although the sample size was too low for a complete study, the results indicate that this investigation may deserve additional research: 3 of 4 females in the poor diet group mounted a male while only 1 of 5 females in the rich diet group mounted a male.

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. Dr. J. Chad Johnson stands out in particular in this regard because we were able to discuss his research over dinner a number of times and also work with him in the field and lab.

Aside from conducting research, we explored Grand Teton and Yellowstone National parks to learn about ecosystem dynamics, the role of disturbance and succession, and the influences of geologic process in shaping landscapes and the communities that occupy them.
Figure 2. (a) Students applying identification markers to captured sage cricket, (b) Marked sage cricket released to its capture site, (c) Students admiring view from the AMK Ranch shoreline.
CLASS OVERVIEW

This course offers in-service teachers an opportunity to learn about geology and geoscience education through a 2-week inquiry-based field course across Wyoming, South Dakota and Nebraska. In 2011 this course utilized the UW-NPS facilities for 3 days in mid-June. The group discovered local glacial features, evaluated the uplift and subsidence history of the Grand Tetons and Jackson Hole, respectively, and built upon growing geological abilities and knowledge of the geological evolution of the Rocky Mountain region. The 2011 course included seven teacher participants (5 from Nebraska and 2 from North Carolina), one education and media facilitator from the ANDRILL Program at the Univ. of Nebraska-Lincoln (UNL), and two instructors. This course is offered as part of UNL's Nebraska Math and Science Summer Institute (NMSSI) Program, receiving support from this program, from the Dept. of Earth and Atmospheric Sciences, and private donations. The primary aim of this course is to improve educators’ ability to teach inquiry in their classrooms, gain knowledge and understanding of geoscience, and to demonstrate effective teaching methods that can integrate geoscience into K-12 learning environments. The UW-NPS facilities provide an excellent opportunity for participants to discover the natural history of the Teton Range.

Participants became active members of a field-based learning community comprising individuals with expertise and experience in geoscience and pedagogy. Through a collaborative teaching and learning structure, course participants learned about geoscience, pedagogy, group dynamics,
and discovered Rocky Mountain history. The experience was enhanced through the evaluation, assessment and reflection on the inquiry-based approach demonstrated as an effective means of teaching geoscience.

**CLASS OBJECTIVES**

Major goals of these courses are: 1) to enhance the 'geoscience experience' for pre-service and in-service science educators, 2) to teach inquiry concepts and skills that K-12 educators are expected to understand and teach (as outlined in national standards), 3) to engage science educators in field-based geoscience education and inspire them to use inquiry and geoscience as unifying themes in their classes/teaching activities, 4) to provide participants with an opportunity to pursue authentic geoscience fieldwork, and 5) to enhance pedagogical understanding and provide all participants with a 'tool-kit' of effective inquiry-based, and discovery-learning teaching practices. Grand Teton National Park provides excellent exposure to a wide range of geological features and processes that built this impressive landscape.
PRESERVATION TREATMENT GUIDE FOR
AMK RANCH (UW-NPS RESEARCH CENTER)

MARY M. HUMSTONE, AMERICAN STUDIES PROGRAM
UNIVERSITY OF WYOMING ♦ LARAMIE

Figure 1. Students, instructors and National Park Service staff at a site visit to the Lucas-Fabian cabin in Grand Teton National Park (Mary Humstone, 2011)

CLASS OVERVIEW

During summer 2011, the University of Wyoming American Studies Program offered “Field Studies in Historic Preservation: Preparing a Preservation Treatment Guide for the Historic AMK Ranch.” This 3-credit, upper-level undergraduate course introduced students to the process of documenting and assessing the condition of historic buildings and developing treatment protocols. The majority of the course was devoted to inspecting buildings, interviewing property managers, researching solutions to common problems and writing a “Preservation Treatment Guide” for use by National Park Service and University of Wyoming personnel. Students also studied log building maintenance and repair at other historic sites within Grand Teton National Park and conducted experiments and demonstrations at the AMK Ranch. Through this field course, students were given the opportunity to assist in fulfilling a contract with the National Park Service and to learn about how the park manages its historic and cultural resources. The course was taught by University of Wyoming Research Scientist Mary Humstone, with assistance from building conservation specialist Harrison Goodall of Langley, Washington, and Grand Teton National Park Cultural Resource Specialist Katherine Longfield.
**Course Background**

The four students enrolled in the course conducted several days of research on historic preservation and building conservation methods before traveling to Grand Teton National Park. Students stayed at the UW-NPS Research Center (AMK Ranch) for nine days, most of which were spent on site. Under the guidance of Harrison Goodall, students completed *Building Condition Assessment Forms* for each of the 16 historic buildings on the property, noting the overall condition of each building as well as the condition of the roof, exterior walls and finish, foundation, windows and doors, porches and steps, site drainage and grade and surrounding vegetation. They also took documentary photographs of each building.

Following the initial assessment, students met with Research Center director Hank Harlow and caretaker Rich Viola to learn about maintenance procedures and building conservation challenges. Because the AMK Ranch is a federal property that is listed on the National Register of Historic Places, work on the buildings must comply with the *Secretary of the Interior’s Standards and Guidelines for Treatment of Historic Properties*, and must be approved by the Wyoming State Historic Preservation Office (WYSHPO). Property managers at this and other historic properties in the park need clarification on how to apply the standards to specific building conservation treatments.

The students identified several problems that were common to many of the buildings on the AMK Ranch, including improper roof flashing, site drainage, vegetation adjacent to buildings, varmints (bats and ants) and areas of wood rot. With Goodall’s help they developed treatment procedures to address the major problems.

One area of particular concern to Harlow and Viola was the black fungus that was growing on the building logs. The team determined that, due to the application of linseed oil every few years, the log buildings at the AMK Ranch were generally in good condition, especially compared with other log buildings in the park. However, while the linseed oil protects the logs, it acts as a food source for fungal growth which in turn causes the logs to darken. Additionally, linseed oil breaks down in ultraviolet (UV) light and flakes off, leaving logs unprotected. The layers of linseed oil must be removed for additional treatments of UV blocker or borate (a natural log preservative, fungicide, and insecticide) to be effective.

The students conducted several experiments in cleaning the logs, using different products and different methods of abrasion. They also demonstrated proper log daubing techniques for the staff at AMK.

In addition to the work directly related to the preservation guide, students had an opportunity to meet with National Park Service cultural resources staff to learn how the park evaluates, manages and interprets its cultural resources. Students visited the Western Center for Historic Preservation at the White Grass Ranch, as well as several other historic properties in the park, to compare treatments of log buildings.

The product of this field course is a *Preservation Treatment Guide for AMK Ranch* that includes photographs and building condition assessments for 16 buildings, procedures for remedying the major conservation problems, and a maintenance checklist. The guide will be used by NPS personnel, not only at AMK Ranch but at other locations in the park.

Through this field course students learned how to conduct assessments of historic buildings and prepare a professional report. They also learned about park policies and procedures regarding historic preservation.

![Figure 2. Students meet with Rich Viola, caretaker at AMK Ranch, to discuss maintenance and conservation issues. (Mary Humstone, 2011)](image)
Figure 3. Students prepare a log wall for testing to compare the effects of different log cleaning techniques. (Mary Humstone, 2011)

Figure 4. UW student Andrea Lewis cleans logs with abrasive brush after applying a cleaning solution. (Mary Humstone, 2011)

Figure 5. Harrison Goodall shows student Cassie Loveland how to apply daubing to the logs of the boathouse at AMK Ranch. (Mary Humstone, 2011)

Figure 6. Student Cassie Loveland emerges after conducting moisture-level tests underneath the Berol Lodge at AMK Ranch. (Mary Humstone, 2011)
GEOLGY OF YELLOWSTONE AND GRAND TETON NATIONAL PARKS

TRINA KILTY ♦ TRENT MORELL ♦ GEOSCIENCES DEPARTMENT
LARAMIE COUNTY COMMUNITY COLLEGE ♦ CHEYENNE

Figure 1. Students as they entered Grand Teton and Yellowstone National Parks.

CLASS OVERVIEW

This was a 3 credit hour field course in geology offered through Laramie County Community College. The title of the course is Geology of Yellowstone National Park (GEOL 1035-60).

- Course Description: A study of Yellowstone’s and the Grand Teton’s earth materials and processes including rocks, minerals, streams, glacial history, geologic structures, earthquakes, and plate tectonics. Students acquired scientific knowledge about the formation of Yellowstone’s landscape, geothermal features, soils, and geologic hazards. Students recorded observations and took notes in a field book that was be assessed as part of their grade.
- Course Objective: Students gained an understanding and appreciation of the geologic processes that form the Yellowstone and Teton landscapes. Participation in daily hikes, lectures, field note preparation and readings allowed students to comprehend the geology of the area.
- We had 12 students participate in the course this year. The maximum enrollment is 13.
- Students learned the basic geologic processes involved in the creation and continuous shaping of the Yellowstone and Grand Teton ecosystem. Participating students had at least an introductory geology, physical geography or other Earth science class; or, had a specific interest in geosciences. Through the use of the text, Windows into the Earth: The Geologic Story of Yellowstone and Grand Teton National Parks (Smith 2000); recording field notes and making sketches in their field books; and, by exploring and seeing geologic features and processes in the field during daily field trips, students got a front row seat to the show that is Earth in action.
**Course Background**

This is our fifth year to complete a successful geology field course in Yellowstone and the Grand Tetons; the first time coordinating and staying at the UW-NPS Research Station at the AMK Ranch. The course has typically run during our interim session between spring and summer semesters – generally in late May to early June.

**Grand Teton National Park**

The field trips began in Grand Teton National Park where students were introduced to the Teton and associated faults, glacial processes, and geologic hazards such as: earthquakes, landslides and floods.

- Students were introduced to the Teton fault and the resulting topography due to these geologic processes over the last 17 million years or so.
- Alpine glaciation extending from the Yellowstone plateau and from the Teton range was discussed, and glacial remnants – both from erosion and deposition were observed and contemplated by the students.
- We drove to the site of the Gros Ventre landslide where students hiked the debris field, conducted rock identification, and took extensive field notes and observations on this event.
- Stream processes were covered as we talked about meandering nature of the Snake River and its migration patterns through time; evidence left behind by stream terraces, oxbows and meander scars.
- As we covered the individual geologic processes in the area, our goal was to get students to think critically about how they have all acted in concert to create what we saw at the present time. A historical geology perspective was important throughout this endeavor.

- We finished up our Teton tour with a hike around Jenny Lake – up to Hidden Falls and then a bird’s eye view from Inspiration Point.
**YELLOWSTONE NATIONAL PARK**  
(Including West Yellowstone and the Hebgen Lake Earthquake)

- The latter part of the trip focused on the geology of Yellowstone and surrounding areas.
- We started the Yellowstone tour off with a trip through the Park and then out the west entrance into West Yellowstone. Here we studied the processes and consequences involved in the Hebgen Lake earthquake event that took place in 1959.
- While studying the Hebgen Lake earthquake event we visited some “textbook” fault scarps, and toured through the Madison River canyon to observe the results of the magnitude 7.5 quake that struck the area on that fateful night in the summer of 1959.
- The Madison Canyon landslide at the end of the canyon provided a great compare and contrast analysis when looking back at the Gros Ventre slide we studied earlier in the Tetons. Students are pushed to put some critical thought into comparing these two events; which at the conclusion of the course, became one of their essays questions on the final exam.
- We also discuss how the Hebgen Lake event altered hydrothermal features in Yellowstone N.P.

![Figure 6. Hiking along the Red Canyon fault scarp near Hebgen Lake.](image)

- In previous years, we have had the privilege to meet with one of Yellowstone’s Geologists and gain an inside perspective on the current events, research, and other projects going on within the Park.
- In 2012, we had the opportunity to meet with Cheryl Jaworowski, a full-time, Yellowstone National Park Geologist who is stationed at the Park Headquarters in Mammoth.
- Cheryl led us on a tour of the Mammoth terraces while also engaging our students in a mapping exercise. One of her current projects is to find an easy and scientifically repeatable method to map changing hydrothermal vents and pool boundaries at Mammoth.

![Figure 7. Students observing the cabin destruction site along Hebgen Lake.](image)

- Our students had an abundance of input on the possibilities of doing this, and also conducted the exercise with paper maps, pencils, cameras, FlipVideo recorders and GPS units. The results will be compiled and put into a GIS map this fall to be sent back to Cheryl with an accompanying report on the students’ observations of this project.

![Figure 8. Yellowstone N.P. Geologist, Cheryl Jaworowski, explaining the mapping exercise to our students at Mammoth.](image)
The trip concluded with the last two days observing hydrothermal features at Lower, Midway and Upper Geyser Basins.

- Students then completed a final essay exam before heading back to Cheyenne.
- 2012 resulted in another enjoyable and successful field course in geology. We look forward to future trips and collaborating with the UW-NPS Research Station at the AMK Ranch.

Figure 9. Students using maps to sketch out current locations of hydrothermal vents and drainage areas.

Figure 10. Brilliant thermophiles give the illusion of a lava flow at Midway Geyser Basin.

Figure 11. Home Sweet Home at the AMK Ranch.
**Class Overview**

**Geol 1240 Geology of the Yellowstone-Teton Region** is offered as a 1 credit, 3-day trip each September, through Central Wyoming College (CWC). Each year the itinerary varies and students may earn 2 credits toward graduation by repeating the course. CWC Student Activities covered the cost of transportation for this year’s trip. Students participating on these trips do not need to be geosciences majors, although this year six of the seven involved have a strong interest in a geoscience-related career.

In 2011, the emphasis was on the Teton area and base-camp was held at the AMK Ranch. The 2011 Itinerary included:

- Dubois – Wind River/Absaroka Overlook
- Togwotee Pass – Absaroka Volcanics
- Togwotee Pass – Harebell Quartzite Conglomerate (History of the Tetons Exercise)
- String Lake – Teton Fault Hike
- Jenny Lake – boat ride
- Inspiration Point Hike - History of Tetons
- Old Faithful & West Thumb – biogeochemistry
- Lewis Falls – Obsidain Flow Structure
- Signal Mountain – Glacial features overlook
- Gros Ventre Landslide – Geologic Hazards Exercise

The wet weekend was a nice relief from the summer heat. Our first exercise at the Harebell Formation Conglomerate consisted of field observations and a “geologic cartoon” matching exercise that requires only observations and logic (no prior geology knowledge).

After making observations on site, we proceeded to the Grand Teton NP Visitor’s Center to discuss and review the exercise. Always being prepared with an alternative site is good, as we were able to continue our discussion under the protection of the covered walkway around the center!

The weather cleared enough for an informative hike along the Teton Fault, above String Lake.

The highlight of our trip was a boat ride on Jenny Lake to the Inspiration Point trailhead where we discussed the different types of ancient “hard” rocks that make up the bulk of the Tetons. It was a beautiful fall day that left us all inspired to learn more about the area.

We were also able to compare and contrast the Teton area geology with some of the hydrothermal features of Yellowstone, including some first-time viewing of an Old faithful eruption.

The final day of the trip focused on geologic hazards, with visits to Signal Mountain for an overview of the Teton Valley landscape, a brief stop at the Jackson Lake Dam and a final exercise at the Gros Ventre Landslide.

We are grateful for the use of the UW-NPS Research Station as our base camp for this trip.
Special Topics in Ecology: Ecology of Greater Yellowstone

Instructors ♦ Tony Stancampiano ♦ Roger Choate
Oklahoma City Community College ♦ Oklahoma City, OK

Class Overview

Special Topics in Ecology: Ecology of Greater Yellowstone is a sophomore level college course emphasizing basic ecological principles with specific application to the ecosystems found in Grand Teton and Yellowstone National Parks. This course is offered during spring intersession using a hybrid format. The field portion of the course took place from May 20-29, 2011.

This year 13 students participated in the course. After completing a 4 unit online study, students embarked on a journey to the AMK Ranch with overnight camping stops in Bayfield, Colorado and Logan, Utah. The 6 day stay at AMK allowed students to experience, in the field, all of the material they had learned in the previous 2 weeks in the online portion of the class. The online learning consists of a series of lectures and associated exercises providing knowledge from multiple areas including:

Figure 1. View of the Grand Teton Range.
We spend each day, while in Wyoming, on a series of hikes in areas that exhibit the features, flora, and fauna discussed in the online sessions. Weather permitting, we prefer to split our time between the two parks on an every other day schedule.

In terms of logistics, the AMK is ideally located to serve as our headquarters. This setting is truly inspirational to students. The raw beauty of this locale provokes a spiritual feeling and almost palpable calling to investigate. Students learn so much more than the science. Cooperation, tolerance, scheduling, budgeting, meal planning and preparation, and consideration of the elements are but a few of the ‘extra’ skills learned while at the AMK.

Areas visited include, but are not limited to, the following:
- Lewis Falls
- Kepler Cascades
- Lonestar Geyser
- Old Faithful
- Upper Geyser Basin - Firehole River
- Midway Geyser Basin - Grand Prismatic Spring
- Lupine Meadows Trailhead
- Amphi theatre Lake Trail
- LeHardys Rapids
- Hayden Valley
- Grand Canyon of the Yellowstone
- Lamar Valley
- Indian Pond
- Jenny Lake Area
- Inspiration Point
- Taggart Lake
- Laurance S. Rockefeller Preserve
- Willow Flats
- Gros Ventre Slide

The AMK ranch and the University of Wyoming make this opportunity possible for students at OCCC. Dr. Hank Harlow and his staff, particularly Celeste Havener, facilitate our housing and accommodations at the AMK. Upon our arrival, Dr. Harlow addresses the students to inform them of general information, current events, personal safety in the parks, bear biology, history of the AMK, and related ecology/biology topics.

Figure 2. Tony Stancampiano giving a field lecture to students.
CLASS OVERVIEW

Utah State University Department of Watershed Sciences runs an introductory course for all incoming graduate students (13 in Fall 2011) 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.

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, Water quality monitoring.