UNIVERSITY OF WYOMING

NATIONAL PARK SERVICE RESEARCH CENTER

30th ANNUAL REPORT 2006 & 2007

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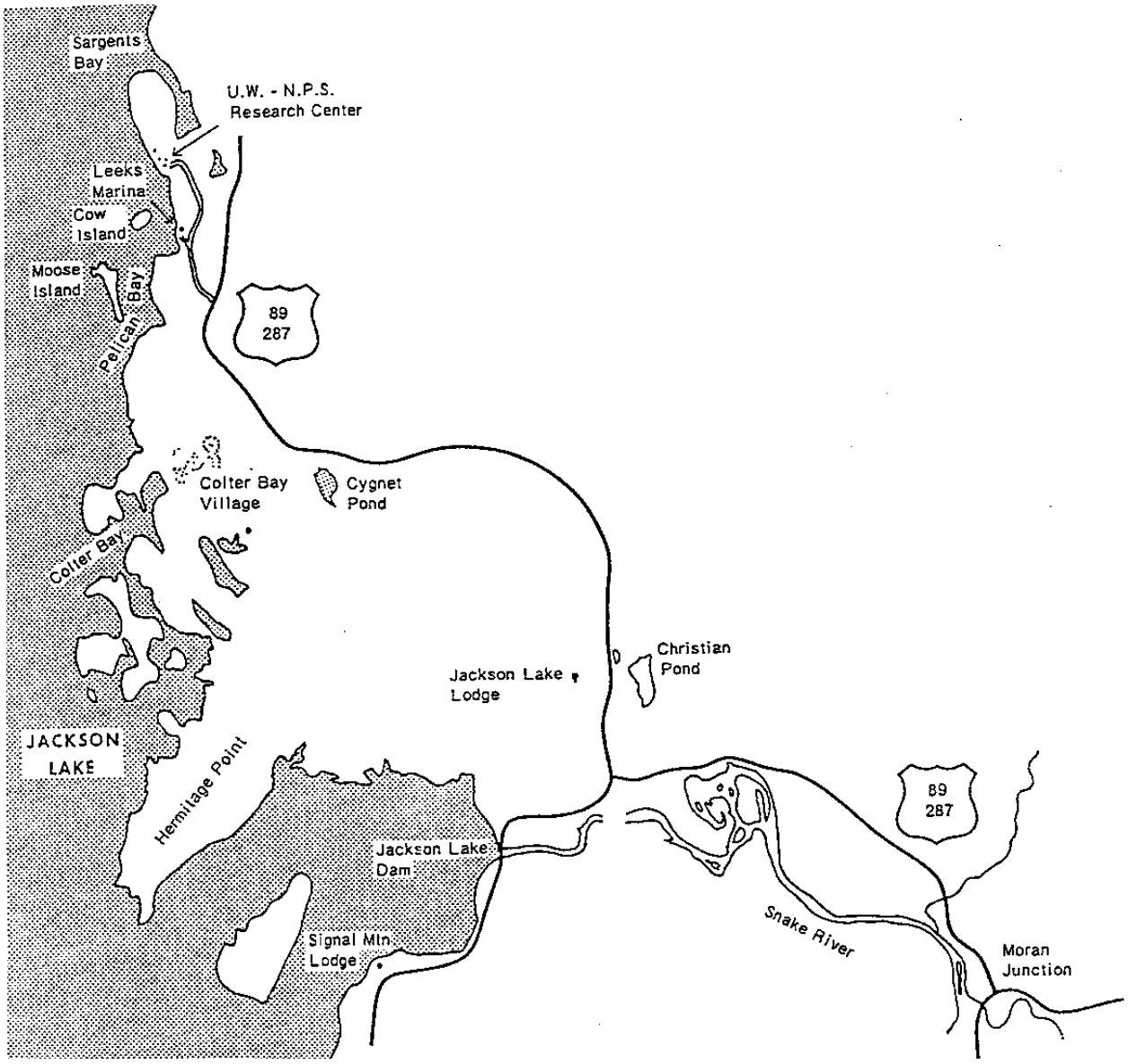

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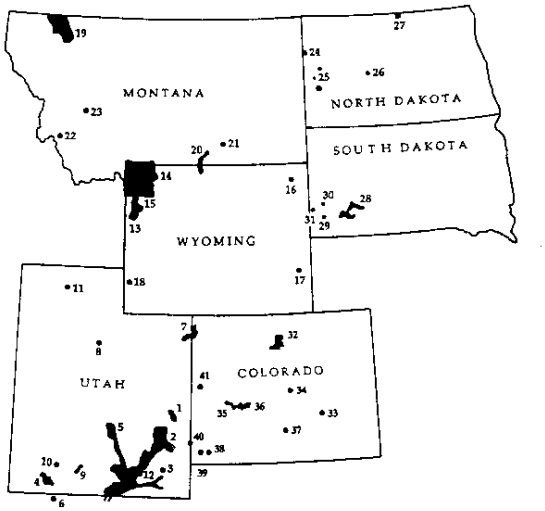

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28. Badlands National Park
29. Wind Cave National Park
30. Mount Rushmore National Memorial
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✦ UTAH
1. Arches National Park
2. Canyonlands National Park
3. Natural Bridges National Monument
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5. Capitol Reef National Park
6. Pipe Spring National Park
7. Dinosaur National Monument
8. Timpanogos Cave National Monument
9. Bryce Canyon National Park
10. Cedar Breaks National Monument
11. Golden Spike National Historic Site
12. Glen Canyon National Recreation Area

✦ WYOMING
13. Grand Teton National Park
14. Yellowstone National Park
15. John D. Rockefeller, Jr. Memorial Parkway
16. Devils Tower National Monument
17. Fort Laramie National Historic Site
18. Fossil Butte National Monument

✦ MONTANA
19. Glacier National Park
20. Bighorn Canyon National Recreation Area
21. Little Bighorn Battlefield National Monument
22. Big Hole National Battlefield
23. Grant-Kohrs Ranch National Historic Site

✦ NORTH DAKOTA
24. Fort Union Trading Post National Historic Site
25. Theodore Roosevelt National Park
26. Knife River Indian Villages National Historic Site
27. International Peace Garden

✦ COLORADO
32. Rocky Mountain National Park
33. Bent's Old Fort National Historic Site
34. Florissant Fossil Beds National Monument
35. Black Canyon of the Gunnison National Monument
36. Curecanti National Recreation Area
37. Great Sand Dunes National Monument
38. Mesa Verde National Park
39. Yucca House National Monument
40. Hovenweep National Monument
41. Colorado National Monument

TABLE OF CONTENTS

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INTRODUCTION

2006 & 2007 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 58 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).

FEATURE ARTICLE

LINKING EXOTIC SNAILS TO CARBON CYCLING IN KELLY WARM SPRINGS, GRAND TETON NATIONAL PARK

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✦ ABSTRACT

Biotic calcification has yet to be considered in most freshwater carbon budgets, despite previous calculations that suggest the importance of calcifying animals in altering inorganic carbon cycling. The freshwater snail, *Melanoides tuberculata,* has achieved a high abundance and a biomass of 34.2 g AFDM m^{-2} after invading Kelly Warm Springs in Grand Teton National Park approximately five years ago. This high biomass suggests that introduced populations of *Melanoides* may alter ecosystem processes. We measured *Melanoides* growth rates and biomass to calculate the production of biomass, shell mass, and CO_2 for comparison with ecosystem carbon pools and fluxes.

Melanoides calcification in Kelly Warm Springs produced up to 10.4 mmol CO_2 m^{-2} day^{-1} during summer months. Despite extremely high primary production and respiration in Kelly Warm Springs (-379 mmol CO_2 m^{-2} day^{-1} and 445 mmol CO_2 m^{-2} day^{-1}, respectively), CO_2 produced from biotic calcification increased total CO_2 production in Kelly Warm Springs from 65.9 to 76.3 mmol CO_2 m^{-2} day^{-1}. This rate of CO_2 production via biotic calcification is within the range of those previously calculated for freshwater systems and suggests the importance of considering the role of calcification in inorganic carbon budgets for areas dominated by calcifying organisms.

✦ INTRODUCTION

Most aquatic carbon dioxide (CO_2) budgets assume that any changes in total CO_2 concentrations are from primary production and community respiration, after accounting for groundwater inputs and evaporation rates (Wetzel 2001, Chauvaud *et al.* 2003). The ability of animals to alter elemental cycling has been well researched and reviewed (Vanni 2002) and there has been growing interest in the ecosystem-level consequences of exotic species invasions in the past several years (Simon and Townsend 2003). However, few studies have quantified the CO_2 production associated with the biological process of calcification (the formation and growth of calcium carbonate exoskeletons) to compare directly with whole ecosystem processes such as gross primary production and community respiration. When calcium carbonate ($CaCO_3$) exoskeletons are formed, nearly one mole of CO_2 is released for every mole of $CaCO_3$ fixed into shell material (Ware *et al.* 1991, Frankignoulle *et al.* 1994):

$$Ca^{2+} + 2HCO_3^- \leftrightarrow CaCO_3 + H_2O\,.$$

The rising frequency of introductions and establishment of mollusks has the potential to increase the contributions of calcification to inorganic carbon budgets on a global scale (Robinson 1999, Chauvaud *et al.* 2003).

CO_2 evasion from some aquatic ecosystems is an important source of CO_2 that may be missing from many regional carbon budgets (Cole *et al.* 1994, Richey *et al.* 2002, Cole *et al.* 2007). Until recently, many estimates of global carbon sources and sinks did not include contributions from freshwater ecosystems. Many streams and rivers in the United States are supersaturated with CO_2 (Jones *et al.* 2003), meaning that they are already sources of CO_2. Further CO_2 production through respiration or biotic calcification may increase the amount of CO_2 released into the atmosphere. Biotic calcification may be an important aspect of stream, lake, and river outgassing of CO_2 that should be considered when calculating contributions to the global carbon budget. Increases in CO_2 concentrations, linked with heavy consumption of primary producers by consumers, can potentially lower the productivity status and may also raise local carbon emission budgets for invaded ecosystems (Cole *et al.* 2000, Duarte and Prairie 2005).

The freshwater snail, *Melanoides tuberculata* (Müller, 1774), has invaded warm aquatic habitats with unknown consequences. *Melanoides* has achieved high abundance and biomass in Kelly Warm Springs, Grand Teton National Park. This high biomass suggests that *Melanoides* has the potential to drastically change the elemental cycling, productivity, and community structure of invaded habitats (Chauvaud *et al.* 2003, Hall *et al.* 2003, Hall *et al.* 2006). While there is evidence that *Melanoides* can decrease the abundance of native macroinvertebrates (Giovanelli *et al.* 2005), the ecosystem-level consequences of *Melanoides* on carbon cycling is unknown. Introduced populations of *Melanoides* (as well as other exotic mollusks) may dramatically alter the CO_2 production and emissions of invaded habitats through respiration and shell synthesis.

This paper links the calcification rates of an exotic snail population with ecosystem level fluxes and processes. In order to evaluate the impacts of *Melanoides* on carbon cycling in Kelly Warm Springs, we asked: 1) How much CO_2 is released into Kelly Warm Springs through $CaCO_3$ shell synthesis by *Melanoides*?, and 2) To what degree do snails alter inorganic carbon cycling relative to gross primary production and community respiration? To answer these questions, we measured growth rates, biomass and shell mass of *Melanoides* in Kelly Warm Springs to calculate rates of organic and inorganic carbon production, and translated shell growth rates into rates of CO_2 production via calcification. We also compared these snail-driven rates with estimates of gross primary productivity, community respiration, concentrations of carbonate species, and net CO_2 flux into the atmosphere. We predicted that including *Melanoides* calcification rates in the carbon budget would increase the total CO_2 production in Kelly Warm Springs due to their high abundance and biomass.

✦ MATERIALS AND METHODS

Study site and *Melanoides* life history

Kelly Warm Springs is located in Grand Teton National Park (Wyoming, USA) at 43º 38' 21.8" N, 110º 37' 01.9" W (Figure 1) and originates from where the Gros Ventre River crosses a concealed Holocene or Pleistocene fault (Love and Love 1988). Acid neutralizing capacity and pH averaged 3.2 meq L^{-1} and 8.1 from June – September 2006, including measurements taken every three hours during 24-hour sampling periods. The average width and depth of Kelly Warm Springs measured 9.9 m and 0.3 m, respectively. Stream velocity was 7.4 m min^{-1} (standard deviation = 1.3) and discharge was 5.7 m^3 min^{-1} (standard deviation = 0.05). Temperatures in Kelly Warm Springs ranged from 22.6 – 31.3 °C (mean = 27.3 °C) along a 500 m reach.

Because of the comfortable water temperature, Kelly Warm Springs is used heavily as a swimming and kayak training area for Jackson Hole residents and park visitors. The popularity of Kelly Warm Springs has resulted in numerous introductions and the successful establishment of exotic tropical fish and snails; likely through aquarium dumping. Five species of introduced fish have been documented in the USGS Nonindigenous Aquatic Species database: *Xiphophorus helleri* (green swordtail), *Puntius tetrazona* (tiger barb), *Tilapia sp.* (tilapia), *Cichlasoma nigrofasciatum* (convict cichlid) and *Poecilia reticulata* (guppy). All of the species except *P. tetrazona* are categorized as locally established populations (USGS 2005). In summer 2003, we observed *Melanoides* in Kelly Warm Springs, and while we do not know the exact date of introduction, *Melanoides* were absent from invertebrate samples collected in 2001 (R.O. Hall and E.R. Hotchkiss, unpublished data).

Melanoides tuberculata (Gastropoda, Thiaridae) are likely native to eastern Asia but have established populations around the world through at least six different introductions since 1950 (Robinson 1999, Facon *et al.* 2003). Invasive populations of *Melanoides* are closely linked with the aquarium trade. They are limited to warm fresh and brackish waters with temperatures ranging from 14 to 31 °C (Dudgeon 1986, Duggan 2002). *Melanoides* burrow in substrate during the day and become more active at night (Figure 1).

Figure 1. Kelly Warm Springs, Grand Teton National Park, Wyoming in top photograph (July 2006). Bottom photograph shows a close-up of *Melanoides tuberculata* while active at night (July 2007).

Individuals can grow up to 35 mm in length (although extremes of 80 mm have been reported), which is likely equivalent to 3 to 5 years in age (Dudgeon 1986, Duggan 2002, Rader *et al.* 2003). *Melanoides* are parthenogenetic and viviparous; embryos develop in the mother and young range from 1.0 – 4.0 mm in length when they are released from the brood pouch (Berry and Kadri, 1974, Subba Rao and Mitra 1982). A majority of populations sampled worldwide consist entirely of females (Jacob 1957, Dudgeon 1986), but Livshits and Fishelson (1983) reported up to 33% males in small, isolated populations in Israel. *Melanoides* establish in new environments quickly and can out-compete other invertebrates through facilitation (specifically *Biomphalaria* spp., the intermediate host of *Schistosoma mansoni*). Because of this, *Melanoides* have been intentionally introduced in some areas of Latin America and the Caribbean as biological control against schistosomiasis (Pointier and Giboda, 1999, Giovanelli *et al.* 2003).

Melanoides production

During June – September 2006, we sampled benthic macroinvertebrates along a 500 m reach of Kelly Warm Springs. We collected monthly samples from six random sites along the 500 m reach using a stovepipe sampler 15.2 cm in diameter and rinsed samples in the field with a 250-µm sieve (Hall *et al.* 2006). We sorted, counted and measured *Melanoides* and other macroinvertebrates using 1-mm and 250-µm sieves to separate all benthic invertebrates and digital calipers to measure shell lengths the nearest tenth of a millimeter. Each stovepipe sample was sub-sampled following Hall *et al.* (2006). All macroinvertebrates were preserved in 95% ethanol. We also measured and counted *Melanoides* collected in summer 2004 for comparison with summer 2006 population estimates.

We developed a length/mass regression for both biomass and shell mass using dried, unpreserved *Melanoides* collected in June 2006 to calculate biomass estimates for the population in Kelly Warm Springs. We dried, weighed, ashed (at 500 °C for four hours) and re-weighed 157 individuals from a range of size classes. Predictive equations for 27 size classes were derived using SAS PROC REG (SAS Institute 2002-2003). We calculated size-specific biomass and shell mass for *Melanoides* collected in 2004 (4 stovepipe samples) and monthly during summer 2006 using the relationship between shell length, shell mass, and biomass. In order to understand the severity of this invasion in terms of organic carbon cycling, we also quantified the percent of macroinvertebrate biomass that consisted of *Melanoides* in comparison to native species.

We measured *in situ* growth rates of *Melanoides* during July and August 2006. We placed 4 – 8 individuals from similar size classes (controlled for biomass to avoid over-crowding)

with a small rock and attached algae in 56 x 43 mm growth cages with 244-µm nylon mesh (Toby TeaBoy Ltd., Hall *et al.* 2006). We removed any other macroinvertebrates that were embedded in the algae. Size classes were determined by shell length and binned in 0.5 mm increments. We secured the growth cages in Kelly Warm Springs for three week incubations (Hall *et al.* 2006). We immediately preserved individuals from each growth cage after collection at the end of the three week period. We re-measured shell lengths to calculate mass, from which we estimated growth rates as

$$\text{Growth rate}\left(\text{day}^{-1}\right) = \frac{\ln\left(\text{mass}_t\right) - \ln\left(\text{mass}_0\right)}{t},$$

where mass_0 is the initial mass of the individuals in the growth cage, mass_t is the mass of the individuals at the end of the growth period, and t is the length of the growth period (in days). This equation was used for both shell mass and biomass calculations.

Because growth rates highly depend on temperature, we also measured the range of temperatures throughout the entire growth period using temperature dataloggers secured to the bottom of Kelly Warm Springs at our 0 m and 500 m sites (HOBO Water Temp Pro v2, Onset Computer Corporation). We calculated size-specific growth rates for the Kelly Warm Springs population using SAS PROC REG to find the best predictive regression (SAS Institute 2002-2003).

After measuring size-specific growth rates and biomass for *Melanoides* in Kelly Warm Springs, we calculated secondary production for the summer season as

$$\text{Somatic Secondary Production} = \sum_{i=1}^{n} g_i B_i,$$

where g_i is instantaneous growth (day^{-1}) and B_i is biomass (g m^{-2}) for the ith size class of snails (Benke 1984).

We also incorporated fecundity for *Melanoides* to estimate the relative contribution of reproduction versus growth to total biomass production in Kelly Warm Springs. All of our fecundity calculations were based on the assumption that juvenile snails were 1.5 mm in length at the time of their emergence from the brood pouch. We measured the dry and ash-free dry mass of the smallest *Melanoides* collected from Kelly Warm Springs for calculations of biomass and shell mass production. Reproduction in native and invasive regions occurs continuously and often peaks in response to environmental variables (Berry and Kadri 1974, Dudgeon 1986, Pointer *et al.* 1992). We chose a conservative reproduction rate of 182 year^{-1} for all individuals between 12.0 and 25.0 mm in length (Berry and Kadri 1974, Subba Rao and Mitra 1982).

Carbon cycling in Kelly Warm Springs

We measured community respiration and gross primary production (g O_2 m^{-2} day^{-1}) using the two station open channel method for oxygen (Odum 1956). We placed two Hydrolab MiniSondes in Kelly Warm Springs at each end of a 500 m reach for three day cycles during July and August 2006 to measure changes in dissolved oxygen (DO) concentrations. Using measurements of width, depth, travel time, and k_{O_2}, we calculated instant metabolism throughout seven different 24-hour cycles (Hall *et al.* 2007) as

$$\text{Instant Metabolism}\left(\text{g O}_2\ \text{m}^{-2}\ \text{min}^{-1}\right) = z\left[\frac{(C_t - C_0)}{t} - kDO_{Def}\right],$$

where C_t and C_0 are the dissolved oxygen concentrations at upstream and downstream sites (g O_2 m^{-2}), t is water travel time between sondes (min), k is the reaeration coefficient for O_2 (min^{-1}), DO_{Def} is the average of the dissolved oxygen deficit measured upstream and downstream (g O_2 m^{-3}), and z is stream depth (m).

We used these instant metabolism measurements to calculate GPP (gross primary production) as

$$\text{GPP}\left(\text{g O}_2\ \text{m}^{-2}\ \text{day}^{-1}\right) = \left[\text{I} * \sum\left(\text{M} - \text{M}_{\text{PM}}\right)\right],$$

where I is the measurement interval (min), M is instant metabolism, and M_{PM} is average night metabolism (the mean of instant metabolism rates during the nighttime). We calculated CR (community respiration) as

$$\text{CR}\left(\text{g O}_2\ \text{m}^{-2}\ \text{day}^{-1}\right) = \left[\text{M}_{\text{PM}} * 1440\right],$$

where 1440 is total minutes day^{-1}. We used the common assumption that CR during the daytime was equal to CR measured at night. We did not adjust for groundwater inputs because conservative tracer (NaCl) concentrations did not decline along our study reach. The one station open channel method was used during two periods in July. We converted O_2 to CO_2 using a photosynthetic quotient of 1.2 (Raine 1983).

In order to accurately measure the amount of air-water gas exchange with respect to O_2 and CO_2 fluxes, we used tracer additions of sulfur hexafluoride (SF_6), a biologically inert gas. We also added a conservative tracer, NaCl, to calculate travel time and any dilution from potential groundwater inputs along the reach (Wanninkhof *et al.* 1990). SF_6 is not naturally present in aquatic ecosystems and evades at a rate that can be used to calculate O_2 and CO_2 evasion (Wanninkhof *et al.* 1990, Cole and Caraco 1998). We collected triplicate dissolved gas samples at 5 stations along an 800 m reach downstream from the release site and measured the decline in SF_6 concentrations using a gas chromatograph with an electron capture detector (Shimadzu Gas Chromatograph 14A). k_{SF6}, the piston velocity (m min^{-1}), was calculated from the three separate SF_6 releases and the decline in SF_6. We used our average k_{SF6} to calculate k_{O2} and k_{CO2} using the ratios of gas exchange coefficients and Schmidt numbers for the gas of interest (Wanninkhof 1992, Cole and Caraco 1998).

$$\frac{k_{gas1}}{k_{gas2}} = \left[\frac{Sc_{gas1}}{Sc_{gas2}}\right]^n,$$

where k is the gas exchange coefficient, gas_1 is SF_6, gas_2 is CO_2 or O_2, Sc is the Schmidt number, and n depends on processes dominating diffusion (Wanninkhof 1992, Cole and Caraco 1998). We assumed n = 1 (Portielje and Lijklema 1995, Wanninkhof and Knox 1996).

We collected data on several water chemistry and physical parameters on a weekly basis and during diel sampling throughout summer 2006 at upstream (0 m) and downstream (500 m) sites along our reach. These data inlcuded temperature, acid neutralizing capacity (ANC) calculated by titration (Wetzel and Likens 2000), pH (Orion 3-star portable pH meter with a ROSS Ultra® pH Electrode, Thermo Scientific), conductivity and dissolved oxygen (Hydrolab MiniSondes, Hach Environmental). We collected duplicate 60 mL water samples from our upstream and downstream sites that were filtered, frozen, and later analyzed for concentrations of common cations and anions (Dionex ICS-2000 Ion Chromatography System with AS40 Automated Sampler and Perkin Elmer model 372 Atomic Absorption Spectrophotometer). We measured stream depth (z) and width (w) several times throughout the summer. We also measured stream velocity (V) and discharge (Q).

Using pH, temperature and acid neutralizing capacity, we calculated dissociation constants for carbonic acid, concentrations of carbonate species, and total dissolved inorganic carbon. Carbonic acid dissociation constants (pK1 and pK2) were calculated using temperature adjustments from Cai and Wang (1998). We calculated the concentrations of different carbonate species using measurements of carbonate acid neutralizing capacity, pH, and carbonic acid dissociation constants, following Millero (1979).

$$\left[H_2CO_3^*\right] = H_2CO_3 + CO_2 = \frac{\left(\frac{A_C a_H}{K1}\right)}{\left(1 + \frac{2K2}{a_H}\right)},$$

$$\left[HCO_3^-\right] = \frac{A_C}{1 + \frac{2K2}{a_H}},$$

$$\left[CO_3^{2-}\right] = \frac{A_C K2}{a_H + 2K2},$$

where [] represents the effective concentration in mmol m^{-3}, A_C is carbonate acid neutralizing capacity (mmol m^{-3}) and a_H is the activity of H^+. Total carbonate is the sum of $[H_2CO_3^*]$, $[HCO_3^-]$ and $[CO_3^{2-}]$. We calculated partial pressure of CO_2 (in atm),

$$pCO_2 = \frac{\left[H_2CO_3^*\right]}{K_H},$$

using our indirect measurements of $[H_2CO_3^*]$ and Henry's constant for CO_2 (K_H, mol m^{-3} atm^{-1}) corrected for temperature and elevation (Langmuir 1997).

Our measurements of CO_2 fluxes from Kelly Warm Springs were calculated by multiplying the CO_2 deficit by the site-specific piston velocity for CO_2.

$$CO_2 \text{ Flux } \left(\text{mmol m}^{-2}\text{ min}^{-1}\right) = \alpha k\left((pCO_2 K_H) - [CO_2]_{sat}\right),$$

where α is the chemical enhancement factor, k is the piston velocity for CO_2 (m min^{-1}), pCO_2 is the partial pressure of CO_2 (mmol CO_2 m^{-3}), K_H is the Henry's constant for CO_2 (mol m^{-3} atm^{-1}), and $[CO_2]_{sat}$ is the concentration of CO_2 (mmol CO_2 m^{-3}) at saturation (Cole and Caraco 1998). We adjusted K_H for changes in temperature and elevation when we calculated CO_2 saturation (Langmuir 1997). We used an average of current atmospheric levels of CO_2 (380 µatm) for measurements of saturation (Tans 2007).

Contributions of *Melanoides* to carbon cycling

After calculating pCO_2, CR, and the rate of air-water gas exchange in Kelly Warm Springs, we measured the rate of CO_2 flux into the atmosphere and the extent to which *Melanoides* were responsible for making Kelly Warm Springs a local source of CO_2. Using growth rates in combination with the $CaCO_3$ content of varying shell sizes, we calculated the amount of $CaCO_3$ produced by *Melanoides* and, consequently, the CO_2 emitted through shell synthesis into Kelly Warm Springs during the summer months (Chauvaud *et al.* 2003).

We calculated the ratio (Ψ) of released CO_2 to fixed $CaCO_3$ using adjustments for temperature and salinity by Frankignoulle *et al.* (1994). Approximately 0.6 moles of CO_2 are released for every mole of $CaCO_3$ precipitated in sea water and the ratio in freshwater is nearly 1.0, but Ψ lowers with increasing temperature (Ware *et al.* 1991). Using a temperature- and salinity-adjusted Ψ (0.85) for Kelly Warm Springs, we converted calcification rates to CO_2 production by *Melanoides*.

✦ RESULTS

***Melanoides* production**

The density of *Melanoides* in Kelly Warm Springs was 24,000 individuals m^{-2} (standard deviation = 13,000) in summer 2006. The biomass of *Melanoides* in 2004 was 17.8 g AFDM m^{-2} (standard deviation = 12.9), with a density of 17,000 m^{-2} (standard deviation = 7,000). The relationship between shell length and biomass can be described using the equation: [Biomass (g AFDM m^{-2})] = $0.0021[\text{Shell Length}]^{3.1153}$ ($n = 27$, $r^2 = 0.96$, $p < 0.0001$). *Melanoides* biomass was 34.2 g AFDM m^{-2} (standard deviation = 18.2) in 2006. The relationship between shell length and shell mass can be described using the equation: [Shell mass (g $CaCO_3$ m^{-2})] = $0.0223[\text{Shell Length}]^{2.9664}$ ($n = 27$, $r^2 = 0.99$, $p < 0.0001$). Shell lengths ranged from 1.4 to 33.9 mm (Figure 2).

Melanoides persisted at high densities 1.5 km downstream of the spring pool and at low densities along 0.5 km of a lower reach before Kelly Warm Springs merged with Ditch Creek. Total macroinvertebrate biomass in Kelly Warm Springs was 39.1 g AFDM m^{-2}, including 4.9 g AFDM m^{-2} of native mollusks, arthropods, and annelids (standard deviation = 2.65). *Melanoides* made up 87% of the total invertebrate biomass during summer 2006.

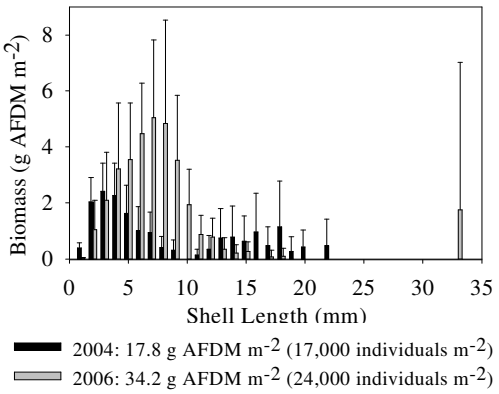

Figure 2. Frequency of biomass represented by each *Melanoides* size class in Kelly Warm Springs during summer 2004 and summer 2006. Error bars represent standard deviations.

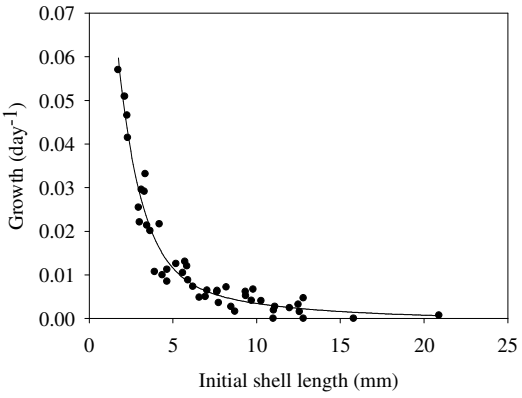

Figure 3. Size-specific growth rates for *Melanoides* in Kelly Warm Springs measured *in situ* from June – September 2006. Growth rates are best predicted using the following equation: [growth rate (day^{-1})] = $0.0142e^{-0.1454[\text{shell length}]} + 0.1686e^{-0.7165[\text{shell length}]}$ ($n = 46$, $r^2 = 0.9507$, $p < 0.0001$).

Growth rates were measured for Kelly Warm Springs *Melanoides* ranging from 1.5 to 13 mm in length. Growth rates were best predicted using the following equation: [growth rate (day^{-1})] = $0.0142e^{-0.1454[\text{shell length}]} + 0.1686e^{-0.7165[\text{shell length}]}$ ($n = 46$, $r^2 = 0.95$, $p < 0.0001$). Because we did not measure individuals with an initial length less than 1.5 mm in our growth chambers, we assumed that they have the same growth rates as snails in the 1.5 mm size class, even though the growth rate of smaller snails is likely higher. By weighting size-

specific growth rates with the relative abundance of each size class, we calculated an average growth rate of 0.02 (day^{-1}). We also assumed that individuals with an initial length greater than 13 mm had a growth rate of zero (day^{-1}). These large snails have a low abundance and we were unable to measure significant growth during our three week incubations (Figure 3).

Secondary production of *Melanoides* biomass in Kelly Warm Springs was 0.31 g AFDM m^{-2} day^{-1} in 2006, with a P:B (production:biomass) of 3.3 $year^{-1}$ (without accounting for fecundity or potential seasonal changes in growth). The density of fecund individuals was 370 m^{-2} during summer 2006, yielding an estimated annual production of 67,000 young m^{-2} $year^{-1}$ and a daily production rate of 0.07 g AFDM (of young) m^{-2} day^{-1}. Combining production from the growth of the current population and the predicted fecundity of individuals 12.0 to 25.0 mm in length, *Melanoides* produced 0.4 g AFDM m^{-2} day^{-1} and had a P:B of 4.1 $year^{-1}$ during summer 2006. *Melanoides* in Kelly Warm Springs produced 12.2 moles $CaCO_3$ m^{-2} day^{-1} through biotic calcification.

Carbon cycling in Kelly Warm Springs

The differences in CR and GPP between one and two station calculations were similar to the ranges measured between various dates during summer 2006. After comparing GPP and CR calculated using both the two station and the one station approach for the dates when we deployed two MiniSondes, we included our one station calculations from the end of July in our overall estimates of metabolism for Kelly Warm Springs. One and two station CR measurements differed by an average of 6.4% (n = 3, standard deviation = 6.8), while the average difference between one and two station GPP measurements was 9.6% (n = 5, standard deviation = 5.5).

Our releases of SF_6 yielded a k_{SF6} value of 0.00155 m^{-1} (95% confidence interval for all three releases = 5.66 x 10^{-5}) and a k_{600} value of 0.00136. Gross primary productivity (GPP) and community respiration (CR) measurements over 14 days in July and August averaged -379 mmol CO_2 m^{-2} day^{-1} (standard deviation = 131) and 445 mmol CO_2 m^{-2} day^{-1} (standard deviation = 37.5). Net ecosystem production (NEP) was 65.9 mmol CO_2 m^{-2} day^{-1} (standard deviation = 128.9). Despite a much higher GPP from 21-22 July in comparison to our other measurements (the measurements responsible for the high standard deviation), we do not believe these calculations are due to measurement error and included these data in our metabolism calculations for Kelly Warm Springs.

Kelly Warm Springs was consistently super-saturated with CO_2 (with respect to current atmospheric levels of 380 ppm). CO_2 partial pressure values ranged from 476.0 to 5421.5 µatm, with a mean of 2725.8 µatm over 24-hour cycles. CO_2 evasion rates ranged from 0.0015 to 0.0556 mmol CO_2 m^{-2} min^{-1}, with higher fluxes during late evening and early morning and lower fluxes in the afternoon (Figure 4). Kelly Warm Springs contributed to an average flux of 37.2 mmol CO_2 m^{-2} day^{-1} (standard deviation = 5.6).

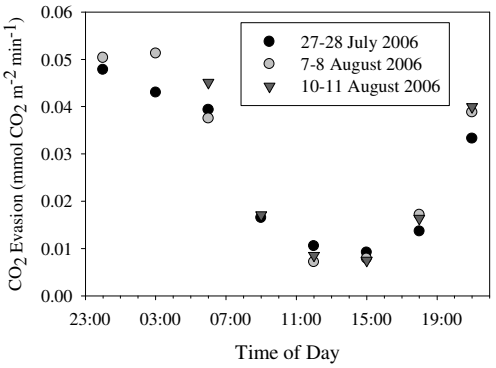

Figure 4. Net CO_2 evasion over 3 different 24-hour periods in July and August 2006. The average CO_2 flux from Kelly Warm Springs was 37.2 mmol CO_2 m^{-2} day^{-1}.

Contributions of *Melanoides* to carbon cycling

Using our direct measurements of *Melanoides* population density, growth rates and size frequency distributions, shell mass in Kelly Warm Springs was 1.9 moles $CaCO_3$ m^{-2} and calcification rates averaged 12.2 mmol $CaCO_3$ m^{-2} day^{-1}. During summer months, we estimated that biotic calcification by *Melanoides* contributed 10.4 mmol CO_2 m^{-2} day^{-1} to the water column inorganic carbon pool. We assumed that CO_2 produced as a byproduct of calcification was constant throughout day and night.

Compared to the daily swings of CO_2 production and consumption in Kelly Warm Springs, calcification produced a relatively small amount of CO_2 (Figure 5). However, this CO_2 released from biotic calcification increased total CO_2 production estimates for Kelly Warm Springs. Including calcification in the inorganic carbon budget for Kelly Warm Springs would increase net

ecosystem production of CO_2 from 65.9 mmol CO_2 m^{-2} day^{-1} to 76.3 mmol CO_2 m^{-2} day^{-1}. Because the bicarbonate system in streams is dominated by HCO_3^-, a large proportion of the CO_2 produced via biological processes was transformed to HCO_3^-. Relatively little CO_2 was lost due to diffusion and reaeration (only 37.2 mmol CO_2 m^{-2} day^{-1}, including losses from high-CO_2 groundwater inputs upstream), despite Kelly Warm Springs being a net source of CO_2 to the atmosphere (Figures 4 & 6).

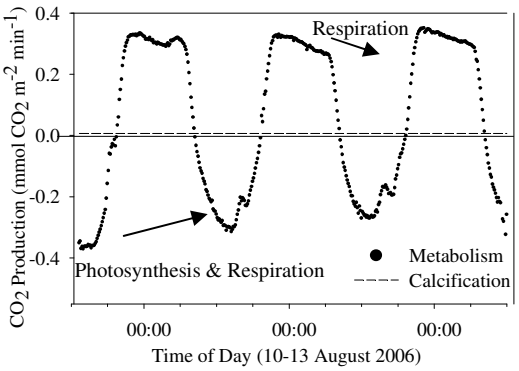

Figure 5. Comparison of CO_2 production by stream metabolism versus calcification.

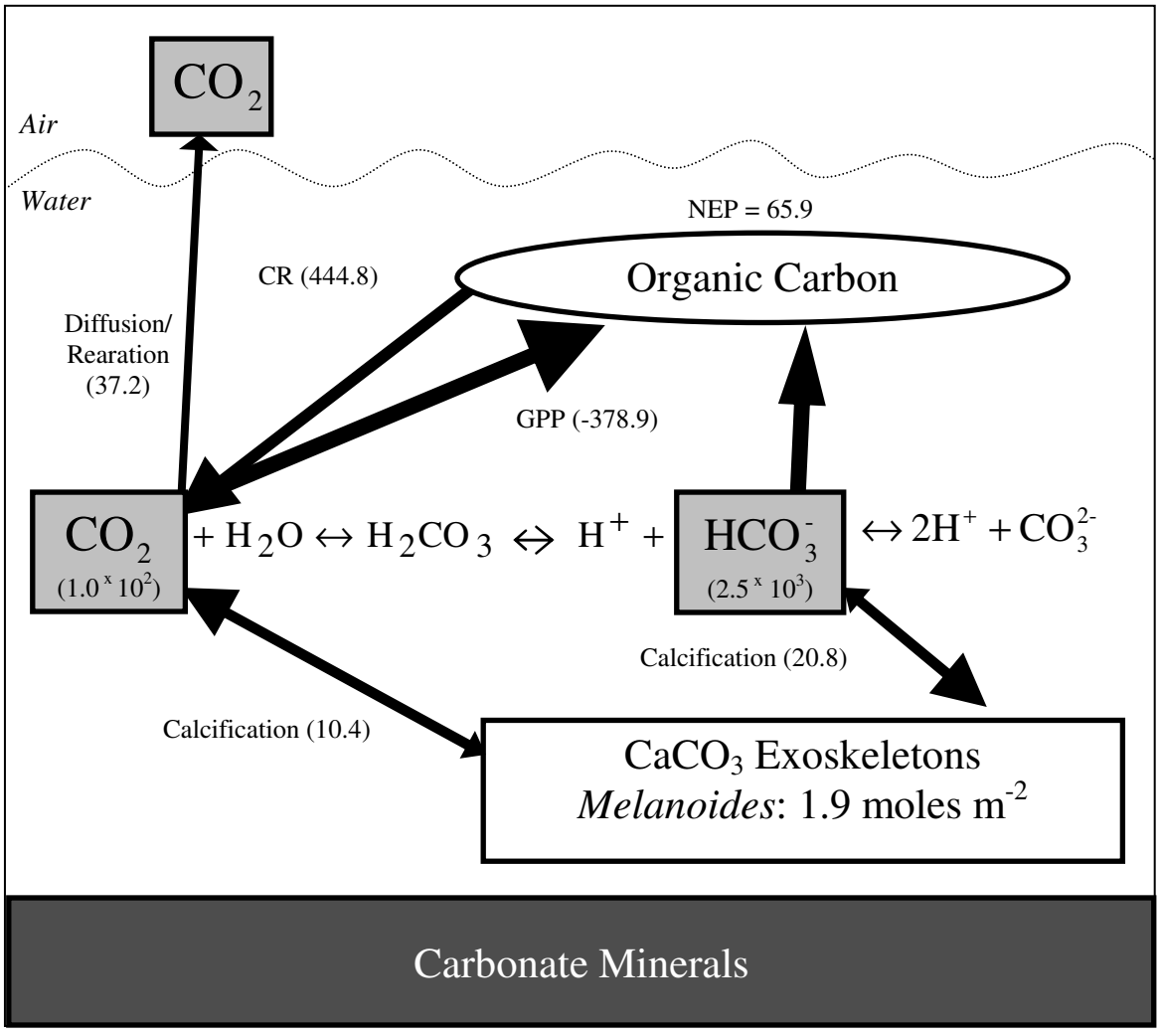

Figure 6. Carbonate pools and fluxes within and from Kelly Warm Springs, Wyoming. Arrows represent fluxes (mmol of CO_2 m^{-2} day^{-1}) and represent the relative contributions of each process to CO_2 production. Boxes are standing stock. Note that primary production by biota in the organic carbon pool can take up CO_2 or HCO_3^-, depending on the species. We did not measure dissolution of shells or carbonate minerals on the benthos for this specific study and assumed they were at steady state.

✦ DISCUSSION

Melanoides production

Warm temperatures and high primary production in Kelly Warm Springs have likely facilitated one of the highest densities reported for *Melanoides* in the literature to date. Biomass production and shell calcification rates for *Melanoides* individuals were slower than rates published for other invasive snail species, but were important in terms of total invertebrate biomass due to the high density of *Melanoides* established in Kelly Warm Springs.

Melanoides tend to grow slowly and have lower fecundity compared to other successful invasive freshwater snails (Facon *et al.* 2006) Therefore, it is no surprise that the *Melanoides* annual P:B of 4.1 was lower than 9 and 12 $year^{-1}$ calculated for the invasive New Zealand mud snails in the greater Yellowstone area (Hall *et al.* 2006). Our calculations of annual P:B for the measured ranges of *Melanoides* fecundity (4.1 to 4.9 $year^{-1}$) are on either end of the reported values of 4.4 in Lake Kariba, Zimbabwe (Kiibus and Kautsky 1996) and 4.81 in Ping Long, Hong Kong (Dudgeon 1986).

While we calculated the density of *Melanoides* from only four stovepipe samples collected in 2004 and measurements in 2006 were not statistically higher ($t = -0.9976$, $df = 6$, $p = 0.3570$), overall trends suggest the population has continued to increase over the past few years. Giovanelli *et al.* (2005) found *Melanoides* populations capable of exponential growth to over 1,000 individuals m^{-2} just a few months after establishment, so it is reasonable to assume that the introduction of *Melanoides* did take place around 2001.

Carbon cycling in Kelly Warm Springs

Kelly Warm Springs was a highly productive yet net heterotrophic stream during summer 2006. The 500 m reach was super-saturated with CO_2 with respect to atmospheric concentrations during the entire study period; and Kelly Warm Springs acted as a net source of CO_2 throughout diel cycles and the summer months in general. Rates of primary production and respiration in Kelly Warm Springs were higher than most streams (Mulholland *et al.* 2001) as well as Polecat Creek, another highly productive stream in the greater Yellowstone ecosystem (Hall *et al.* 2003). Despite extremely high rates of productivity, Kelly Warm Springs was net heterotrophic during six of the seven 24-hour cycles we recorded changes in dissolved oxygen.

As with many freshwater ecosystems, Kelly Warm Springs was consistently super-saturated with respect to atmospheric pCO_2. While some of this CO_2 saturation can be attributed to a P:R (GPP:CR) of -0.85, much of this CO_2 likely comes from the upwelling of CO_2-rich spring water above our study reach. This constant source of inorganic carbon, along with warm temperatures, may be important factors behind the high productivity in Kelly Warm Springs.

While methods have been developed to quantify inorganic carbon dynamics within aquatic ecosystems as well as evasion rates of CO_2 into the atmosphere, it is still uncertain how much of this CO_2 evasion is driven by biological versus physical and geological processes. We show here that photosynthesis and respiration, which alter pH in aquatic systems, can drive 24-hour cycles in CO_2 concentrations and, consequently, CO_2 evasion.

Contributions of *Melanoides* to carbon cycling

Melanoides calcification and CO_2 production rates in Kelly Warm Springs were similar to rates calculated for other aquatic invertebrates, but were small in comparison to daily inorganic carbon fluxes driven by photosynthesis and respiration. However, the rate of CO_2 production via shell synthesis was significant in comparison to daily net ecosystem production (NEP) of CO_2. When considering the role of invasive snails in freshwater inorganic carbon cycling, the introduction and establishment of *Melanoides* in Kelly Warm Springs has increased net biological CO_2 production and, consequently, CO_2 evasion from the water into the atmosphere.

Beyond dominating the invertebrate organic carbon pool, the shell mass of *Melanoides* may be an important inorganic carbon reserve that could alter biogeochemical cycling. *Melanoides* have thick shells (and grow to a much larger size than any of the other mollusks present in Kelly Warm Springs) that will take several years to dissociate after death, especially in Kelly Warm Springs with high calcium (Ca^{2+}) concentrations

and pH, which impede CO_2 dissolution (Strayer and Malcom 2007). Decreases in $CaCO_3$ precipitation can also reverse this trend of CO_2 production and act as a CO_2 sink, especially during exoskeleton dissolution (Orr *et al.* 2005).

Melanoides CO_2 production via biotic calcification was similar to other mollusks, including the invasive freshwater bivalves *Dreissena polymorpha* and *Corbicula fluminea* (Chauvaud *et al.* 2003). We calculated additional annual CO_2 production estimates for several different marine calcifying organisms for further comparisons, most of which were in a similar range to *Melanoides* CO_2 production after accounting for the difference in Ψ between salt and freshwater systems (Table 1). If *Melanoides* consumed a larger proportion of primary producers in Kelly Warm Springs, it is possible that they would have more of an impact on ecosystem inorganic carbon cycling and CO_2 fluxes (Schindler *et al.* 1997). On the other hand, it is unlikely that ecosystems could support higher densities and/or higher production rates of snails without a preceding increase in GPP.

CO_2 production by *Melanoides*, while only a fraction of daily inorganic carbon cycling in relation to GPP and CR, was 13.6% of the net biological CO_2 production in Kelly Warm Springs (Figure 6). Despite the large proportion of CO_2 that was quickly transformed to HCO_3^- within the carbonate pool, we estimated the potential impacts of losing calcifying *Melanoides* from Kelly Warm Springs. Compared to the total net CO_2 production from biological processes (NEP + calcification), diffusion and reaeration were responsible for the evasion of 48.7% of the net biological CO_2 production. Holding all other processes equal, the loss of calcifying *Melanoides* would decrease Kelly Warm Springs CO_2 evasion rates from 37.2 to 32.1 mmol CO_2 m^{-2} day^{-1}.

This study demonstrates the potential role of invasive species as a source of CO_2 to stream inorganic carbon budgets as well as the ecosystem-level impacts of an exotic snail. *Melanoides* can contribute substantially to total biological CO_2 production through calcification, which must be calculated independently from stream metabolism. Biotic calcification did increase calculations of total CO_2 production and evasion in Kelly Warm Springs. In freshwater systems that are already super-saturated with CO_2, successful invasions by calcifying organisms may contribute to higher CO_2 evasion rates. The escalating introduction and spread of invasive mollusks worldwide will have important consequences when considering the biological processes responsible for CO_2 evasion from aquatic systems.

Table 1. Approximate CO_2 production via calcification by several different freshwater and marine organisms. Freshwater organisms are noted with a "*" and calcification values calculated from other sources by Chauvaud *et al.* (2003) are noted with a "+".

Organism	**CO_2 Production (moles CO_2 m^{-2} $year^{-1}$)**	**Citation**
*Dreissena polymorpha** (zebra mussels)	0 – 18.0	Chauvaud *et al.* 2003+
Heteropod mollusks	4.7×10^{-4} – 16.6×10^{-4}	Fabry 1990
Pteropod mollusks	3.3×10^{-3} – 15.6×10^{-3}	Fabry 1990
Bryozoans	0.4	Smith & Nelson 1994
Potamocorbula amurensis (Asian clam)	1.8	Chauvaud *et al.* 2003
*Corbicula fluminea** (freshwater Asian clam)	1.8 – 10.8	Chauvaud *et al.* 2003+
Bryozoans, coralline algae, echinoderms and mollusks	2.4	Smith 1972
Seagrass epiphytes	3.2	Chauvaud *et al.* 2003+
Crepidula fornicata (slipper limpet)	3.6	Martin *et al.* 2006
*Melanoides tuberculata** (red-rim melania)	3.8	This study
Ophiothrix fragilis (brittle star)	4.8	Migné *et al.* 1998
Coral reef systems	6.0	Gattuso *et al.* 1998
Crustose coralline algae	9.7 – 66.9	Chisholm 2000
Foraminifera	12.0	Chauvaud *et al.* 2003+

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✦ LITERATURE CITED

Benke, A.C. 1984. Secondary production of aquatic insects. Pages 289-322 in *Ecology of aquatic insects*. V. H. Resh and D. M. Rosenberg, eds. Praeger Publishers, New York.

Berry, A.J. and A.B.H. Kadri. 1974. Reproduction in the Malayan freshwater cerithiacean gastropod *Melanoides tuberculata*. Journal of Zoology, London 172: 369-381.

Cai, W.-J. and Y. Wang. 1998. The chemistry, fluxes, and source of carbon dioxide in the estuarine waters of the Satilla and Altamaha Rivers, Georgia. Limnology & Oceanography 43: 657-668.

Chauvaud, L., J.K. Thompson, J.E. Cloern and G. Thouzeau. 2003. Clams as CO_2 generators: The *Potamocorbula amurensis* example in San Francisco Bay. Limnology & Oceanography 48: 2086-2092.

Chisholm, J.R.M. 2000. Calcification by crustose coralline algae on the northern Great Barrier Reef, Australia. Limnology & Oceanography 45: 1476-1484.

Cole, J.J., N.F. Caraco, G.W. Kling and T.K. Kratz. 1994. Carbon dioxide supersaturation in the surface waters of lakes. Science 265: 1568-1570.

Cole, J.J. and N.F. Caraco. 1998. Atmospheric exchange of carbon dioxide in a low wind oligotrophic lake measured by the addition of SF_6. Limnology & Oceanography 43: 647-656.

Cole, J.J., M.L. Pace, S.R. Carpenter and J.F. Kitchell. 2000. Persistence of net heterotrophy in lakes during nutrient additions and food web manipulations. Limnology & Oceanography 45: 1718-1730.

Cole, J.J., Y.T. Prairie, N.F. Caraco, W.H. McDowell, L.J. Tranvik, R.G. Striegl, C.M. Duarte, P. Kortelainen, J.A. Downing, J.J. Middleburg and J. Melack. 2007. Plumbing the global carbon cycle: Integrating inland waters into the terrestrial carbon budget. Ecosystems 10: 171-184.

Duarte, C.M. and Y.T. Prairie. 2005. Prevalence of heterotrophy and atmospheric CO_2 emissions from aquatic ecosystems. Ecosystems 8: 862-870.

Dudgeon, D. 1986. The life cycle, population dynamics and productivity of *Melanoides tuberculata* (Müller, 1774) (Gastropoda: Prosobranchia: Thiaridae) in Hong Kong. Journal of Zoology, London 208: 37-53.

Duggan, I.C. 2002. First record of a wild population of the tropical snail *Melanoides tuberculata* in New Zealand natural waters. New Zealand Journal of Marine and Freshwater Research 36: 825-829.

Fabry, V.F. 1990. Shell growth rates of pteropod and heteropod molluscs and aragonite production in the open ocean: Implications for the marine carbonate system. Journal of Marine Research 48: 209-222.

Facon, B., J.-P. Pointer, M. Glaubrecht, C. Poix, P. Jarne and P. David. 2003. A molecular phylogeography approach to biological invasions of the New World by parthenogenetic Thiarid snails. Molecular Ecology 12: 3027-3039.

Facon, B., B.J. Genton, J. Shykoff, P. Jarne, A. Estoup and P. David. 2006. A general eco evolutionary framework for understanding bioinvasions. Trends in Ecology & Evolution 21: 130-135.

Frankignoulle, M., C. Canon and J.-P. Gattuso 1994. Marine calcification as a source of carbon dioxide: Positive feedback of increasing atmospheric CO_2. Limnology & Oceanography 39: 458-462.

Gattuso, J.-P., M. Frankignoulle, I. Bourge, S. Romaine and R.W. Buddemeier. 1998. Effect of calcium carbonate saturation of seawater on coral calcification. Global and Planetary Change 18: 37-46.

Giovanelli, A., M. V. Vieira and C.L.P.A Coelho da Silva. 2003. Apparent competition through facilitation between *Melanoides tuberculata* and *Biomphalaria glabrata* and the control of schistosomiasis. Memórias do Instituto Oswaldo Cruz 98: 429-431.

Giovanelli, A., M.V. Vieira and C.L.P.A. Coelho da Silva. 2005. Interaction between the intermediate host of Schistosomiasis in Brazil, *Biomphalaria glabrata* (Say, 1818) and a possible competitor, *Melanoides tuberculata* (Müller, 1774): A field study. Journal of Molluscan Studies 71: 7-13.

Hall, R.O., J.L. Tank and M.F. Dybdahl. 2003. Exotic snails dominate nitrogen and carbon cycling in a highly productive stream. Frontiers in Ecology and Environment 1: 407-411.

Hall, R.O., M.F. Dybdahl and M.C. VanderLoop. 2006. Extremely high secondary production of introduced snails in rivers. Ecological Applications 16: 1121-1131.

Hall. R.O., S. Thomas and E.E. Gaiser. 2007. Measuring primary production and respiration in freshwater ecosystems. Pages 175-203 in *Principles and Standards for Measuring Primary Production*. T.J. Fahey and A.K. Knapp, eds. Oxford University Press, Oxford.

Jacob, J. 1957. Cytological studies of Melaniidae (Mollusca) with special reference to parthenogenesis and polyploidy. I. Oogenesis of the parthenogenetic species of *Melanoides* (Prosobranchia-Gastropoda). Transactions of the Royal Society of Edinburgh. 63: 341-352.

Jones, J.B., E.H. Stanley, and P.J. Mulholland. 2003. Long-term decline in carbon dioxide supersaturation in rivers across the contiguous United States. Geophysical Research Letters 30:10.1029/2003GL017056.

Kiibus, M. and N. Kautsky. 1996. Respiration, nutrient excretion and filtration rate of tropical freshwater mussels and their contribution to production and energy flow in Lake Kariba, Zimbabwe. Hydrobiologia 331: 25-32.

Langmuir, D. 1997. *Aqueous Environmental Chemistry*. Prentice Hall, Upper Saddle River, New Jersey.

Livshits, G. and L. Fishelson. 1983. Biology and reproduction of the freshwater snail *Melanoides tuberculata* (Gastropoda: Prosobranchia) in Israel. Israel Journal of Zoology. 32: 21-35.

Love, J.D. and J.M. Love. 1988. *Geological road log of part of the Gros Ventre River valley including the lower Gros Ventre slide*. Geological Survey of Wyoming: Laramie, WY.

Martin, S., G. Thouzeau, L. Chauvaud, F. Jean, L. Guérin and J. Clavier. 2006. Respiration, calcification, and excretion of the invasive slipper limpet, *Crepidula fornicata* L: Implications for carbon, carbonate, and nitrogen fluxes in affected areas. Limnology & Oceanography 51: 1996-2007.

Migné, A., D. Davoult and J.-P. Gattuso. 1998. Calcium carbonate production of a dense population of the brittle star *Ophiothrix fragulis* (Echinodermata: Ophiuroidea): role in the carbon cycle of a temperate coastal ecosystem. Marine Ecology Progress Series 173: 305-308.

Millero, F.J. 1979. The thermodynamics of the carbonate system in seawater. Geochimica et Cosmochimica Acta 43: 1651-1661.

Mulholland, P.J., C.S. Fellows, J.L. Tank, N.B. Grimm, J.R. Webster, S.K. Hamilton, E. Martí, L. Ashkenas, W.B. Bowden, W.K. Dodds, W.H. McDowell, M.J. Paul and B.J. Peterson. 2001. Inter-biome comparison of factors controlling stream metabolism. Freshwater Biology 46: 1503-1517.

Odum, H.T. 1956. Primary production in flowing waters. Limnology & Oceanography 1: 102-117.

Orr, J.C., V.J. Fabry, O. Aumont, L. Bopp, S.C. Doney, R.A. Feely, A. Gnanadesikan, N. Gruber, A. Ishida, F. Joos, R.M. Key, K. Lindsay, E. Maier-Reimer, R. Matear, P. Monfray, A. Mouchet, R.G. Najjar, G.-K. Plattner, K.B. Rodgers, C.L Sabine, J.L. Sarmiento, R. Schlitzer, R.D. Slater, I.J. Totterdell, M.-F. Weirig, Y. Yamanaka and A. Yool. 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature 437: 681-686.

Pointier, J.-P., B. Delay, J.L. Toffart, M. Lefèvre and R. Romero-Alvarez. 1992. Life history traits of three morphs of *Melanoides tuberculata* (Gastropoda: Thiaridae), an invading snail in the French West Indies. Journal of Molluscan Studies 58: 415-423.

Pointier, J.-P. and M. Giboda. 1999. The case for biological control of snail intermediate hosts of *Schistosoma mansoni*. Parasitology Today 15: 395-397.

Portielje, R. and L. Lijklema. 1995. Carbon dioxide fluxes across the air-water interface and its impact on carbon availability in aquatic systems. Limnology & Oceanography 40: 690-699.

Rader, R.B., M.C. Belk and M.J. Keleher. 2003. The introduction of an invasive snail (*Melanoides tuberculata*) to spring ecosystems of the Bonneville Basin, Utah. Journal of Freshwater Ecology 18: 647-657.

Raine, R.C.T. 1983. The effect of nitrogen supply on the photosynthetic quotient of natural phytoplankton assemblages. Botanica Marina 26: 417-423.

Richey, J.E., J.M. Melack, A.K. Aufdenkampe, M.V. Ballester and L.L. Hess. 2002. Outgassing from Amazonian rivers and wetlands as a large tropical source of atmospheric CO_2. Nature 416: 617-620.

Robinson, D.G. 1999. Alien Invasions: The effects of the global economy on non marine gastropod introductions into the United States. Malacologia 41: 413-438.

SAS Institute. 2002-2003. *SAS/STAT User's Guide*, Release 9.1.3. Cary, North Carolina.

Simon, K.S. and C.R. Townsend. 2003. Impacts of freshwater invaders at different levels of ecological organisation, with emphasis on salmonids and ecosystem consequences. Freshwater Biology 48: 982-994.

Smith, S.V. 1972. Production of calcium carbonate on the mainland shelf of southern California. Limnology & Oceanography 17: 28-41.

Smith, A.M. and C.S. Nelson. 1994. Calcification rates of rapidly colonizing bryozoans in Hauraki Gulf, northern New Zealand. New Zealand Journal of Marine and Freshwater Research 28: 227-234.

Strayer, D.L. and H.M. Malcom. 2007. Shell decay rates of native and alien freshwater bivalves and implications for habitat engineering. Freshwater Biology 52: 1611-1617.

Subba Rao, N.V. and S.C. Mitra. 1982. Bioecology of two melaniid snails (Mollusca: Gastropoda) in ponds near Calcutta. Journal of the Zoological Society of India 1&2: 21-32.

Tans, P. 2007. Global monthly mean CO_2 data. NOAA/ESRL. www.esrl.noaa.gov/gmd/cgg/trends

U.S. Geological Survey. 2005. Nonindigenous Aquatic Species Database, Gainesville, FL. http://nas.er.usgs.gov.

Vanni, M.J. 2002. Nutrient cycling by animals in freshwater ecosystems. Annual Review of Ecology and Systematics 33: 341-370.

Wanninkhof, R., P.J. Mulholland and J.W. Elwood 1990. Gas exchange rates for a first order stream determined with deliberate and natural tracers. Water Resources Research 26: 1621-1630.

Wanninkhof, R. 1992. Relationship between wind speed and gas exchange over the ocean. Journal of Geophysical Research 97: 7373-7382.

Wanninkhof, R. and M. Knox. 1996. Chemical enhancement of CO_2 exchange in natural waters. Limnology & Oceanography 41: 689-697.

Ware, J.R., S.V. Smith and M.L. Reaka-Kudla. 1991. Coral reefs: sources or sinks of atmospheric CO_2? Coral Reefs 11: 127-130.

Wetzel, R.G. and G.E. Likens. 2000. *Limnological Analyses*. 3rd edition. Springer Verlag, New York.

Wetzel, R.G. 2001. *Limnology*. 3rd edition. Academic Press, San Diego, CA.

GRAND TETON NATIONAL PARK

HARRISON R. CRANDALL: ARTIST, PIONEER AND PATRON OF GRAND TETON NATIONAL PARK

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✦ INTRODUCTION

Harrison R. Crandall (or "Hank" as he preferred; Fig. 1) is best known for his paintings and photographs of the Teton Range, and ranch scenes of Jackson Hole, Wyoming. However, Hank's multi-faceted life, which spanned the period from 1887-1970, was far more interesting and important than is generally recognized. He was the first artist and commercial photographer to operate a studio in the Jackson Hole area, but he was also a valley homesteader, an important supporter and patron in the establishment of the Grand Teton National Park, and a pioneer concessionaire of National Park art and souvenirs before the advent of mass tourism. Hank's natural artistic talent was accompanied by a complex personality—a mixture of the spirited individualism required of a mountain adventurer and dry-land homesteader, a loving and dedicated family man who promoted shared labor and leisure, and an environmentally attuned visionary who helped many to interpret the meaning of the Grand Teton National Park experience.

Figure 1. Hank Crandall with his skis ca. mid-1920's (left), and Hank painting the Tetons ca. 1950 (right) (© Crandall)

✦ Hank Crandall's Art—Photographs and Oil Paintings

Hank's artistic and technical expressions were the result of a unique combination of his personal vision, early 20th Century academic conventions, and the equipment, emulsions, and chemistry that was available at the time (H. Pownall, 1991; H. Pownall, personal communication 2008). Photography was a staple of the Crandall Studio business. Hank had the ability to capture the photographs that people wanted as remembrances of their Teton experience, and many of these subjects have become the iconic images of Jackson Hole (Fig. 2). His favorite subjects included Teton landscapes (Fig. 3), wildflowers, Native Americans, and western life style scenes complete with buck-rail fences, cowboys and cowgirls (Flood 1996; Q. Pownall, personal communication 2008).

Hank's vision of the Jackson Hole landscape resulted in photographs with luminous mountains and a bright sky (Pownall, 1991). Hank was most proud of his hand painted wildflower panels (Fig. 4), and Native American portraits (Fig. 5) (Crandall, Hildegard 1970). Today, the strong secondary market for Hank's photographs is explained, in part, by the consistently high quality of his photographic prints. Hank demanded quality in the field and the darkroom, which is best explained by his own words, "It is my aim and ambition to only turn out the best pictures that are possible to be made, as I figure a poor picture is worse than nothing" (Flood 1996). In the darkroom, large and expensive prints were torn up if they were not just right (H. Pownall, personal communication 2007).

Figure 2. Cowboy Pastime—an iconic Hank Crandall photograph of ranch life in Jackson Hole (© Crandall)

Figure 3. Hank Crandall Teton landscapes—Sepia-tone photograph of Mount Moran (left), and hand painted photograph, "North View of the Grand Teton" (right)

Figure 4. Hank Crandall hand painted, wildflower panel photographs—"Wild Rose" (left), and "Fringed Gentian" (right).

Figure 5. Hank Crandall hand painted photo—Native American (© Crandall

Hank used a variety of camera types, and a wide range of film sizes—from small to large formats. His favorite equipment included panel cameras for sheet film. Negative sizes ranged from 3¼x4¼, through 4x5, 5x7, 8x10 and 7x17 inches. The 3A Kodak roll film size was right for contact prints on post card stock paper. He also used 16 mm and 35 mm roll films (H. Pownall 1991; H. Pownall personal communication 2008). Many of Hank's photographs from the 1920s and 1930s were made on orthochromatic emulsions, which was the type of film that was available to him. Orthochromatic film was considered to be "color blind" in the sense that a scene was recorded in gray tones that were different from what the eye sees. The film was more sensitive to blue than red, which produced a very light sky. Hank occasionally used lens filters when photographing with panchromatic films, but he preferred not to try for the artificial effects that filters tended to generate (H. Pownall 1991; H. Pownall personal communication 2008).

During print exposure, Hank's dodging and burning-in patterns required the nimble hands of an orchestra conductor—he sought the precise emphasis that would achieve his scenic

vision (H. Pownall, 1991; H. Pownall personal communication 2008). The process of creating a hand painted photo began with a photographic print made on single-weight Kodak mural paper that was deliberately underexposed in order to render it to about 25 percent of the contrast and density of a normal black and white photo. The lighter image allowed the opaque color oils to be more easily superimposed over top of the photographic image (H. Pownall personal communication 2008). While many photographers produced hand tinted photos before the advent of color films, Hank's color applications were unique. The photographs were heavily over-painted with vivid oil colors—in a sense, the underlying photographic image was treated like the canvas of an oil painting.

Painting the Teton Range was always foremost among Hank's artistic goals. The great majority of Hank's oil paintings were Teton landscapes (Fig. 6). However, proving up the homestead, creating and running an art studio, and raising a family consumed much of Hank's time. Therefore, many of his oil paintings were completed after his retirement from the Crandall Studio business. It was during these more tranquil moments that Hank was able to focus on evolving his technique, and the style of his paintings shifted from realism to a more subjective vision (Q. Pownall personal communication 2007). Hank's paintings were very popular, and continue to grace many homes in Jackson Hole (Jackson Hole News & Guide 2006; Winchell 2007), and they were distributed across the United States as National Park souvenirs.

✦ Hank Crandall as Patron of the Grand Teton National Park

Hank considered the Teton Range to be his "ideal landscape"—a place that he loved, and a landscape with the power to cause him to move his family in order to fully live the Teton experience. Some suggest that Hank surrendered some of the national notoriety that he might otherwise have achieved in order to remain focused on his Teton art despite the lack of a mass market for the subject at the time. Given Hank's deep commitment to the Tetons, it is easy to understand why he was an ardent supporter of establishing the Grand Teton National Park. Hank was the Park's greatest publicist—he was to the Teton Range and Jackson Hole what F.J. Haynes was to Yellowstone National Park (NPS 2007). Many of Hank's photographs were gifted to the Grand Teton National Park for promotional purposes (Fig. 7). Hank's photographs helped sway the U.S. Congress into establishing the Park (Jackson Hole News & Guide 2006). Moreover, with the agreement to sell their homestead, the Crandall's transferred a key property for the creation of the preserve. Horace M. Albright, the Director of the National Park Service at the time that the Grand Teton National Park was dedicated, commented on Hank's commitment to the Park ideal, "Hank Crandall never wavered in his adherence to plans, including the creation of a Grand Teton National Park, to preserve the best of Jackson Hole for present and future generations" (Albright 1971).

Figure 6. Hank Crandall oil paintings of Mount Moran—early painting ca. 1930's (left), late painting ca. 1960's (right).

Figure 7. Hank Crandall photo of Grand Teton National Park dedication ceremony—Horace Albright, Director of the National Park Service (left), Billy Owen, famous climber of the Grand Teton (center), and Park Superintendent Sam Woodring (right) (© Crandall)

✦ Hank Crandall—Life and Times

Hank Crandall was born on 23 November 1887, in Newton, Kansas, to Sarah Conover Crandall and Robert Wyatt Crandall (Crandall and Crandall 1976). He was the ninth of ten children (Q. Pownall 1991). Hank's father ran a nursery and berry farm on the plains of Kansas despite having lost his arm while serving in the Union Army during the Civil War.

Hank began dreaming of westward travel and adventure at an early age. In grade school, he was inspired by the landscape photographs found on the pages of his geography textbooks. In particular, he recalled a picture of the Teton Range by William Henry Jackson. Hank resolved to visit those seemingly distant mountains (Crandall, Hildegard 1970).

The opportunity to move west came at the age of 25, when Hank's brother filed for a homestead in the sand hills of Idaho. Hank was sent to sit on the claim. He traveled to Idaho on a freight train, which was carrying a Kansas family's household goods. Hank was allowed the price of the train fare in return for feeding and milking the family's cow along the route (Crandall and Crandall 1976). He lived in a shanty on the claim for little more than 3 months until the land was deemed worthless for farming (Crandall and Crandall, 1976). After abandoning his brother's claim, Hank moved to Los Angeles, California, and begin his formal art training. He enrolled at the School of Art and Design, where he studied for several years (Crandall and Crandall, 1976; Crandall, Hildegard 1970). Hank took on several jobs to defray the cost of his education, including painting theatre backdrops and murals. During his summer vacation, he lived at Lake Tahoe, where he played trombone in a local dance band (Crandall and Crandall, 1976; Q. Pownall, personal communication 1991).

Hank served in the Navy Band during World War I. After the war, he moved to American Falls, Idaho, where he met his future wife—Hildegard R. Winter (Hilda as Hank preferred; Fig. 8). She was born on 27 April 1898, at Menno, South Dakota. In 1911, her family moved to a homestead west of American Falls. After secretarial school, she went to work for a local bank (Crandall and Crandall 1976).

Figure 8. Hildegard Crandall with snowshoes ca. 1920's (© Crandall)

Hank took a job with the U.S. Biological Survey in Boise, Idaho, just long enough to buy a Model T Ford. The Model T provided the means to fulfill his childhood dream of visiting the Teton Mountains (Crandall, Hildegard 1970). During the summer of 1920, Hank and Hilda took off on a two week adventure through Yellowstone National Park. On their return route, they traveled through Teton country. In order to get the Model T over the Teton Pass, they had to push it up the steep switchbacks (Crandall, Hildegard 1983).

Hank and Hilda were married in October of 1921 (Crandall, Hildegard 1980). The newlyweds moved to Pocatello, Idaho, where Hank opened a commercial sign shop, and Hildegard took a secretarial job at a bank (Crandall, Hildegard 1983). However, the Crandalls did not reside in Pocatello for long as they were saving money to move to the Tetons and Jackson Hole (Crandall, Hildegard 1983).

When spring arrived in 1922, Hank enclosed the back of the Model T with plywood so that they could carry all their belongings to their new life in Jackson Hole (Crandall and Crandall, 1976). They carried a complete camping outfit (Crandall, Hildegard 1983), and photographic supplies (Flood 1996). Hank and Hilda took their friends, Red Kelly and Miss Bye, along on their trip to Jackson Hole, and they spent the summer camping (Crandall and Crandall, 1976). Red Kelly served as Hank's photographic assistant, and with their canoe, they paddled across lakes, and hiked up into the Teton canyons (Crandall and Crandall 1976; Crandall, Hildegard 1980).

Hank and Hilda camped the entire summer of 1922, living in a tent, and moving from place to place in what is now the Grand Teton National Park, including Jenny Lake, String Lake and Jackson Lake (Crandall, Hildegard 1980). Hank's primary interest was to paint the Tetons, but the first summer was spent scouting for photographs (Crandall, Hildegard 1980). Hank did not know what the Tetons had in store for him since he was only a student artist, with no established "fame or fortune" (Crandall, Hildegard 1970).

Hank had a fine camera that was formatted for making real photo postcards—a "3A Special Eastman Kodak" (Crandall, Hildegard 1970). Photos of the mountains and valley were taken from every angle (Crandall, Hildegard 1980). Film and prints were developed at String Lake Camp, a fully equipped camp that was recently abandoned by a Hollywood film crew (Fig. 9). Hank used a canvas umbrella tent as a darkroom. His darkroom contained several plywood developing trays, which were made watertight by lining them with oil cloth. The negatives were mounted in wooden contact printing frames, and the photographic print paper was exposed through the negative by sticking the apparatus through the canvas flap for the appropriate dose of sunlight. Then, the film was developed and fixed in home mixed solutions. The prints were washed in String Lake and dried on tightly stretched bed sheets. Then, they were trimmed, stamped with "postcard" on the back, and sold at Charlie Fessler's General Store in Moran village. Selling postcards was a tenuous start, but Hank was optimistic about making a living selling his Teton art.

Figure 9. String Lake Camp ca. 1922 (© Crandall)

By the fall of 1922, friends had persuaded Hank and Hilda to stay the winter at Moran village. Moran, located near the base of the Jackson Lake Dam, was a lively village, which consisted of Ben Sheffield's spacious main lodge surrounded by rustic cabins, a store, auto garage, campground and corral. Moran served as a camp for the construction crews that were working on Jackson Lake Dam, and as a stop for travelers. Charlie Fessler owned the Moran General Store, and he suggested a cabin for Hank and Hilda in exchange for cutting fuel wood and ice from Jackson Lake (Fig. 10) (Crandall and Crandall 1976; Crandall, Hildegard 1980).

Hank negotiated a lease to open a studio and photo developing business at Moran village in the late 1920s. For more than 20 years, Hank operated a darkroom service where he and his apprentices would spend most evenings developing and contact printing film for the local dude ranch guests.

Figure 10. Hank Crandall cutting ice on Jackson Lake ca. 1922 (© Crandall)

During their first winter at Moran, Hank and Hilda became well acquainted with the local homesteaders (Crandall, Hildegard 1980). On Saturday nights, they would meet with friends and attend a party at one of the nearby ranches. The party often began with a 10-mile long ride on a mail sleigh (a large horse drawn sled on four runners covered with canvas and containing a sheep herder's stove). At the ranch house, about 20 adults would play cards until midnight, and then the music started and folks danced until daybreak. The Crandall's often helped furnish the music—Hank played the trombone, and Hildegard played the piano.

Hank and Hilda went on a ski trip to take photographs in the spring of 1923. They visited Tony Grace who owned the Danny Ranch (now called the Jenny Lake Ranch), which was located close to String Lake (Crandall, Hildegard 1980). They learned that land adjacent to Danny Ranch was available for homesteading. Upon hearing the good news, Hank "ran as if there was fire back of him" and "hitched" a sleigh ride to the land office. They filed for a 120 acre homestead, which was located northeast of Jenny Lake (Crandall and Crandall 1976; Crandall, Hildegard 1983).

Hank and Hilda lived in a Sibley tent during their first summer on the homestead, complete with a wood-burning stove in the kitchen area (Crandall, Hildegard 1983). Later, they stayed in a larger tent in order to cook for log builders and carpenters (Crandall, Hildegard 1980). Building projects included a 2-room cabin, an art studio and a dance pavilion (Crandall, Hildegard 1980; Crandall, Hildegard 1983). The cabin was heated by a kitchen range, and a pot-bellied stove (Crandall, Hildegard 1980). A wash tub was set up in front of the stove for bathing. Kerosene lamps were used (Crandall and Crandall 1976). Most of the furniture was homemade—only Hildegard's piano was store bought (Crandall, Hildegard 1980).

In the summer, water for domestic use and photo processing had to be carried from String Lake. In the winter, snow was collected in a 50-gallon barrel, melted in big pots, and filtered through a cloth (Crandall, Hildegard 1980). Fresh vegetables could be purchased in Kelly, so no attempt was made to grow a garden (Crandall, Hildegard 1980). Also, Hank would "lay in" food and supplies from Idaho—anything that could be stored in a root cellar. Hank hunted game in order to provide meat for the family, but he did not enjoy hunting much, so it was usually put off until about the last day of the hunting season. Also, fresh meat could be purchased from a merchant, who delivered meat from Wilson to the nearby Danny Ranch. Hildegard tried to raise a few chickens, but the local wildlife ended up taking most of them (Crandall, Hildegard 1980).

Hank and Hilda were not ranchers, so they undertook several commercial ventures to provide a little income. In 1924, they opened the "String Lake Dance Pavilion" on the homestead (Crandall and Crandall 1976; Crandall, Hildegard 1980). The open-air dance hall had a 70-foot long floor made of lodgepole pine planks. The walls were lodgepole logs that extended about 4 feet off the floor, with the upper portion of the walls being canvas (Crandall and Crandall 1976; Crandall, Hildegard 1980). The Dance Pavilion was open for business during the summer months—from mid-June until the end of August (Crandall, Hildegard 1980). Hank and Hilda's musical talents were already in high demand throughout the valley. Their band consisted of Hank on trombone, Hilda on piano, Charlie Hedrick on fiddle, and Louie Flemming or Cliff Ward on the drums (Crandall and Crandall 1976; Crandall, Hildegard 1980; Crandall, Hildegard 1983). The Saturday night events were so popular that dances were added on Wednesdays. Square dancers came from miles around, and included valley residents and "dudes" from the local dude ranches. There

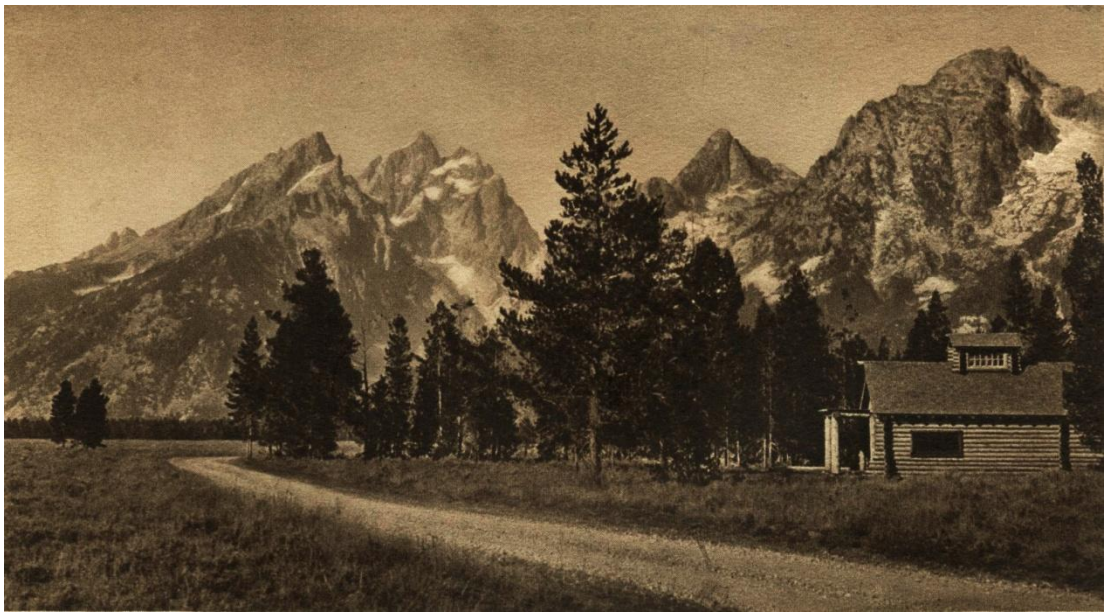

Figure 11. Crandall Studio building at the original homestead location

were few tourists, as the roads were not sufficiently improved. At midnight, around huge campfire, "lunch" was served, which included a sandwich, pie and coffee. After refreshments, folks danced until at least 2:00 a.m. (Crandall and Crandall 1976).

Hank took care of business during the day and played in the band at night. The dance pavilion was discontinued after about 2.5 years because Hank wanted to concentrate all resources on opening his art studio. In 1925 and 1926, wood from the pavilion was recycled and diverted to the construction of the Crandall Studio (Fig. 11) (Crandall, and Crandall 1976; Crandall, Hildegard 1980). The studio was conveniently located on the homestead near the road, but not too far from the cabin, so that regular staffing was not required (photo processing was being done at a small separate one-room structure). Hank designed the rustic lodgepole studio to withstand heavy winter snow loads, and outfitted the interior with a sky-lighted, detailed log pattern (Fig. 12). The structure was constructed entirely by local artisans (Q. Pownall personal communication 2007; H. Pownall personal communication 2007). Today, the studio building represents an enduring architectural statement, and is considered to be one of the landmark rustic buildings in Jackson Hole.

Figure 12. Interior of the Crandall Studio building ca. late 1920's (© Crandall)

In 1927, the Crandall studio was opened. Business depended on a few tourists and guests from the dude ranches. When a vintage car would approach, the noise was sufficient to announce the arrival of a potential customer. When a car would drive up, Hank would yell "Hrrrrrrry, Hrrrrrrrrry, biznesssssss!" The studio door was always kept open (Crandall and Crandall 1976; Crandall, Hildegard 1980). In the early years, tourist traffic was extremely light, so there were few customers (Crandall, Hildegard 1980).

Hank also sold Kodak photo finishing for the local dude ranches (Crandall and Crandall 1976; Crandall, Hildegard 1983). When the studio first opened, Hank sold only the few photographs that he had taken the summers before. However, soon thereafter, Hank began hand painting his photographs, which became very popular in Jackson Hole (Crandall and

Crandall 1976). Later, the studio sold paintings, post cards, photographs (sepia tone, black and white, and hand painted), cameras and film, poster prints, wood carvings of wild animals, animal skins (elk, bear and mountain lion), Navaho rugs, baskets, jewelry by western artisans and guidebooks (H. Pownall personal communication 2007; Q. Pownall personal communication 2008). Care was taken to offer a finer quality of souvenirs—some were imported from Germany. There was also a small film changing darkroom. Hank did little of the actual salesmanship, leaving that to other members of the family and employees (Q. Pownall personal communication 2007; H. Pownall personal communication 2007). Hank also produced and sold several photo picture books of the Tetons, including "The Tetons in Pictures" (Crandall, Harrison ca. 1930) and "The Tetons in Color" (Crandall, Harrison 1953).

The winters were typically spent printing, developing and stamping the photographs that Hank had taken the previous summer. When photographic supplies arrived, they had to be carried in from Moran. The Crandalls would put on snowshoes—Hank would pull the toboggan and Hilda would push. Hildegard's secretarial skills were important for business correspondence and record keeping. Otherwise, she kept very busy braiding rugs, cooking and keeping the fires burning (Crandall and Crandall 1976).

Hank and Hilda spent a total of seven years on the homestead, although they did take trips out during the winter to explore other ways to make a living, as the postcard business was not very profitable (Crandall and Crandall 1976). In 1928, the Snake River Land Company offered to buy the homestead, and the Park tendered a twenty-year concession lease to operate a picture and curio shop at Jenny Lake. Hank and Hilda quickly accepted the offers. By selling the homestead, Hank retained his dream of having an art studio in the Tetons, and the proceeds made it possible to establish the studio business on a year-round basis (Crandall, and Crandall 1976; Crandall, Hildegard 1980; Crandall, Hildegard 1983). Hank and Hilda wintered that year in Jackson where life would be a little more comfortable. Thereafter, the Crandalls lived at their summer quarters in back of the Crandall studio at Jenny Lake, but over wintered outside of the valley. In 1932, and for 17 years thereafter, their winter home was in Boise, Idaho.

Hank and Hilda's first child, Quita, was born in Jackson, Wyoming, on 16 October 1928. Quita's natural artistic talents were recognized at an early age, and she went on to become an accomplished artist. During Quita's formative years, her father tutored her at the studio, and she was encouraged to draw and paint the wildflowers of the Tetons. Quita hand painted many of the Crandall photographs, especially the wildflower panels. She also served as a Crandall Studio salesperson, and, later, helped manage the Crandall Studio at Moran. Following her formal art education at Stephens College (Missouri) and the Pratt Institute (New York), she became a graphic artist for the University of Wyoming, and a freelance artist for commercial publications (ca. 1960-1968). Her main career in the fine arts began in 1970. Her favorite subjects include the scenic wonders of Wyoming, including landscapes, animals in wild settings, cowboys, ranchers and Native Americans. Quita, as she signs her paintings, has exhibited her oil and pastel paintings widely, and has received many art awards in Wyoming (Kovinick and Yoshiki-Kovinick 1998).

Quita married Herbert (Herb as he prefers) D. Pownall in 1950. Herb worked extensively with Hank in the darkroom as an apprentice. Herb's formal photographic training began with courses at Iowa State College, and his experience using Press Cameras during journalism assignments, but working in the Crandall darkroom turned out to be a rewarding experience for a young photographer. At the Crandall Studio, Herb had to learn Hank's unique, market tested techniques and standards, which were different than those provided by his collegiate courses (H. Pownall personal communication 2008). Quita and Herb managed the Crandall Studio at Moran from 1952 until the last summer of operation in 1954. The National Park Service removed the Moran village in 1955, and moved many of the cabins to Colter Bay (NPS 2007). Quita and Herb moved to Laramie, Wyoming, where Herb was employed by the University of Wyoming to set up the campus photographic service (H. Pownall personal communication 2008).

Hank and Hilda's second daughter, Nancy, was born during the summer of 1930 (Crandall, Hildegard 1980). Nancy also worked

with her father in the studio by hand painting photographs and assisting in the darkroom. She was also a salesperson at the studio (Flood 1996; Q. Pownall personal communication 2008). Like her sister, Nancy went to Stephens College, but eventually graduated from the University of Wyoming. She went on to become a junior high school teacher. Nancy passed away in 1998 (Q. Pownall personal communication 2008).

After the founding of the Grand Teton National Park in 1929, Hank became the Park's "Official Photographer" (Flood 1996). The National Park Service negotiated Hank's concession based on the successful F.J. Haynes photographic concession in Yellowstone National Park (Q. Pownall personal communication 2007; H. Pownall personal communication 2007). The Crandall Studio was moved from its original location on the homestead to near the shore of Jenny Lake. Later, in about 1960, the studio was moved back a short distance from the Lake to its present location. The studio is listed on the National Register of Historic Places, and is currently a National Park Service visitor center (Q. Pownall personal communication 2007; H. Pownall personal communication 2007).

The Studio business was rather lean from 1932 until the mid-1940s because tourism was limited by the Great Depression and World War II, and the Grand Teton National Park's tourist trade was not well established (Crandall, Hildegard 1983). During these lean summers, Hank was able to spend more of his time painting (Crandall and Crandall 1976). Hank maintained a studio at his home in Boise, and during the long winters, he refined his art (Q. Pownall personal communication 2007).

In 1941, Hank and Hilda began building a new home and studio at "Paint Brush Point" near the north end of Blacktail Butte, just east of Moose, Wyoming. Paint Brush Point became the family's year-round home—complete with world-class views of the Tetons. Unfortunately, Hank's workshop at Paint Brush Point burned in late December of 1954, and most of his collection and photographic negatives were lost in the fire (Crandall, Hildegard 1980).

Hank retired in 1959, after operating his studio business for 34 years. He sold the Crandall Studio and Park business concession. In retirement, Hank had the time to focus on his oil painting—an activity he did not have sufficient time to take very seriously while running the business (Crandall, Hildegard 1970; 1980). Hank recovered from a serious illness and surgery in early 1969, and returned to painting. Hank passed away at Paint Brush Point on 14 December 1970 (Crandall, Hildegard 1970; 1980).

✦ CONCLUSIONS

Hank Crandall came to the Teton Range and Jackson Hole for reasons that were intensely personal—to live and work in the landscape that he loved. However, his lifetime achievement can now be viewed as transcending his personal story, or even his own generation. Hank left a legacy of National Park art that helped create an early vision of the Tetons that will continue to inspire and inform generations to come. The souvenirs sold in his studio gave countless National Park visitors a tangible remembrance of their trip or vacation. His unique hand painted photographs and oil paintings will continue to grace many fine American homes. His homestead will always remain preserved land at the heart of the Grand Teton National Park.

✦ ACKNOWLEDGEMENTS

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✦ LITERATURE CITED

Albright, H.M. 1971. Letter to the Editor, *Jackson Hole News*. January 7, 1971.

Crandall, Harrison R. 1953. *The Tetons in Color*. Hank R. Crandall, lithographed by Security Lithograph Company, San Francisco, California. 26 pp.

Crandall, Harrison R. ca. 1930. *The Tetons in Pictures*. Crandall Studios, Grand Teton National Park, lithographed by Graves & Potter, Inc., Pocatello, Idaho. 75 pp.

Crandall, Hildegard. 1983. Diary of Our Adventures in Jackson Hole—Five Years on the Homestead. Signed written history document, October 5, 1983. Jackson Historical Society & Museum, Jackson, Wyoming.

Crandall, Hildegard. 1980. Interview Summary. Jackson Historical Society & Museum, Jackson, Wyoming.

Crandall, Hildegard. 1970. Compiled Notes Collected by H.D. Pownall for the Jackson Hole Guide. Jackson Historical Society & Museum, Jackson, Wyoming.

Crandall, Hildegard and Crandall, Harrison R. 1976. Notes About Hildegard and Harrison. Jackson Historical Society & Museum, Jackson, Wyoming.

Flood, E.C. 1996. Harrison R. Crandall Photographer. Cowboys & Indians: The Premier Magazine of the West. Summer, 1996. pp. 49-54.

Jackson Hole News & Guide. 2006. Show Stars One of 1st Artists to Paint Tetons. June 14, 2006.

Kovinick, P. and M. Yoshiki-Kovinick. 1998. *An Encyclopedia of Women Artists of the American West*. University of Texas Press, Austin, Texas.

NPS (National Park Service). 2007. Grand Teton Historic Resource Study, Chapter 15: Tourists. http://www.cr.nps.gov/history/online_books.

Pownall, Herbert. 1991. Notes on the Museum Qualities of Hank R. Crandall Photographs. Jackson Historical Society & Museum, Jackson, Wyoming.

Pownall, Quita. 1991. Notes on the Crandall Family. Jackson Historical Society & Museum, Jackson, Wyoming.

Winchell, T. 2007. Personal Communication. Owner, Fighting Bear Antiques, Jackson, Wyoming.

GTNP BREEDING BIRD MONITORING PROJECT: THE 2006 SEASON
YEAR-TO-YEAR VARIATION IN AVIAN BREEDING DENSITIES IN GRAND TETON NATIONAL PARK

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✦ ABSTRACT

Census work was carried out in mid-June on 10 of the 30 breeding bird monitoring sites formally established in the mid 1990s. The censuses conducted in 2006 spanned a range of habitats from grassland and sage through willows and cottonwoods to pine and spruce-fir forest. Collectively, the sites cover all habitats within Grand Teton National Park, from lowest to highest elevations, and have produced records of 158 bird species since project initiation. Dry conditions prevailed in GTNP in late winter 2006 and extended into the spring and summer. Similarly, dry conditions were widespread in the overwintering areas of many of the migrants breeding within the park, from southern and southwestern USA south into northern and western Mexico.

The 2006 breeding birds showed overall lower densities, with especially low numbers in those species typical of wetland habitats. On the other hand, many species characteristic of drier habitats within the park and with geographic ranges extending south and west of the park were more common than usual. Comparisons are drawn, for different suites of birds, between 2006 densities and the long term average densities at the monitoring sites. Some attempt is made to distinguish between on-site and off-site influences on breeding bird densities, although these efforts remain tentative.

✦ INTRODUCTION

Monitoring of breeding bird densities in Grand Teton National Park has been ongoing in an organized fashion since the early 1990s, although data from some sites dates back a half-century (e.g. Salt 1957a,b; see overviews by Cody 1996, 1999, 2005). A suite of thirty monitoring sites was formalized in the mid-1990s (Cody 1997). These sites, spread over the full range of habitats within the park, have been assessed for breeding birds with varying schedules; some sites have been evaluated yearly, continuously for the last 17 years, others have been visited more sporadically. The goals of continued monitoring efforts of the breeding birds are several fold: to assess long term trends and detect changes in breeding bird numbers, to evaluate any differences in breeding density variability between neotropical migrants and resident birds, and to record patterns of habitat use and variations of breeding densities over habitat gradients.

In 2006 10 monitoring sites were surveyed over 10 d in mid-June:

1. Site 2: Jackson Lake Junction (JLJ) Sedge Meadow
2. Site 4: JLJ Grass-sage
3. Site 5: Antelope Flats sage burn/nonburn
4. Site 9: RKO Dry Willows
5. Site 10: JLJ Wet Willows
6. Site 11: Oxbow Willow-aspen
7. Site 15: Spread Ck Cottonwoods

8. Site 19: AMK Lodgepole Pine
9. Site 20: Taggart Lk Lodgepole Pine Burn
10. Site 25: Jenny Lk Spruce-fir

Bird census protocols followed those specified earlier for this project (e.g. Cody 1997). Each site is visited three times for several hours, at three different times of the day (early morning, late morning, afternoon). Bird activity records, movements, vocalizations and nesting are entered on a site map, from which estimates of territory numbers and breeding bird densities can be extracted.

Spring conditions in the northern part of Jackson Hole were dry (2006 April-June precipitation down 32% from the long-term average--LTA) and somewhat warmer than usual (cumulative mean monthly temperature up 3% from LTA, and spring monthly maxima and minima were 2-3 ^{o}C higher than normal). Snowmelt date, the date by which snow no longer persists on the ground, at Jackson Lake Dam (NCDC climate station Moran 5 WNW; L. Robinson prop.) was close to average, namely Julian Date (JD) 116 (= April 22nd.); cf. long-term average JD of snowmelt = 112 ±10SD. Winter conditions were dry also throughout the southwestern U.S. in early 2006 (NOAA-NCDC summaries) from Arizona to southern California, an area encompassing much of the wintering grounds for a number of GTNP breeding birds. In southern California NCDC stations from Santa Barbara to San Diego recorded collectively just 54% of their LTA precipitation. Further south in western Mexico, also an area that supports large wintering bird populations from the western U.S., including the central Rocky Mountains, there were winter drought conditions (NOAA web site). Weather stations (north to south over ca. 1400 km) from Mazatlan SIN, Durango DGO, Tepic NAY, Cd. Guzmán JAL, Morelia MICH and Acapulco GRO recorded winter precipitation from November 2005 to March 2006 at or very near zero, although summer rainfall in the wettest months of August and September was at or above average at least in the southern part of this range.

2006 GTNP Bird Populations

Censuses in 10 of the established monitoring sites produced several new site records and numerous shifts in density of individual species relative to previously tallied high and low values. At Site 4, JLJ Grass-sage, Turkey Vulture (*Cathartes aura*) was a first for the site, and is a species that we have recorded with increased frequency over the last several years over the drier sage flats of Jackson Hole. Site 5 straddles the burned and unburned areas of the Antelope Flats, the Mormon Row fire of 1994. Now the species that utilized the burn in its early years (e.g. Long-billed Curlew *Numenius americanus*, Mourning Dove *Zenaida macroura*, Common Nighthawk *Chordeiles minor*, feeding Sage Grouse *Centrocercus urophasianus*) are long gone, and the 12 y-old recovering burn is mostly grassy and dominated by Savannah Sparrow *Ammodramus sandwichensis*, Vesper Sparrow *Poocetes gramineus*, and Western Meadowlark *Sturnella neglecta*. The unburned part of the plot is tall sage, and in 2006 supported a Sage Thrasher *Oreoscoptes montanus* for the first time.

Site 9, the RKO Dry Willows site, recorded its lowest ever densities of Common Yellowthroat *Geothlypis trichas* (1 pr; LTA 3.83 pr) and White-crowned Sparrow *Zonotrichia leucophrys* (0.9 pr; LTA = 2.27 pr). In 2006 all three *Spizella* sparrows were recorded at the site (Chipping Sparrow *S. passerina*, Brewer's *S. breweri*, and Clay-colored *S. pallida*), although none is common there. 2006 was clearly a good year for Clay-colored Sparrows, as it was recorded at several sites; the species seems to be recovering from several decades of absence or great rarity, as it was relatively common in GTNP in the 1960s and 1970s. Site 10, the JLJ Wet Willows site, now has 17 y of continuous monitoring records. The site was drier than usual in 2006, with no rails or Marsh Wren *Cistothorus palustris*. The SW beaver pond was shrunken in size and just 3 pr of duck, of three species, nested there (the norm is 6pr). The N beaver pond, the dam being the northern boundary of the study site, supported a Northern Waterthrush *Seiurus novaboracensis*, but overall the number of locations within GTNP at which Northern Waterthrush can usually be heard singing was much reduced in this dry year. Pine siskins *Spinus pinus* utilized this site at high density from 2000-2005, following a major outbreak of a defoliating moth (of unknown providence, *fide* Dr. Clifford Ferris). The siskins foraged avidly on the pupating moths, whose cocoons were leaf-wrapped on the upper willow branches. The Oxbow willow-aspen, Site 11, continued the theme of scarcer wetland species and commoner "dryland" species, with the

absence on Common Snipe *Gallinago gallinago* and presence of Lazuli Bunting *Passerina amoena*. The exceptional species at the site, however, was Gray Catbird *Dumetella carolinensis*, with 3 pr in residence; the LTA for the species at this site is 0.72 pr, and the previous density high was just a single pair.

The cottonwood census at Site 15, Spread Creek, again reflected the overall conditions of the year, with dryland species Clay-colored Sparrow and Common Nighthawk present, and species with a preference for a more mesic lower stratum of vegetation, the two usual hummingbird species, Fox Sparrow *Melospiza iliaca*, and White-crowned Sparrow absent or nearly so. Moving to the pines, Site 19, AMK Lodgepole Forest, the commonest species here is Dark-eyed Junco *Junco hyemalis*, slightly over 1 pr/ha. In 2006 the numbers were at a hitherto unrecorded low of 5 pr (LTA 6.5 pr, max. 8pr). The second commonest species here is Yellow-rumped Warbler, at it also was at somewhat lower than usual density.

The 1985 lodgepole pine burn at Taggart Lake has been followed via the monitoring site there. Many of the species that depended on the standing dead snags for nest sites, species common 1994-2001, are now gone, since the standing dead are nearly all fallen. The list includes Mountain Bluebird *Sialia curruca*, House Wren *Troglodytes aedon*, Violet-green and Tree Swallows (*Tachycineta thalassina, T. bicolor*). The lodgepole regrowth is vigorous but patchy, with some of the seed-sprouted stems 6+ m tall. New species have invaded with post-fire recovery, with the advent of Swainson's Thrush in 1996, followed by Western Tanager *Piranga ludoviciana*, Yellow-rumped Warbler *Dendroica coronata* and Warbling Vireo *Vireo gilvus* in 1997. Many of the typical lodgepole pine forest, however, have yet to reappear after 22 y: Red-breasted Nuthatch *Sitta canadensis*, Brown Creeper *Certhia americana*, Cassin's Finch *Carpodacus cassinii*, Mountain Chickadee *Parus gambeli*.

The last site of those censused in 2006 is Site 25: Jenny Lake Spruce-Fir. This site burned 9/2/99, some 5 y after it was established as a monitoring site. Post-fire around two-thirds of the canopy was gone, and most of the shrubs layers below it. Species recorded post-fire but not pre-fire include Downy, Black-backed and Three-toed Woodpeckers (*Picoides pubescens, P. arcticus, P. tridactylus*). Least Flycatcher *Empidonax minimus*, Tree and Violet-green Swallows, House Wren, Mountain Bluebird, Cedar Waxwing *Bombycilla cedrorum*, Lazuli Bunting, Green-tailed Towhee *Pipilo chlorurus*, Lincoln's Sparrow *Melospiza lincolnii* and White-crowned Sparrow. Species recorded prior to the burn but not since include Blue Grouse *Dendragapus obscurus*, Great-horned Owl *Bubo virginianus*, Golden-crowned Kinglet *Regulus satrapa*, Hermit Thrush *Catharus guttatus*, White-winged Crossbill *Loxia leucoptera*. Most species present pre-burn persisted afterward, but many at reduced densities. Brown Creeper has recently recolonized the site. In 2006 Western Wood Pewees *Contopus sordidulus* and Hammond's Flycatchers *Empidonax hammondii* were unusually common, while Red-breasted Nuthatch, Western Tanager and Red Crossbill *Loxia curvirostra*, which persisted after the fire, were all absent (and Mountain Chickadee nearly so). As at Site 19, both Dark-eyed Junco and Yellow-rumped Warbler were much rarer than usual (2.5 pr vs LTA 3.7 pr, and 1.25 pr vs LTA 4.9 pr respectively).

2006 Deviations from Long Term Densities

The time-spans over which breeding bird census activities have been pursued at the monitoring sites vary from 7-17 y in the modern era (n.b. some sites were censused by the author and others in the 1960s and 1970s, and one site [#10] even in the 1950s). This permits comparison of 2006 densities with LTA densities at some 10 sites over a range of habitat types. The results of these comparisons are shown in Figs. 1-4. Species are included in these comparisons if they are present at sites in >50% of the census years, and are relatively common (and so more easily censused accurately) within census years.

In Fig. 1 are data for three species of wetland species, more definitively so in the case of the first two (Fig. 1A: Common Snipe, Fig. 1B: Common Yellowthroat), less so in the third (Fig. 1C: Fox Sparrow). In the first two, densities are zero or very low in all habitats except the wettest (Site 10), where they are up very slightly. Fox Sparrow is somewhat scarcer than LTA density in three sites (9, 10, 11). The lower parts of each of the figures give the deviation of 2006 from long term density in terms of standard deviation (SD) units, as a means of gauging the relative significance of the

observed deviation. It appears likely that these wetland species are recorded at reduced densities in 2006 because the monitoring sites are drier and constitute less suitable habitat.

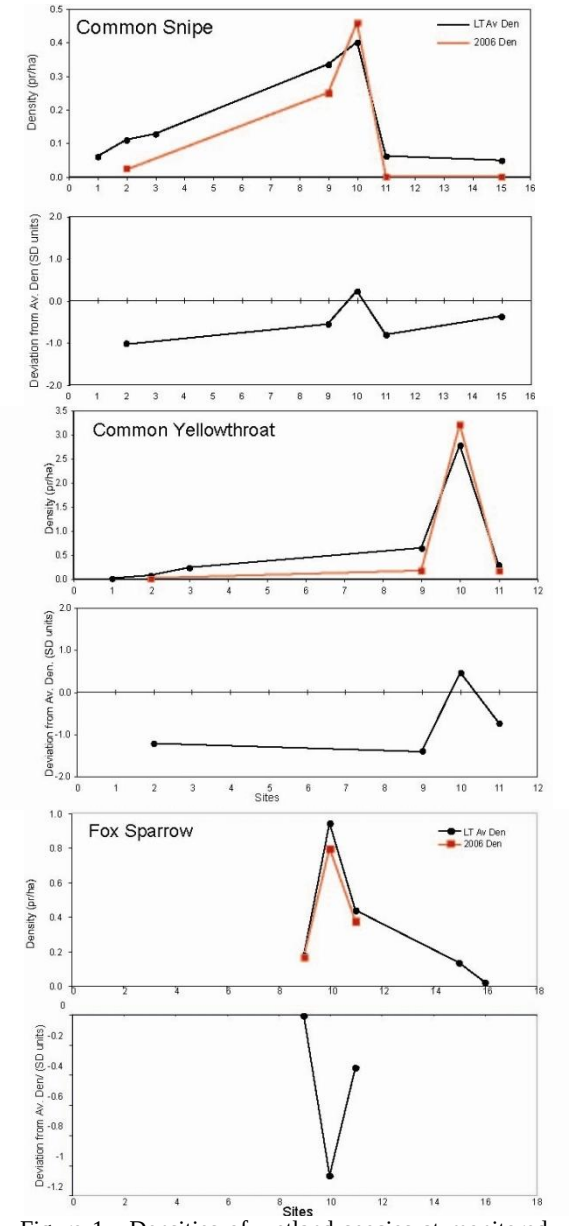

Figure 1. Densities of wetland species at monitored sites in 2006, 1A is the Common Snipe (5 sites), 1B is the Common Yellowthroat (4 sites), and 1C is the Fox Sparrow (3 sites).

Three broad-ranging species are depicted in Fig. 2. American Robin (*Turdus migratorius*; Fig. 2A) has a broad North American range, occupies a wide range of habitats in GTNP, and is a local to short distance migrant. Its 2006 GTNP densities are not dramatically different from LTA densities across the board. The same might be said for Yellow Warbler (*Dendroica petechia*; Fig. 2B), with similar broad ranges across geography and local habitats. It also occupied sites at more or less normal densities, although it is one of the farthest migrants amongst the GTNP breeding birds, reaching NW South America. The third species in the figure, White-crowned Sparrow (Fig. 2C), shows a very different pattern; the species was conspicuously sparse over all of its usual breeding sites, from sagebrush to willows to lodgepole forest, with dramatic (and statistically significant) density declines. The species winters in the SW USA, utilizing shrub and scrublands from California to Texas and into north-central Mexico. These are the regions most affected by the paucity of winter rainfall 2005-6, and it seems likely that the reduced densities of these species in GTNP is attributable not to a reduction in local habitat quality (and certainly not across all habitats), but to poor overwinter survival.

Some breeding species in GTNP are characteristic of generally more arid habitats and regions, such as the Great Basin sagebrush-dominated Desert (Brewer's Sparrow, Fig. 3A), open pine woods, edge and scrub continent-wide (Chipping Sparrow, Fig. 3B), or the mixed conifer and especially oak woodlands of the SW USA south to central Mexico (Warbling Vireo, Fig. 3C). All three of these species show density increases in 2006. Notably, the density increase in Brewer's Sparrow is most apparent in its preferred sagebrush habitat (Site 4), that in Chipping Sparrow most prominent in its preferred conifer habitats (Sites 19-25). Warbling Vireo also shows the larger density shifts in conifers (rather, e.g. than cottonwoods Site 15). It might well be that the effects of drier on-site conditions have negatively impacted broad-leafed vegetation more than the needle-leaved sites. However, this, if it occurs, is not reflected in overall bird densities, which were down 5% in both broad-leaved and needle=leaved vegetation in 2006.

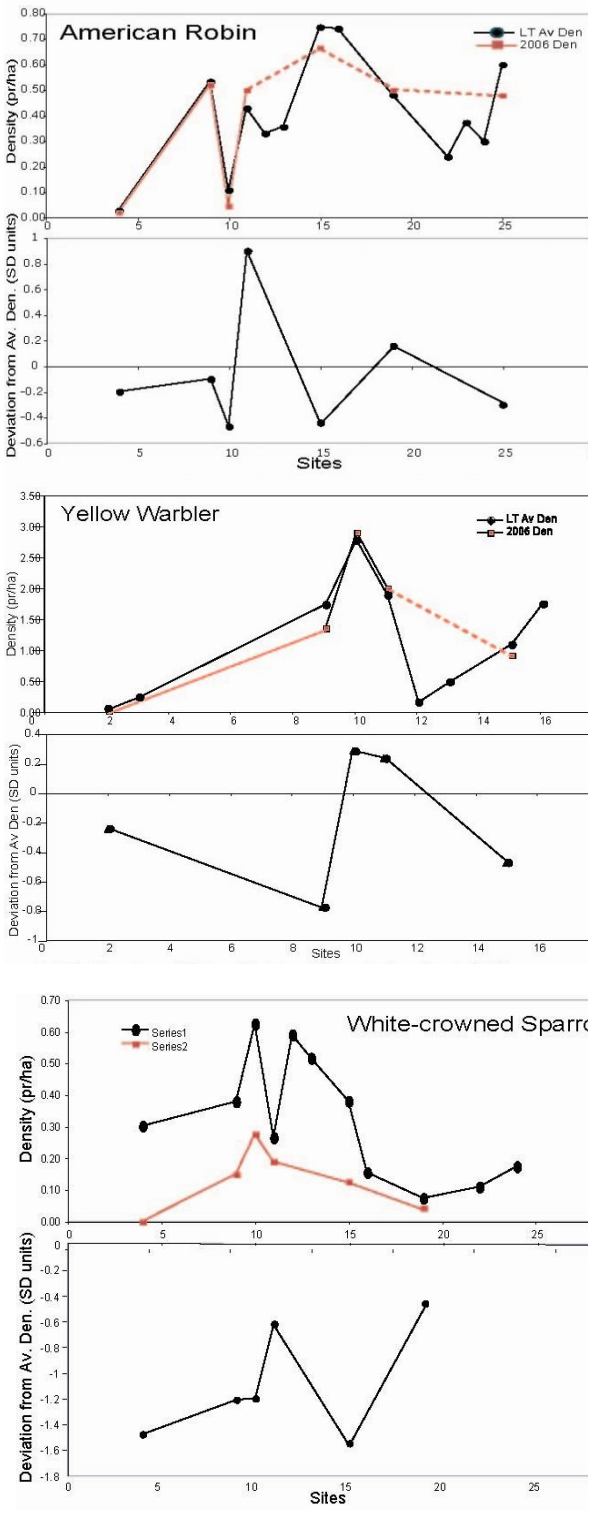

Figure 2. Densities of broad ranging species at monitored sites in 2006. 2A is the American Robin (7 sites), 2B is the Yellow Warbler (5 sites), and 2C is the White-crowned Sparrow (11 sites).

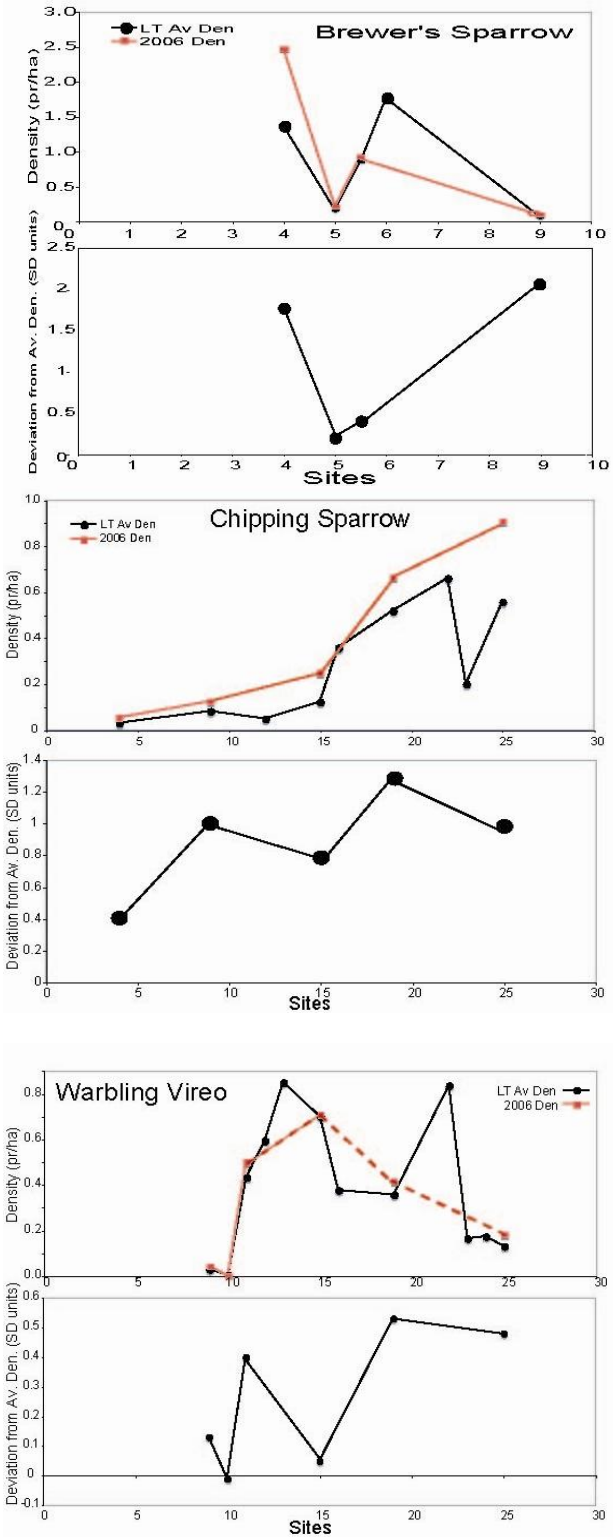

Figure 3. Densities of desert and sagebrush dwelling species at monitored sites in 2006, 3A is the Brewer's Sparrow (4 sites), 3B is the Chipping Sparrow (9 sites), and 3C is the Warbling Vireo (11 sites).

Fig. 4 depicts data from three species whose preferred habitat is the conifer forests. In Fig. 4A Western Wood Pewee apparently had a very good summer in GTNP in 2006, with densities well above average and especially high in its preferred conifer forest habitats. This species also is a long distance migrant, and winters in South America; thus it may have escaped to poor wintering conditions likely suffered by species within SW North America. Yellow-rumped Warbler has a similar range of occupied habitats as the pewee (Fig. 4B), but its 2-006 densities show a very different pattern: it bred at lower than usual densities across the habitat range, and especially in the taller conifers. Unlike the pewee, this warbler winters further north than almost any other paruline, and it is a particularly common winter bird in southern California, throughout the southwest and into northern and central Mexico. Thus it likely experienced poor overwintering conditions due to unusual aridity, and its lowered densities in GTNP seem better ascribed to this rather than depletion in local habitat quality. Lastly, Fig. 4C shows Dark-eyed Junco, which occurred in its GTNP sites at reduced densities in 2006. Juncos were most common in their preferred pine habitats, far less common in the more marginal (for them) cottonwoods. This again, like the warbler, is a short-distance migrant, with some juncos wintering throughout the Rocky Mountain foothills as far north as the central Rockies and even Jackson Hole. Low junco densities in the cottonwoods (Site 15) might be attributable to the dry spring, perhaps an important factor in the life of these phreatophytes, or alternatively to poor survival of the winter. It is likely that these alternatives might be readily distinguished if measures of productivity in local GTNP habitats were part of the monitoring scheme.

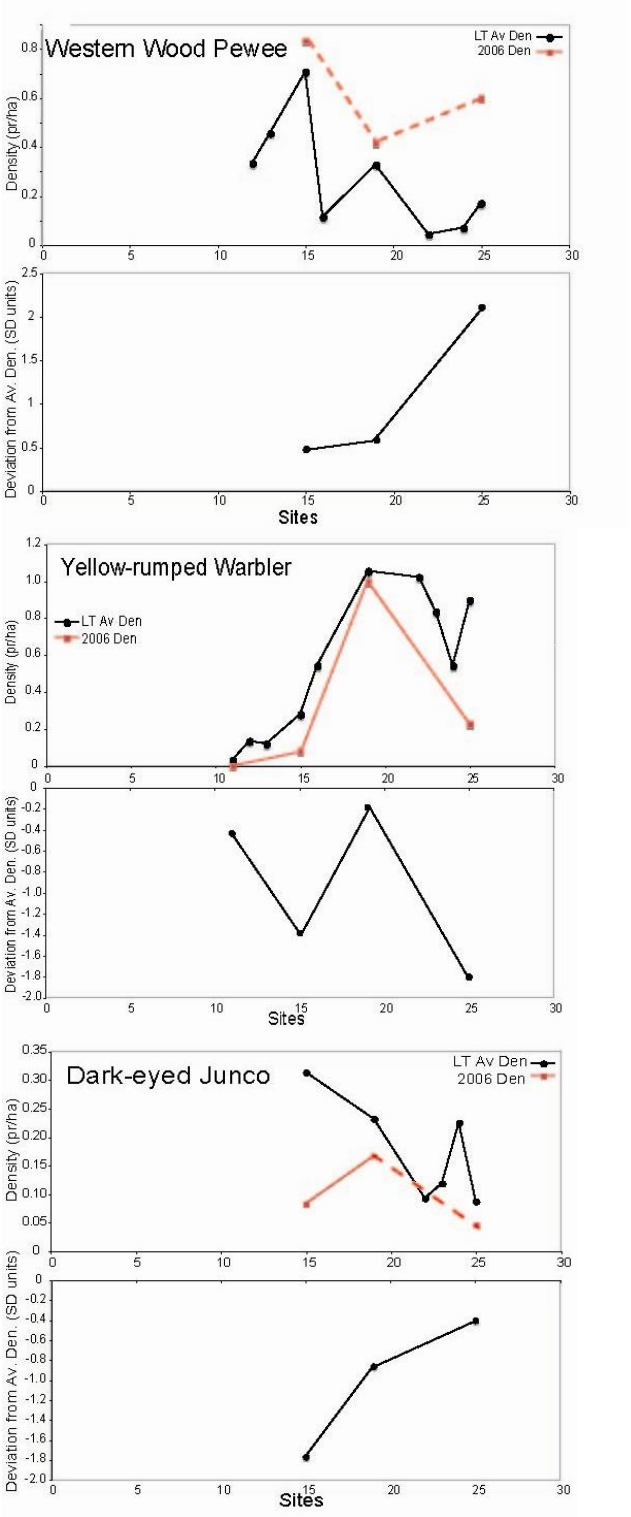

Figure 4. Densities of species that prefer conifer habitat at monitored sites in 2006, 4A is the Western Wood Peewee (8 sites), 4B is the Yellow-rumped Warbler (10 sites), and 4C is the Dark-eyed Junco (6 sites).

✦ ACKNOWLEDGEMENTS

Thanks to the many birdwatchers who have contributed in the past to the monitoring project which, while it gains credence and power each year with additional data, lacks the personpower to make a comprehensive annual count at each site. Prof. H. Harlow kindly made available the wonderful facilities of the National Park Service Research Station at the AMK Ranch for the duration of the field work.

✦ LITERATURE CITED

Cody, M.L. 1996. Bird communities in the central Rocky Mountains. Ch. 11, pp. 291-342 *in* Cody, M. L. & J. A. Smallwood, Long-Term Studies of Vertebrate Communities. Academic Press, Orlando, FL.

Cody, M.L. 1997. Monitoring Bird Populations in Grand Teton National Park. Final Report, National Park Service. v.1,2.

Cody, M. L. 1999. Assembly rules at different scales in plant and bird communities. Ch. 6, pp. 165-205 *in* Weiher, E., & P. Keddy (eds.), Ecological Assembly Rules. Cambridge Univ. Press, Cambridge, UK.

Cody, M. L. 2005. Seasonal bird traffic between Grand Teton National Park and western Mexico. Pp. 32-43 *in* Ralph, C. J. & Rich, T. D. (eds.), Bird Conservation, Implementation and Integration in the Americas: Proceedings of the Third International Partners in Flight Conference. V.1. Gen. Tech Paper PSW-GTR-191, Pac. SW Res. Stn., USDA Forest Service, Washington, DC.

NOAA World Climate Summaries: http://www7.ncdc.noaa.gov/IPS/MCDWPubs

Salt, G. W. 1957a. An analysis of avifaunas in the Teton Mountains and Jackson Hole, Wyoming. Condor 59: 373-393.

Salt, G. W. 1957b. Song, Lincoln's, and fox sparrows in a Tetons willow thicket. Auk 74: 258 .

MEASUREMENTS OF BED LOAD TRANSPORT ON PACIFIC CREEK, BUFFALO FORK AND THE SNAKE RIVER IN GRAND TETON NATIONAL PARK, WYOMING

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✦ INTRODUCTION

Dams disrupt the flow of both of water and sediment through a watershed. Channel morphology is a function of discharge and sediment load, and perturbations caused by dams often alter channel form, causing significant geomorphic and, potentially, ecological changes (e.g. Petts and Gurnell, 2005). At the first order, dams often produce a flow regime that is profoundly altered in the timing, magnitude, and frequency of flows (Magilligan and Nislow, 2005). Yet, the nature of channel adjustments will be specific to both the physical setting, size of the river, dam characteristics, and nature and severity of the flow regulation (Church 1995; Knighton, 1998).

Channel change analysis of the regulated Snake River in Grand Teton National Park (GTNP) has demonstrated that there have been periods of both channel narrowing and widening, but that there is no long-term progressive change (Nelson, 2007). Nevertheless, accumulation of gravel near some tributary mouths is of concern to river navigation and accumulation of gravel in braided reaches drives channel avulsions and floodplain formation. Though prior research has evaluated hydrologic changes associated with the operations of Jackson Lake Dam (JLD) (Marston et al., 2005; Nelson, 2007; Schmidt and White, 2003), little work has been done to characterize changes in the flux of sediment passing through the regulated Snake River. Thus, the processes that link dam operations with present channel characteristics are poorly understood.

In an effort to advise managers of JLD, we have developed estimates of bed load flux that can be tied to dam release schedules. These estimates are based on calibrated gravel transport relations for Pacific Creek and Buffalo Fork, the major tributaries to the Snake River downstream from the dam, and a similar relation for the Snake River at the downstream end of the study reach, the Deadmans Bar boat ramp. This report describes the data collected on Pacific Creek and Buffalo Fork in 2006 and on the Snake River at Deadmans Bar during the 2007 spring runoff season.

✦ METHODS

Three measurement sites were established within Grand Teton National Park for the purposes of measuring bed load transport rates. On Pacific Creek, we measured bed load transport downstream from USGS gage 13011500 (Pacific Creek at Moran WY) and approximately 650 m upstream from the confluence with the Snake River. On Buffalo Fork we sampled bed load transport rates downstream from USGS gage 13011900 (Buffalo Fork above Lava Creek near Moran WY) and approximately 2 km upstream from the

confluence with the Snake River. On the Snake River, we measured transport approximately 500 meters downstream from the Deadmans Bar boat ramp. Discharge for the Snake River measurement site was calculated by summing the discharges measured at the gages on Pacific Creek, Buffalo Fork and the Snake River (Snake River near Moran, station number 1301100).

Bed load transport was measured at the three study sites using a Toutle River Sampler (TR-2), a type of pressure difference sampler with a 52 x 305 mm inlet nozzle and 1.4 expansion ratio. We modified the TR-2 by adding a front stayline to the sampler to reduce the scooping tendency associated with many large pressure-difference samplers. The stayline was attached to the mouth of the TR-2, making it possible to rapidly "jerk" the sampler off the bed prior to raising the sampler from the river bottom. A cataraft-based sampling platform was used to deploy the sampler (Fig. 1). We mounted a crane to a 4.9 m long cataraft and fitted the crane with an E-reel to lower the sampler to the channel bed.

The sampling boat was held stationary in the channel at predetermined intervals using roller-towers and a semi-permanent fixed cable. The system allowed us to safely repeat measurements at specified locations over a range of flows. We selected our sampling sites by considering the following factors, listed in order of importance: crew safety (i.e. the cross-section is not immediately upstream from a debris jam), simplicity of flow patterns through the cross-section, proximity to the Snake River confluence, and accessibility.

We collected samples in accordance with the Equal Width Increment method (EWI), as outlined by Edwards and Glysson (1988). Each complete measurement was comprised of one pass across the channel, consisting of 10-12 samples taken at equally spaced intervals. The duration of time the sampler remained on the bed varied between samples, from 30 – 240 sec, but remained constant at each interval for a given sample. The determination of the time interval used for sampling reflects a compromise between the need for a long sampling duration and the capacity of the sampling bag. Field studies suggest that measurements may become inaccurate once the sampler bag is filled beyond 40% of its capacity. Therefore, the length of time the sampler is left on the channel bottom at a single vertical must be shorter than the length of time it takes the sampler to approach its limiting capacity at the vertical where the most sediment is moving. We regularly reassessed the sampling time interval as flow and sediment transport conditions changed.

Figure 1. Sampling bed load transport rates on Pacific Creek: (A) moving the boat across the cable using the roller-towers; (B) deploying the sampler; and (C) retrieving the sampler from the bed with a partially filled bag of sediment.

Bed load samples were processed in the Fluvial Geomorphology Lab at USU. Coarse organic material was removed by hand from each sample prior to sieving. We then sieved the portion of each sample that was greater than 2 mm into $2^{0.5}$ fractions to determine the grain size distribution of the bed load. First, we used a hand-held rocker sieve to separate those size fractions greater than 11.3 mm. The remainder of each sample was then split using a splitter. We processed the split fraction using a shaker sieve. All sediment less than 2 mm was weighed. Because these particles are transported in suspension as well as bed load, they were disregarded when constructing calibrated bed load transport models.

✦ RESULTS

We sampled bed load transport rates during the 2006 spring runoff season on Pacific Creek and Buffalo Fork and during 2007 spring runoff season on Snake River at Deadmans Bar . Samples were collected over a range of discharges at each sampling site: 26 –144 m^3/s on Pacific Creek (35 – 200% of the 2-yr flood), 45 – 117 m^3/s on Buffalo Fork (35 – 105% of the 2-yr flood), and 48 - 181 m^3/s on Snake River (20 – 60% of the 2-yr flood). In total, 24 samples were collected on Pacific Creek, 39 on Buffalo Fork and 62 on Snake River. Sample from the three sites ranged in size from a few hundred grams to as much as 136 kg on Pacific Creek during peak flows.

Patterns in bed load transport rates differed among the three measurement sites (Fig. 2). On Pacific Creek and Snake River at Deadmans Bar, bed load transport tracked well with changes in discharge. On Snake River, measurements of bed load transport rates ranged from < 1 to 200 $gm^{-1}s^{-1}$. Although we were able to collect samples during flows of at least the magnitude of the 2-yr flood on both tributaries, this was not the case at Deadmans Bar, where the width of the channel and water velocities limited our ability to collect samples at higher flows.

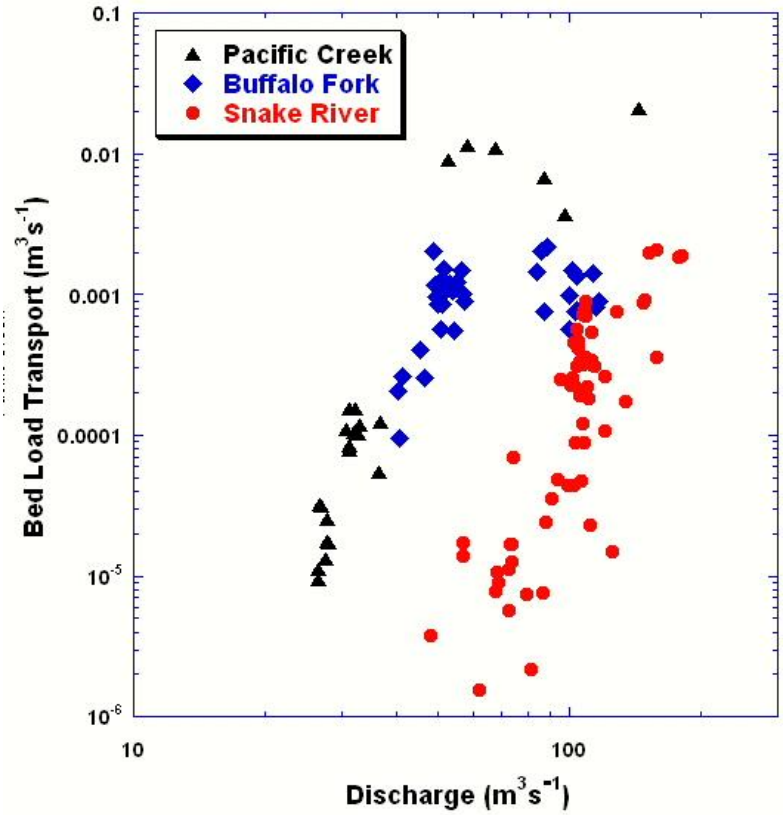

Figure 2. Bed load transport data collected on during 2006 on Pacific Creek and Buffalo Fork, and during 2007 on the Snake River.

On Pacific Creek, we measured much higher bed load transport rates than at either of the other two sampling sites, with measured rates ranging from 1 to 1300 $gm^{-1}s^{-1}$. These high transport rates reflect a unique spring runoff event that marked our sampling season: the peak flow of record on Pacific Creek, 164 m^3s^{-1}, occurred on May 23, 2006. While we did not sample transport rates during the instantaneous peak, we did collect measurements on the day of the peak just prior to and after the time at which record flows were recorded at the gaging station. The measurements made in the vicinity of the peak discharge showed the most scatter of the samples collected at the Pacific Creek measurement site. It was during this period of high flows that sampling time were shortest (30 sec per vertical), because the capacity of our sampler bag was quickly exceeded.

On Buffalo Fork, measured bed load transport rates ranged from 25 to 180 $gm^{-1}s^{-1}$. The Buffalo Fork bed load transport measurements displayed substantially more scatter than the data collected at either of the two field sites. The range of bed load transport rates measured from June 7 to June 9 was comparable to the range of transport rates measured from June 17 to June 21, despite the fact that magnitude of discharge was half as great during the later period of time (Fig. 2). This trend in the data appears to demonstrate counter-clockwise hysteresis, where transport rates were larger on the falling limb than on the rising limb. Although this finding runs contrary to typical patterns, there is some precedence for counter-clockwise hysteresis in natural rivers (Reid et al., 1985). However, it is difficult to discern the exact nature of the pattern on Buffalo Fork because our measurements of bed load transport were discontinuous.

✦ SUMMARY

Bed load transport rates were measured on both Pacific Creek and Buffalo Fork over a range of discharges 2006 and on the Snake River in 2007. These data are being used to calibrate transport relations, and ultimately to estimate the influx and efflux of sediment through the Snake River, from Jackson Lake Dam to Deadman's Bar. This data will allow us to predict and better understand the impacts of alternative dam release schedules on the Snake River in Grand Teton National Park.

✦ ACKNOWLEDGEMENTS

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✦ LITERATURE CITED

Church, M.A. 1995. Geomorphic response to river flow regulation: case studies and time-scales. Regulated Rivers: Research and Management 11(1), 3-22.

Edwards, T.K., G.D. Glysson. 1988. Field Methods for Measurement of Fluvial Sediment.U.S. Geological Survey Techniques of Water-Resources Investigations, Book 3, Chapter C2.

Knighton, D., 1998. Fluvial forms and processes: A new perspective. Hodder Arnold Publications.

Magilligan, F.J., K.H. Nislow. 2005. Changes in hydrologic regime by dams. Geomorphology 71; 61-78.

Marston, R.A., J.D. Mills, D.R. Wrazien, B. Basset, D.K. Splinter. 2005. Effects ofJackson Lake Dam on the Snake River and its floodplain, Grand Teton National Park, Wyoming, USA. Geomorphology 71, 79-98.

Nelson, N.C. 2007. Hydrology and Geomorphology of the Snake River in Grand Teton National Park, Wyoming. M.S. Thesis, Utah State University.

Petts, G.E. and A.M. Gurnell. 2005. Dams and geomorphology: Research progress and future directions. Geomorphology 71, 27-47.

Reid, I., L.E. Frostick, J.T. Layman. 1985. The incidence and nature of bedload transport during flood flows in coarse-grained alluvial channels. Earth Surface Processes and Landforms.

Schmidt, J.C., M.A. White. 2003. The hydrologic regime of the Snake River in Grand Teton National Park and associated channel change, Draft Report. Cooperative Agreement CA-1200-99-007. Utah State University.

DIGITIZATION OF THE GRAND TETON NATIONAL PARK HERBARIUM 2006 - 2007

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✦ INTRODUCTION

Examples of digitization projects in the history of science are understood to have lasting consequences for the intellectual history of their fields (Petersen, 2005; Roes 2001). Following this trend, herbarium collections around the world are beginning to be digitized with positive results for their institutions (Begnoche, 2002; Ong, 2002). Librarians, with their long history of making collections accessible, are participating in this trend (Foster, 2005). This project expands the University of Wyoming Libraries work in the digitizing of a unique collection of plant specimens.

The Grand Teton National Park (GTNP) herbarium is a historical record of the plant specimens collected in the National Park. Since the1920s, it has provided a physical record of vascular flora within the Park and includes examples of many rare and endangered species. Digitization of this collection reduces the necessity for handling the fragile specimens, helps maintain their current condition and contributes to management decisions. This digital collection will expand the herbarium use to local communities and extends its influence nationally.

✦ METHODS

The initial work was done at the University of Wyoming/National Park Service Research Station (UW/NPS) in Grand Teton National Park. The camera and other equipment were housed in a dedicated photography room. Specimens were transported from the Herbarium in the Park to UW/NPS, photographed and returned. Data was entered into the database, backed up on CD ROMs and sent to the server at the University of Wyoming Campus.

The equipment used on this project was a Canon 16.7 mega pixel EOS-1Ds Mark II camera utilizing a full-size 24x36mm CMOS sensor that eliminates focal length conversion factors, and features dramatically improved image quality. The libraries also purchased a 50 mm macro lens to use with the camera for the close up actual size images of plant specimens. Portable studio equipment includes two external flash units and an opaque photography tent used to diffuse light for optimal imaging conditions. The library also provides and maintains a computer, two monitors, and portable storage devices for the project.

Descriptive metadata, including the scientific name and collection location, was recorded in the accompanying spreadsheet as each specimen was photographed and tied to the image file with a unique identification number. Technical metadata was captured during photographing including shutter speed, aperture, camera information and imaging software used. We followed the Colorado Digitization Project (CDP) best practices throughout the project (CDP 2003; CDP 2005).

✦ RESULTS AND DISCUSSION

Photography of herbarium specimens continued during the summer of 2006. The total number of photographs taken was 6342 of which 360 were overexposed. In 2007 the overexposed specimens were photographed again. Our workflow changed after our first season as we learned that trying to edit the records and take the images at the same time was too time consuming. We now edit the information at the UW Libraries using a process that will ensure quality control.

Currently we have processed approximately 3650 of the 6342 specimen's images. The Rocky Mountain Herbarium on the University of Wyoming campus has supported this effort by providing botany students interested in the project who are able to help edit the database entries. We also have library staff members helping with the data entry as well as the librarians responsible for the project. Editing is proving to be the most challenging aspect of the project so far. We have decided after reviewing previous work that database records need to be compared with their corresponding images twice. Each specimen is examined once to enter the data and a second time to make sure that the information was entered correctly.

Images of each specimen are matched to their corresponding record using the image number field in the Access database. Once the image and record are matched, the information from the specimen label can be entered into the database. Upon completion of editing the database, the specimens and their associated metadata will be ready for publication on the web. In order to present the specimens on the web for public viewing, digital imaging software needs to be used. The University of Wyoming Libraries has purchased Insight, digital imaging software available from LUNA Imaging. The web interface will allow users to search the metadata records as well as look at images of the specimens at various magnifications without long download times. Figure 1 is an example of a database page for a specimen. See Figure 2 for an example of a specimen photograph. Figure 3 is an example page from the LUNA software.

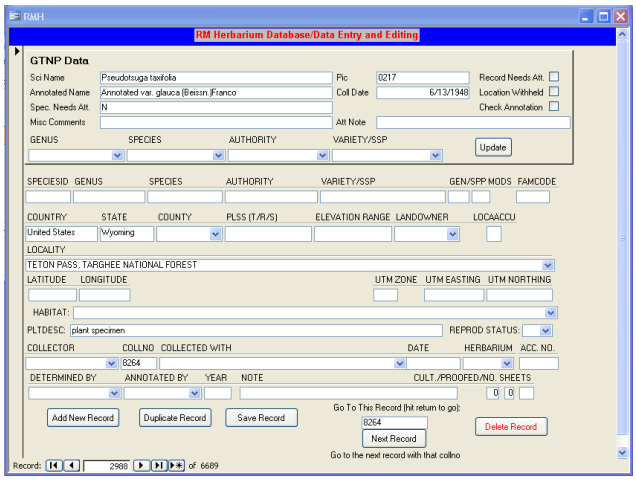

Figure 1 is an example of a database page for a specimen.


Figure 2 is an example of a specimen photograph.

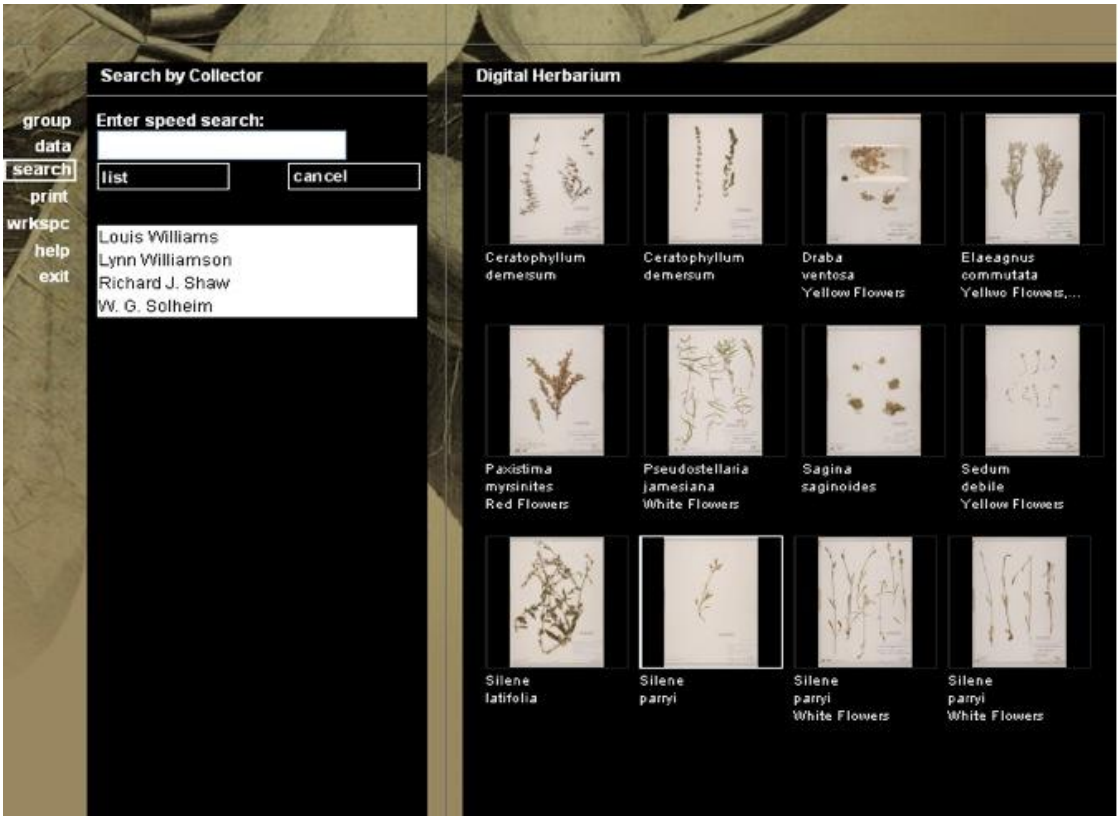

Figure 3 is an example page from the LUNA software.

It is the intention of the University of Wyoming Libraries to support the database at the Laramie campus on a Library server. The project uses architecture designed to allow technology upgrades. Images and attached metadata will be available to the public in a prevailing file format that allows a reasonable download time for the average user, such as the currently popular TIFF or JPEG formats, but may be migrated in the future as file specifications evolve. The master copy is preserved in a RAW format. This kind of data intensive work takes a lot of computer technology including data storage and server space. The 780+ Gigabyte GTNP project is hosted on a 3.0 GHz Dell network server connected to a 4 Terabyte Dell storage area network (SAN). The GTNP images are backed up using the library's disk-to-disk backup scheme. Backup images are located on a 6 Terabyte StoreVault 500 unit. In the immediate future the libraries will be replicating all the data on the 6 Terabyte StoreVault to an offsite 12 Terabyte StoreVault unit as part of the UW Libraries disaster recovery plan.

Our project will continue during the summer of 2008 as we continue editing the database, decide on searchable fields for the online database and prepare to go live on the web. Easy access will also be available through the Grand Teton National Park webpage to insure accessibility to researchers and the general public.

✦ ACKNOWLEDGEMENTS

UW/NPS provided housing, financial and material support, including funds for a student, Lauren Harrison, to help with data entry. We are grateful for the cooperation and encouragement of GTNP staff. We appreciate the botanical expertise contributed by the Rocky Mountain Herbarium faculty and staff and the support from UW Libraries.

✦ LITERATURE CITED

Begnoche, M. (2002, 11/11/2002). Specimens at herbarium get digital makeover. University Record Online. Available at http://www.umich.edu/~urecord/0102/Nov11_02/21.shtml.

Collaborative Digitization Program, (January 2003). Western States Digital Imaging Best Practices, Version 1.0. Available at http://www.cdpheritage.org/digital/scanning/documents/WSDIBP_v1.pdf.

Collaborative Digitization Program, (January 2005). Western States Dublin Core Metadata Best Practices, Version 2.0. Available at http://www.cdpheritage.org/cdp/documents/CDPDCMBP.pdf.

Foster, N. F. & Gibbons, S., (January 2005). Understanding Faculty to Improve Content Recruitment for Institutional Repositories. D-Lib Magazine, Available at http://www.dlib.org/dlib/january05/foster/01foster.html.

Ong, T. J., Leggett, J. J., Wilson, H. D., Hatch, S. L., & Reed, M. D. (2002). Interactive information visualization in the digital flora of Texas. In Visual interfaces to digital libraries (Vol. 2539, pp. 188-198). Berlin: Springer-Verlag Berlin.

Petersen, C., (January 2005). Linus Pauling and the Nature of the Chemical Bond: A Documentary History, D-Lib Magazine, Available at http://www.dlib.org/dlib/january05/01featured-collection.html.

Roes, H., (July/August 2001). Digital Libraries and Education: Trends and Opportunities, D-Lib Magazine, Available at http://www.dlib.org/dlib/july01/roes/07roes.html.

IMPACT OF IRRIGATION CESSATION ON WETLAND COMMUNITIES WITHIN THE ELK RANCH, GRAND TETON NATIONAL PARK, MOOSE, WYOMING

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✦ INTRODUCTION

Riparian ecology research in Arizona and California has documented the likelihood of a subsurface linkage between irrigation, especially flood-irrigation, and riparian function (Smith et al. 1989; Stromberg et al. 1996). Initial groundwater monitoring results from rural New Mexico indicate water tables rose 1 to 2m after the onset of field irrigation and subsurface flow paths towards the Rio Grande River developed soon after (Fernald et al. 2008). Results from a study of wetlands in southeastern Wyoming suggest that declining flood-irrigation levels would lead to a reduction in the total area of wetlands and related areas of wetland vegetation types in the Laramie Basin (Peck and Lovvorn 2001). Stringham et al. (1998) have reported further evidence for a linkage between irrigation and riparian function. These Oregon researchers noted lower water temperatures in stream reaches receiving subsurface return flows from irrigated hayfields than similar reaches flowing through non-irrigated lands. This information is timely because Grand Teton National Park (GTNP) managers have begun an evaluation of historic irrigation operations within the Park and are endeavoring to learn how cessation of flood irrigation will affect Park wetlands. The historically irrigated hayfields at the Elk Ranch provide an opportunity to address the Park Service's informational needs through identification of vegetation composition, soil physical characteristics and groundwater patterns associated with irrigated and naturally occurring wetlands. Successful description of patterns unique to natural wetlands will provide an avenue for predicting which Park wetlands would remain functional should irrigation efforts be brought to a close. Development of criteria for identifying naturally occurring wetlands could also serve as a basis for identifying areas for wetland mitigation and rehabilitation elsewhere in GTNP and the mountain valleys of the Northern Rocky Mountains.

STUDY OBJECTIVES

The primary objectives of this research are to characterize plant communities, soils, and shallow groundwater in flood irrigated hay meadows in the Elk Ranch, test for relationships between vegetation composition, soil characteristics and ground water elevation and determine if those relationships can be used to differentiate between natural and irrigation created wetlands. Shallow groundwater monitoring wells placed in apparent natural and irrigation-based wetlands will be monitored for several years to further test the relationship between wetland species and groundwater persistence.

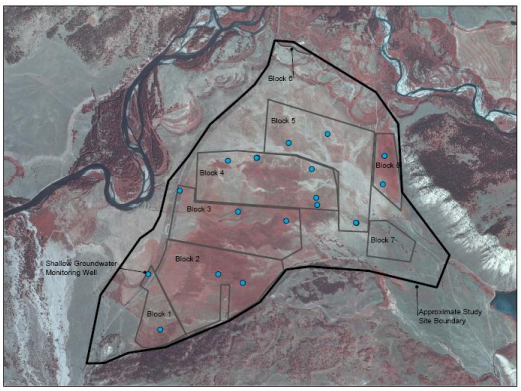

Fig. 1. Location of sampling blocks within the Elk Ranch hay meadows used for characterizing wetland vegetation community composition, soil characteristics and depth to groundwater. Block boundaries follow apparent drainage ways. Blue dots represent randomly located groundwater monitoring wells.

✦ METHODS

2006 - 2007 Field Work:

In March 2006, an infrared USGS aerial photograph was used to stratify the Elk Ranch hayfields into eight similar blocks based on intensity of color (Fig. 1). Eleven macro-plots were randomly located within the various hayfield blocks for field measurements in August 2006. Percent aerial cover of vegetation was estimated following methods described by Daubenmire (1968) at 5 meter intervals along four 20-meter transects centered within each macro-plot. Transects were oriented north, west, south, and east. After aerial cover estimates were completed, one soil sample pit was excavated in the center of each macro-plot for determination of depth to groundwater and measurement of various soil parameters. Excavation went to groundwater contact or a depth of 1.5 meters. Soil horizons where photographed and then characterized by: a) in-field description of texture using the USDA-NRCS standard texturing method, b) color using the Munsell color chart, c) quantity and contrast of mottling, d) quantity and size of roots present in the profile and e) depth to soil saturation. Depth to soil saturation was determined from the surface to the layer where a water film formed on the side of the soil pit. Following the various field measurements, a 150-gram sample was extracted from each soil horizon for further lab analysis. Each sample plot location was documented using a Garmin global positioning unit. Following summarization of the 2006 data a sample adequacy test indicated a minimum of 12 more macro-plots would have to be sampled to detect a 10% difference between the various soil and vegetation parameters. Additional macro-plots were first randomly allocated to blocks that had only one or two macro-plots sampled in 2006. Then additional macro-plot locations were randomly selected in all blocks until each block had a minimum of 4 macro-plots. This effort produced seventeen new macro-plots for sampling in 2007.

During July 2007, sixteen 3.75cm x 150cm pipes were driven to a depth of 120cm at random locations throughout the Elk Ranch hay meadow (Fig. 1). These shallow wells were used to track monthly changes in groundwater in each of the study blocks.

Wetland indicator status of the various plant species encountered on the hayfield was determined from the 2003 US Fish and Wildlife Service Wetland Indicators List (USFWS 2003). Because the same sampling protocol was followed each field season, all vegetation and soil measurements were pooled for the initial statistical analyses. Blocks were used as treatments and macroplots within blocks as replicates (n = 28). For purposes of this report only depth to groundwater, depth to soil saturation, depth to mottles, average obligate/facultative wetland species and shallow groundwater levels are summarized and presented. Preliminary comparisons of aerial cover for individual obligate and facultative wetland indicator species with depth to groundwater, depth to saturation and depth to mottling was inclusive so individual obligate and facultative wetland species cover was combined for each macroplot and then averaged for statistical comparisons. Average obligate/facultative wetland cover for the various blocks was evaluated with ANOVA. The strength of relationship between the various soil attributes and wetland species cover was later evaluated with the standard linear regression model. Because of the unequal number of wells among the blocks within-block differences (July elevation vs. October elevation) were evaluated separately with a paired t test assuming unequal variance. Mean separation (ANOVA results) were performed with the Tukey's pairwise comparison.

Soil Parameter	B1	B 2	B 3	B 4	B 5	B 6	B 7	B 8
Groundwater	**0.4m**	**0.6m**	**0.5m**	**0.6m**	**0.6m**	**0.4m**	**0.7m**	**0.7m**
Saturation	**0.2m^{ab}**	**0.1m^{a}**	**0.2m^{ab}**	**0.3m^{ab}**	**0.6m^{b}**	**0.2m^{ab}**	**0.7m^{c}**	**0.7m^{c}**
Mottling	**0.3m^{ac}**	**0.5m^{ac}**	**0.04m^{ab}**	**0.1m^{ab}**	**0.1m^{ab}**	**0.5m^{ac}**	**0.7m^{c}**	**0.07m^{ab}**

Table 1. Soil attributes measured at the Elk Ranch hayfield in July 2006 and 2007. Measurements are depth from vegetated soil surface. Values in rows with different letters are significantly different at P≤ 0.10.

✦ PRELIMINARY FINDINGS

Two of the three field soil attributes differed significantly (P ≤ 0.10) among the eight blocks representing the Elk Ranch hayfield (Table 1). While there was no difference among any of the blocks in terms of excavated depth to groundwater (Table 1) there were differences among the blocks in terms of depth to soil saturation (P = 0.03) and depth to mottling (P = 0.002). Soils were saturated closest to the surface in Blocks 1, 2 and 6 (0.1m), intermediate in blocks 3 and 4 (0.2m – 0.3m) and deepest in blocks 5, 7 and 8 (0.5m – 0.7m). Depth to mottling was different (P<0.01) but the groupings where much broader; mottling depth in blocks 1, 2 and 6 was essentially equivalent to the depth in the other seven blocks while the presence of mottling was significantly deeper in block 7 than blocks 3, 4, 5 and 8 (Table 1). Groundwater elevation determined from monitoring wells was significantly higher in block 1 during October (P=0.03) than it had been earlier in July (Table 2). However, groundwater elevations were similar between both months in all the other blocks. Comparison of observed groundwater elevation patterns during 2007 indicates groundwater recovery in block 1 and slight improvement in blocks 2 and 7 (Fig.2).

Block	July Depth (m)	Oct Depth (m)
1	1.4^{a}	0.7^{b}
2	1.2	1.1
3	1.0	1.3
5	1.3	1.4
7	1.1	1.0

Table 2. Average groundwater elevation in the Elk Ranch Hay Meadow in July and October 2007. Values in the same row with different letters are significantly different at P ≤ 0.10. Excavated column contains groundwater depths recorded when soil pits were dug in each macro-plot. Blocks 4, 6 and 8 were omitted from the analysis because they had fewer than 2 wells.

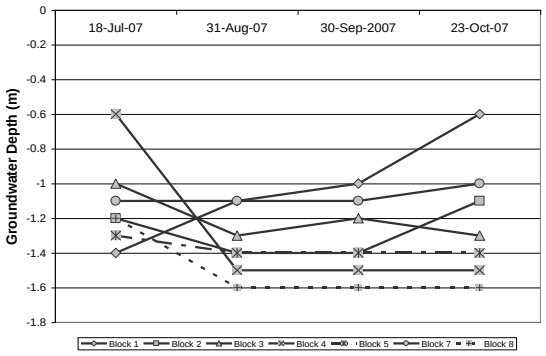

Fig. 2. Monthly groundwater elevations for monitoring wells in the Elk Ranch hayfield. Individual values are the average of all wells with the specific block.

Comparison of obligate/facultative wetland cover between the various blocks revealed significant differences (P = 0.04) in vegetative cover between some of the blocks. Block 1 had more wetland indicator cover than Blocks 5, 7 and 8; block 3 had greater wetland cover than block 5, 7 and 8 and blocks 4 and 6 had more wetland cover than block 7 (Table 3). Regression analysis comparing vegetative cover to depth to saturation and then to depth to mottling indicated a significant relationship (P ≤ 0.01) between depth to saturation and the cover of wetland indicator species (Fig 3). However, there was no meaningful relationship between mottling depth and wetland indicator species cover.

Block	1	2	3	4	5	6	7	8
Species	53^{a}	31^{a}	43^{a}	36^{a}	16^{b}	47^{a}	< 1^{b}	7^{b}

Table 3. Percent cover of wetland indicator species in study blocks within the Elk Ranch hayfield. Individual values are the average of obligate and facultative wetland species occurring in macroplots within each block. Averages with different letters are different at P ≤ 0.10)

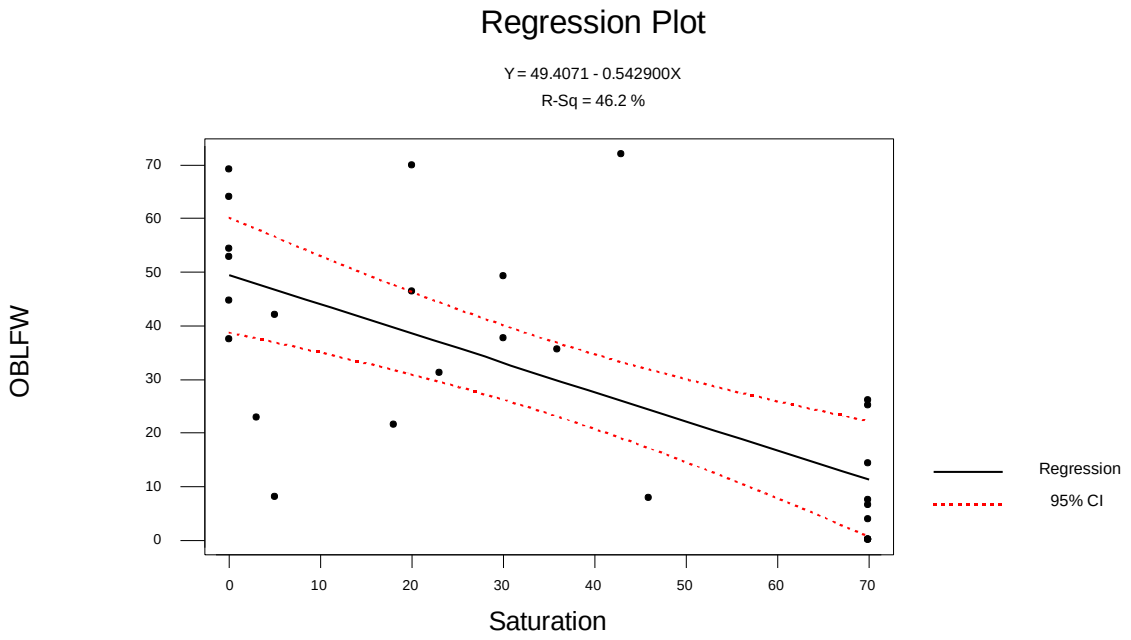

Fig. 3. The calculated relationship between the cover of wetland indicator species and soil saturation in the Elk Ranch hayfield. Soil and vegetation data are from both 2006 and 2007 field seasons.

✦ DISCUSSION

Soil and vegetation information collected over two field seasons reinforces earlier work that certain plant species, e.g. *Carex utriculata*, are useful as indirect indicators of long term, high soil moisture levels. However, the Elk Ranch hayfield data expands on the earlier work by providing a second, physical measure for segregating naturally occurring riparian/wetland vegetative communities from those supported by artificial flows. Grouping the various data sets indicates that areas having soil saturation within 0.3m of the surface support the highest wetland vegetative cover. Furthermore, as depth to saturation increases from 0.5m to 0.7m wetland vegetative cover declines dramatically. While compelling, this criterion is probably inadequate by itself because sampling during or soon after irrigation may suggest soil saturation is close to the surface. The similarities in depth to groundwater among all of the study blocks based on soil pit measurements probably reflects residual groundwater following irrigation in July 2006 and 2007. Furthermore, the lack of differences in groundwater among the various blocks was not supported by groundwater elevation measurements recorded from the 16 monitoring wells throughout the Elk Ranch hayfield. It makes sense then that another measure or measures will be necessary to segregate natural and irrigation induced wetlands. Unfortunately, it is also apparent that there is probably not a single wetland plant species that could be used to compliment the soil saturation criterion. Because groundwater levels are directly linked to soil saturation the possibility exists that tracking groundwater recovery with shallow wells for several years may be key to identifying those wetlands that will remain following cessation of irrigation.

The first field season of groundwater monitoring suggests that groundwater levels increase during the fall in some of the wetlands within the Elk Ranch hayfield. This implies that depth to saturation measures made during September and October could be used to identify naturally occurring wetlands. If the 2007 pattern continues to be observed in subsequent years, it is possible that naturally occurring wetlands are linked to broad subsurface recharge pathways that bring groundwater levels back to the 0.3m saturation depth necessary to support complex wetland vegetative communities. However, at this time it is equally likely that the groundwater

recovery in blocks 1 and 2 result from slow migration of residual irrigation water from "up-stream" hayfields. This highlights the need for additional monitoring in 2008 and 2009 to clarify the potential sources of groundwater recovery. Furthermore, the apparent disconnect between differences in mottling depths in the various blocks and differences in the corresponding obligate/facultative vegetation cover in the study blocks suggests the need for additional information.

Detailed analyses of mottling intensity by depth, mottling frequency by depth and root density by depth from the existing database may provide more clarity to the already identified relationships. However, it is also clear that more information on vegetative cover, mottling depth, mottling intensity, etc. from several additional macro-plots in blocks 6, 7 and 8 is necessary to improve the likelihood of identifying natural wetlands.

✦ ONGOING AND ANTICIPATED EFFORTS

Analysis of all of the field data, soil texture, mottling intensity, etc., from 2006 and 2007 will be completed by May 2008. This information will either substantiate the results reported here or identify information gaps that will be addressed with fieldwork during July and August 2008. In addition to the data analysis effort, 8 more monitoring wells will be added to the network already in place. Four wells will be placed in block 6 and 2 each in blocks 7 and 8. Addition of these wells will provide a minimum of 4 wells per block which will improve the likelihood of identifying the source of subsurface recharge in blocks 1 and 2. Following collection of the 2009 well data the relationship between depth to soil saturation, groundwater recovery patterns and obligate/facultative vegetation cover will be re-assessed to determine if these parameters can be used to identify naturally occurring wetlands.

✦ LITERATURE CITED

Daubenmire, R. 1968. Analysis and description of plant communities. Plant communities: a textbook of plant synecology. New York, NY: Harper and Row, Publishers. p. 39-88.

Fernald, A., S. Guidan, J.P. King and, V. Tidwell. 2008. Effects of ditch and field irrigation seepage on Rio Grande Flow. USDA National Research Initiative Project Directors Annual Report. National Water Conference, Sparks, NV. 4 February 2008.

Peck, D.E. and J. R. Lovvorn. 2001. The importance of flood irrigation in water supply to wetlands in the Laramie Basin, Wyoming, USA. *Wetlands* 21:370-378.

Smith, S. D., J. L. Nachlinger, A.B. Wellington, and C. L. Fox. 1989. Water relation of obligate riparian plants as a function of streamflow diversion on the Bishop Creek Watershed. *In*: Proceedings of the California Riparian Systems Conference. 22-24 September 1988; Davis , CA: Protection, Management, and Restoration for the 1990's. p.360-369.

Stringham, T.K., J.C. Buckhouse and W.C. Krueger. 1998. Stream temperatures as related to subsurface waterflows originating from irrigation. Journal of Range Management. 51:88-90.

Stromberg, J. C., R. Tiller, and B. Richter. 1996. Effects of groundwater decline on riparian vegetation of semiarid regions: the San Pedro, Arizona. Ecological Applications 6:113-131.

US Fish and Wildlife Service. 2003. Wetland Indicators. Web Download. www.nwi.fws.gov/bha/download/1988/region9.txt accessed February 2005.

THE EFFECT OF NITROGEN DEPOSITION AND EDAPHIC CONDITIONS ON MICROBIAL ACTIVITIY IN THE ALPINE ZONE OF THE GRAND TETON NATIONAL PARK

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✦ INTRODUCTION

Atmospheric nitrogen (N) deposition rates show increasing N loadings since the 1980s in the western U.S. associated with increasing N emissions from industrial, urban, and agricultural sources (Fenn et al., 2003). Compared to the eastern U.S., the number of NADP/NTN (National Atmospheric Deposition Program/ National Trends Network) and CASTNet (Clean Air Status Network) monitoring sites is much more limited in the west, and they are rarely located in the highest-elevations, where ecosystems are likely to be more sensitive (Burns 2004). Although N deposition tends to increase with elevation in this region (Williams and Tonnesen 2000), there are considerable uncertainties about the actual N deposition levels in the Rocky Mountains. Model-simulations indicate a "hotspot" of N deposition near Grand Teton National Park (GRTE) (Fenn et al., 2003; Nanus et al. 2003), with feedlot and fertilizer N emissions in Southern Idaho, as potential sources impacting the alpine communities in GRTE. However, little data is currently available on the actual atmospheric N inputs to alpine ecosystems in GRTE, either as snow during winter or wet and dry deposition during the short snow-free period.

Alpine communities are considered very sensitive to changes in N deposition because a combination of short growing seasons, shallow and poorly developed soils, steep terrain, sparse vegetation, and low rates of primary productivity generally limit the N retention capacity of the ecosystem (Fisk et al., 1998; Burns, 2004). These ecosystems are generally considered to be N-limited (Burns 2004), and increases on N availability may be reflected in changes in vegetation composition, biomass, and N content, as well as in changes in soil N status and belowground processes (Bowman et al., 1995). Earlier work at Niwot Ridge in the Colorado Front Range has indicated that the N cycling response to changes in N inputs is greatly influenced by soil climate, especially soil moisture and temperature (Bowman et al., 1993; Fisk and Schmidt, 1995; Fisk et al., 1998). In ecosystems where precipitation mostly falls as snow (such as in GRTE), soil temperature and moisture regime is strongly influenced by the timing, thickness, duration, and redistribution of the snowpack (Brooks et al., 1996; Fisk et al., 1998; Van Miegroet et al., 2000).

Because alpine ecosystems may become N saturated (i.e., lose their capacity to effectively retain N) with relatively small changes in atmospheric N deposition (Baron et al., 2000), there is great interest in identifying early indicators of ecosystem change in response changes in atmospheric N inputs, and establishing critical N loads that can be tolerated by these systems. Most recently, Bowman and coworkers (Bowman et al. 2006) suggested that vegetation changes will precede detectable changes in soil N parameters, based on N addition experiments at Niwot Ridge.

Our research in GRTE is intended to verify the generality of these earlier findings, and test whether soil vs plant parameters are the most sensitive indicators of changes in ecosystem N status.

The overall objective of this two-year project is to assess the impact of atmospheric N deposition on the structure and function of alpine ecosystems in Grand Teton National Park (GRTE), based on field measurements and experimental manipulation of N loadings in alpine sites with contrasting (wet/dry) edaphic conditions and assumed N input regimes. Specific tasks in year one were to determine atmospheric N inputs and N status of a series of sites based on plant and soil parameters. To date relatively little is known about the belowground processes, and in this one-year subproject we collected baseline information on microbial biomass and nitrification potential across the N deposition and soil microclimate matrix. We hypothesized that edaphic conditions control overall abundance of microbial populations, whereas current N deposition and site N status influence the abundance of nitrifier populations and nitrification potential.

✦ METHODS

To test the influence of N deposition and edaphic conditions on above- and belowground N pools and N dynamics, we established a series of plots along a modeled N deposition gradient in GRTE . Based on access via existing trail system, three candidate sites were identified: Moose Basin (High), Paintbrush Canyon /Mica Lake (Low) and Rendezvous Mountain (Medium/Low).

Plot layout

Within each of the three N deposition areas, plots were established in summer 2006 at three sites (located within 0.50 miles from each other) where contrasting edaphic conditions existed (wet vs dry) due to differential snowpack retention. This yielded a two-factorial set-up of initial conditions (3 N deposition levels, 2 edaphic conditions) replicated three times for a total of 18 site locations for which background information on N deposition, site microclimate, vegetation, and soils was collected. Each site was georeferenced by GPS. At each of the 18 site locations two adjacent 2.5m by 2.5m plots will be delineated separated by a 1-m buffer zone. These plots will be assigned as either control or +N treatment in the year two of this project.

N deposition measurements

In early spring 2006, at maximum snow accumulation, snow surveys were conducted at Moose Basin and Rendezvous Mountain in collaboration with the USGS. Due to logistical constraints, no snow survey was collected at Mica Lake. Snow depth, snow water equivalent and chemical composition were determined. We were unable to repeat the snow survey in 2007 due to early melt of the snow pack and avalanche hazard that prohibited access to the sites.

N input during the snowfree period was measured at each of the 18 plot pairs, using ion exchange resin funnels left in the field between 1.5 and 2.5 months (Fenn and Poth, 2004). Resins were retrieved at the end of the field season, extracted with 2N KCl, and the extractant analyzed for NH_4-N and NO_3-N.

To capture the combined N input from snowmelt and wet+dry deposition during the snowfree period, PVC tubes with ion exchange resins were placed close to the ground in early summer 2006 (Susfalk and Johnson, 2003). They will be retrieved in summer 2007 and extracted as described above.

Vegetation Characteristics

Vegetation composition, species richness, aboveground biomass and N content were determined by floristic surveys and destructive sampling in all 36 plots. Vegetation composition and species richness was determined by identifying plant species and accounting for percent cover of each plant within a 1m x 1m subplot located within the 2.5 m x 2.5 m plot. Total percent cover for the entire 1m x 1m plot was then assessed including percent bare ground and percent rock. Aboveground plant biomass was determined by clipping vegetation within two 25 cm by 25 cm frames, drying the materials at 65^{o}C and weighing it. Subsamples were ground and analyzed for N and C using LECO combustion. Belowground biomass and N content was determined from soil cores (0-15 cm depth; 1 per plot), by manually separating roots and analyzing ground biomass for N as described above. Chemical and statistical analysis of the vegetation data is still in progress.

Soil characteristics

Several cores (0-15 cm length, 5 cm

diameter) were taken in each plot to determine bulk density, root biomass, soil moisture content, total and extractable inorganic N, soil nitrification potential and microbial biomass.

Inorganic soil N content in the upper soil was determined by extracting homogenized soil samples with 2N KCl in the field (Van Miegroet, 1995) and analyzing extractant for NH_4-N and NO_3-N. All concentrations are expressed on a dry weight basis using gravimetric soil moisture content measurements on subsamples with rock an debris removed and dried at 105 ^oC .

Soil cores to be used for microbial properties were transported from the field to the lab in coolers and kept refrigerated until processing within 3 days after collection.

Microbial biomass on soil samples taken at each location was determined by standard extraction-fumigation methods (Brookes et al., 1985), and total organic carbon (TOC) analysis of fumigated and unfumigated soils. To date, TOC analysis is still in progress, and no results on microbial biomass will be reported here.

Nitrification potential was determined by incubating 8g of fresh soil soils 50 ml plastic test tubes placed in a constant-temperature incubator (~ 25 ^oC) for 60 days, extracting subsamples after 30 (t_1) and 60 days (t_2) with 2 N KCl , and analyzing extractant for NO_3-N as described above. Changes in NO_3-N concentration relative to in-field extraction (t_0), expressed on a soil dry weight basis, were used as a relative index of nitrification potential.

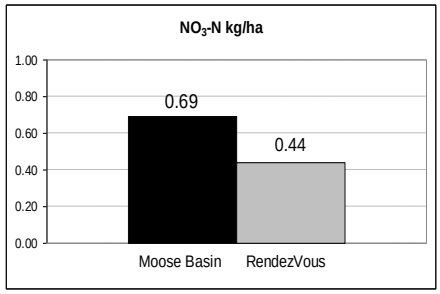
Soil Microclimate

Soil temperature will be measured continuously at each of the 18 locations using miniature data loggers (StowAway Tidbits - Onset Computer Corp), installed within the 1-m buffer zone between 5-15 cm depth, programmed to record temperature at 1 to 2-hour interval, and downloaded at the beginning and end of the snowfree period. Soil moisture regime is determined using 10-cm long soil moisture probes (Decagon ECH_2O probes) installed vertically under the soil surface in the 1-m buffer zone. Periodic measurements were taken in the summer of 2006 using a portable readout device. At six locations (1 replicate per N deposition-edaphic combination) these probes will be hooked up to a datalogger (Decagon EM5 Datalogger), and soil moisture readings recorded continuously at preset intervals. They will be downloaded during in summer 2007 using a PDA.

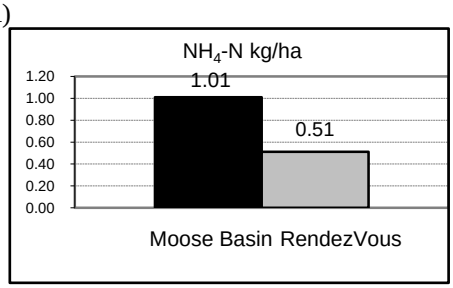
✦ RESULTS

N Deposition Inputs

Results from the 2006 snow survey at Moose Basin and Rendezvous confirm the modeled N deposition gradient (Nanus et al., 2003) with higher atmospheric N inputs to the north of the Park (Moose Basin) and lower levels to the south (Rendezvous) (Figure 1). Inorganic N inputs as snow range between 1 and 2 kg N ha^{-1} with a slightly greater proportion entering as NH_4-N (Figure 1 and 2). Summer N inputs as determined with resin tube collectors deployed for 40 to 90 days in summer 2007 (Fenn and Poth, 2004) do not appear to differ among locations (Figure 3). The summer input data are still preliminary; but accounting for incomplete resin adsorption efficiency and extending the data to the total snow free period, we estimate an additional input of ~0.5 kg N ha^{-1} in summer, again with a slightly higher proportion entering in NH_4 form. Differences in N deposition among the sites appear to be determined by snow accumulation, rather than differences in dry deposition during summer.



(A)



(B)

Figure 1. Nitrate and Ammonium input (kg/ha) determined from 2006 snow survey at Moose Basin and Rendezvous Mountain.

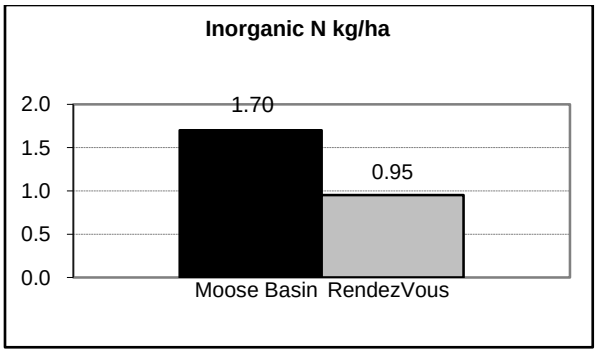


Figure 2. Total inorganic N input as snow in Winter 2006 at the northern and southern part of the Grand Teton National Park.

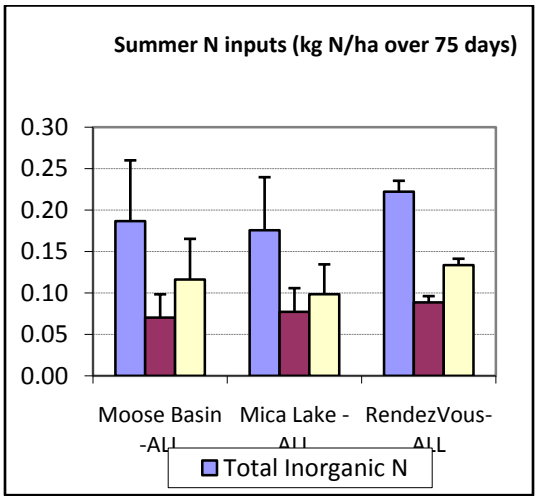


Figure 3. Atmospheric N deposition captured by resin collectors in summer 2007 at the three alpine locations.

Soil Nitrogen Status

There are marked differences in the static and dynamics indicators of soil N status among the three sampling locations. Extractable inorganic soil N is highly variable among locations and edaphic conditions at each sampling location, ranging from 0-10 μg g^{-1} (Figure 4 and 5). Total inorganic N and initial NO_3-N concentration do not follow the observed and modeled N deposition gradient and are generally lower at Moose Basin (Figure 4 and 5). At that site, differences in initial NO_3-N concentration between wet and dry sites are also smaller. At the Mica Lake and Rendezvous sites, differences between edaphic conditions are more pronounced, with higher initial soil NO_3-N concentrations observed at the wetter sites (Figure 5).

The nitrification potential, indicative of the size and activity of the nitrifier population, differs substantially among the three locations and appears to follow the N deposition gradient. Despite initial site exhibits the highest nitrification potential, which is sustained during the 60-days aerobic laboratory incubation (Figure 6). In contrast, nitrification production rates remain low throughout the intire incubation time at Rendezvous (low N site), irrespective of edaphic conditions (Figure 6 and 7). Edaphic conditions also influence the nitrification potential, but the direction and magnitude varies among sites. Whereas wetter conditions favor higher nitrification potential at the low N input site (Mica Lake, Rendezvous), the opposite is true at the higher N input site (Moose Basin), where higher nitrification potentials were measured in soil from dry sites (Figure 7). Our data indicate the differences in N inputs and edaphic conditions interact to influence nitrification potential.

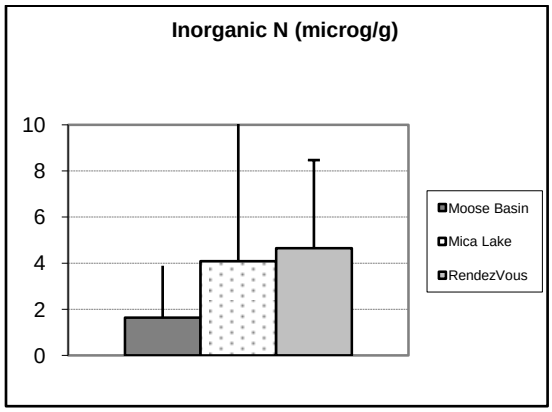


Figure 4. Average extractable inorganic N soil concentration (μg per g dry soil) at the three alpine sites.

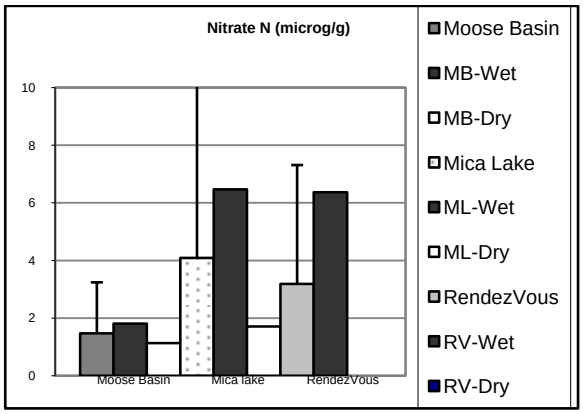


Figure 5. Average extractable NO_3-N concentration (μg per g dry soil) and difference between wet and dry sites at the three alpine sampling locations.

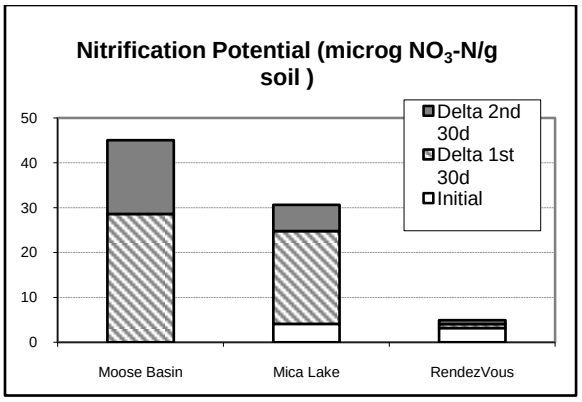


Figure 6. Average nitrification potential after 30 and 60 days of incubation of surface soils from the three alpine locations.

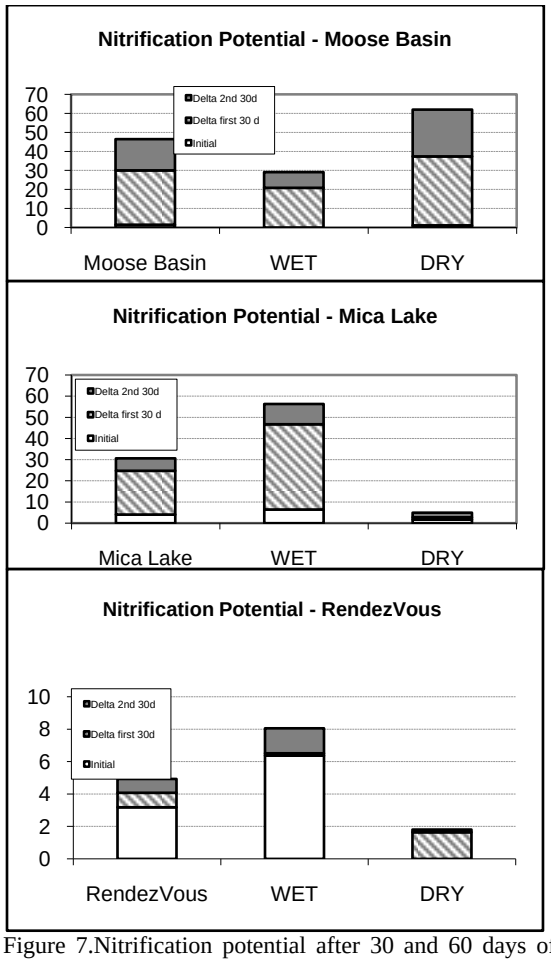


Figure 7.Nitrification potential after 30 and 60 days of incubation of surface soils sampled at dry and wet sites in the three alpine locations.

✦ CONCLUSIONS

Our preliminary data indicate that (1) N deposition inputs to the alpine zone of the Grand Teton National Park are generally low; (2) there is indeed a N deposition gradient; and (3) that there are detectable differences in N dynamics among N input sites that are further modified by local edaphic conditions. While static soil parameters (e.g., extractable inorganic N) reflect differences in edaphic conditions (wet-dry), they do not appear to be good indicators changes in N deposition. Microbial soil parameters (e.g., nitrification potential) on the other hand, are more sensitive indicators of changes in soil function due to a combination of N deposition and soil moisture regime. This study indicates that even small differences in N input (<1 kg N ha^{-1} yr^{-1}) can result in detectable differences in soil nitrifier population, and thus in the ability of soils to respond to increases in N inputs through accelerated NO_3 formation.

✦ LITERATURE CITED

Baron, J.S., H.M. Rueth, A.M. Wolfe, K.R. Nydick, E.J. Allstott, J.T. Minear, B. Moraska. 2000. Ecosystem response to nitrogen deposition in the Colorado Front Range. Ecosystems 3: 352-368.

Brookes, P.C., A. Landman, G. Pruden, and D. Jenkinson. 1985. Chloroform fumigation and the release of soil nitrogen: a rapid extraction method to measure microbial biomass nitrogen in soil. Soil Biology and Biochemistry 17: 837-842.

Brooks, P.D., M.W. Williams, S.K. Schmidt. 1996. Microbial Activity Under Alpine Snowpacks, Niwot Ridge, Colorado. Biogeochemistry 32:93-113.

Burns, D.A. 2004. The effect of atmospheric nitrogen deposition in the Rocky Mountains of Colorado and southern Wyoming, USA – a critical review. Environmental Pollution 127: 257-269.

Bowman, W.D., T.A. Theodose, and M.C. Fisk. 1995. Physiological and production responses of plant growth forms to increases in limiting resources in alpine tundra: implications for differential community response to environmental change. Oecologia 101:217-22.

Bowman, W.D., J.R. Gartner, K. Holland and M. Wiederman. 2006. Nitrogen crucial loads for alpine vegetation and terrestrial ecosystem response: are we there yet? Ecological Applications 16: 1183-1193.

Bowman, W.D., T.A. Theodose, J. Schardt, and R.T. Conant. 1993. Constraints of nutrient availability on primary production of two alpine tundra communities. Ecology 74(7): 2085-2097.

Fenn, M.E. and M.A. Poth. 2004. Monitoring nitrogen deposition in throughfall using ion exchange resin columns: a field test in the San Bernardino mountains. Journal of environmental quality 33: 2007-2014.

Fenn. M.E., R. Haeuber, G.S. Tonnesen, J.S. Baron, S. Grossman-Clarke, D. Hope, D.A. Jaffee, S.Copeland, L. Geiser, H.M. Rueth and J.O. Sickman. 2003. Nitrogen emissions, deposition, and monitoring in the Western United States. BioScience 53(4) 391-403.

Fisk, M.C. and S.K. Schmidt. 1995. Mitrogen Mineraliza6tiona nd Microbial Biomass Nitrogen Dynamics in Three Alpine Tundra Communities. Soil Sci Am J 59:1036-1043.

Fisk, M.C., S.K. Schmidt and T.R. Seastedt. 1998. Topographic patterns of above- and belowground production and nitrogen cycling in alpine tundra. Ecology 79: 2253-2266. Nanus, L., D. Campbell, G. Ingersoll, D. Clow and M.A. Mast. 2003. Atmospheric deposition maps for the Rocky Mountains. Atmospheric Environment 37: 4881-4892.

Susfalk, R.B. and D.W. Johnson. 2002. Ion exchange resin based soil solution lysimeters and snowmelt solution collectors. Communications in Soil Science and Plant Analysis 33 (7&8):1261-1275.

Van Miegroet, H. 1995. Inorganic nitrogen determined by laboratory and field extractions of two forest soils. Soil Science Society of America Journal 59:549-553.

Van Miegroet, H., M.T. Hysell, and A. Denton Johnson. 2000. Soil microclimate and chemistry of spruce-fir tree islands in Northern Utah. Soil Science Society of America 64: 1515-1525.

Williams, M. and K. Tonnessen. 2000. Critical loads for inorganic nitrogen deposition in the Colorado Front Range, USA. Ecological Applications 10(6): 1648-1665.

YELLOWSTONE NATIONAL PARK

HOW MANY RIVER OTTERS INHABIT YELLOWSTONE LAKE? AN ASSESSMENT WITH FECAL AND HAIR DNA ANALYSES

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✦ JUSTIFICATION AND OBJECTIVES

River otters (*Lontra canadensis*) in Yellowstone Lake are different from most other otter populations in that they are heavily dependent on one prey species – Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*; Crait and Ben-David 2006, Crait et al. 2006). Our 2002-2003 studies in Yellowstone Lake showed that cutthroat trout were the most common prey item in otter scats throughout the summer. Overall, trout occurred in 72% and longnose suckers (*Catostomus catostomus*) in 43% of otter feces, based on 515 samples identified to the family-level and 110 samples analyzed to the species-level. Suckers were more prevalent than trout in otter scats only on tributary streams, towards the end of the cutthroat trout spawning season. Introduced lake trout (*Salvelinus namaycush*), which inhabit deep water and are largely inaccessible to otters, occurred in less than 5% of otter scats. In addition, based on fecal deposition rates, we established that otters were more active on spawning streams and less active along the Yellowstone Lake shoreline during the height of the cutthroat trout spawning season, with a return to elevated activity on the lake after spawning had ended (Crait and Ben-David 2006). Therefore, because of the lack of a suitable alternative prey, it is likely that a decline in cutthroat trout (Koel et al. 2005) will translate into a decline in the abundance of otters in this system. Indeed, our 2002-2003 survey indicates the number of river otter latrine sites in the Yellowstone Lake ecosystem is lower than expected based on similar surveys in the Rocky Mountain region (Crait and Ben-David *unpublished data*).

Yellowstone Lake river otters appear to be unique in yet another respect. In 2005, we compared diving physiology of river otters at sea level (San Juan Islands, Washington, USA) with those from the high-altitude (2357 m) Yellowstone Lake population. Preliminary results suggest unique physiological differences in the Yellowstone Lake population relative to lowland otters (Crait et al. *in prep*). Otters from both populations appear to have a higher maximal oxygen (O_2) carrying capacity than terrestrial mammals of similar body size likely due to the increased O_2 demands of diving (Kooyman 1989). However, Yellowstone Lake otters seem to have lower hemoglobin (Hb)-O_2 binding affinity and a higher O_2 carrying capacity than those of the sea level animals. This is likely a compensatory response to moderate hypoxia which may enhance delivery of O_2 to tissues (Banchero and Grover 1972, Storz 2007). Our results suggest that otters in Yellowstone Lake have alterations to their Hb complex or blood chemistry. This is possibly due to increases in 2,3-diphosphoglyceric acid (DPG) in red blood cells (Pomponi et al. 2004) that allow O_2 delivery to tissues at a PO_2 lower than experienced by conspecifics at sea level. Because of this unique physiological adaptation to diving at high altitude, and the potential threat of population declines as a result of loss of their

primary prey, monitoring the status of river otters in Yellowstone Lake should become a priority.

Our objectives are:

1. Estimate the abundance of river otters in Yellowstone Lake in 2002-2003 and in 2006-2008.

2. Estimate survival of river otters in Yellowstone Lake in 2002-2003 and in 2006-2008.

3. Compare estimates of abundance and survival between these two time periods and related them to indices of cutthroat trout abundance.

4. Quantify the relatedness of individuals during the two time periods to assess whether reproductive success has decline between the two time periods.

5. Develop spatially-explicit individual based models that link predation of river otters on cutthroat trout with their subsequent survival, reproduction, and densities.

✦ SIGNIFICANCE

Despite occurring in one of the most protected areas in North America - Yellowstone National Park – river otters inhabiting Yellowstone Lake may be threatened if declines of native cutthroat trout continue. Because of their high dependency on this one prey species, and an apparent lack of ability to switch to alternative prey such as the invasive lake trout, river otters could decline together with their primary prey. Otters will probably persist in other areas of Yellowstone National Park, but these individuals will be less likely to possess the special physiological adaptation for diving at high altitude because they usually forage in shallow streams where such adaptation is less essential. Also, because few otter populations occur in high altitude lakes (Melquist et al. 2003) this adaptation may be unique to Yellowstone Lake otters. Thus, it is imperative to evaluate changes in the abundance of river otters in Yellowstone Lake between 2002-2003 and 2006-2008, develop models linking the abundance of otters with that of Yellowstone cutthroat trout, and develop protocols for future non-invasive monitoring of this unique otter population.

✦ METHODS AND RESULTS TO DATE

Sample collection - From the end of May to mid-August in 2002 and 2003, we surveyed 152.8 km and 177.3 km, respectively, of the lake shoreline from a small boat. A total of 64.7 km in 2002, and 104.4 km in 2003 of tributary streams were surveyed on foot. During these surveys we identified 94 river otter latrine sites. Each site was visited 1-6 times in each summer and a total of 206 fresh feces were collected for DNA analyses. All fresh otter feces collected during each visit to a latrine were preserved in 100% ethanol (EtOH) and stored on ice. In 2006, we revisited 48 of these sites from the end of May to the end of August 7.7 times on average, and collected 85 fresh scats for DNA analyses (Table 1). In 2007, we revisited 47 of the sites 9.0 times on average, and collected 51 fresh feces for DNA analyses (Table 1). In addition, we placed 1 – 3 commercial body-snares modified to capture hair at latrine sites with heavy activity (more than 5 feces per site; Figure 1; DePue and Ben-David 2007). The locking mechanism on these snares has been removed and replaced with a paper clip. This modification allows the wire snare to cinch around the otter and then break free with little tension, while retaining hairs from the animal. These snares capture hair from a single individual and thus avoid problems with cross contamination of samples (DePue and Ben-David 2007). Using these snares we collected a total of 75 hair samples in 2006 and 105 in 2007 (Table 1). No animal (otter or other) were restrained by these traps. In 2008, we will repeat sampling of feces and hair from the end of May to the end of August.

Figure 1 – Clumps of river otter hair snagged off an individual by the barbs on a modified body snare.

Year	Number of visits			Number of feces per site per visit			Number of hairs per site per visit		
	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range
2002	2.20	0.17	1 – 5.00	0.86	0.23	0 – 6.00	NA	NA	NA
2003	2.44	0.10	1 – 6.00	0.53	0.13	0 – 7.50	NA	NA	NA
2006	7.67	0.67	1 – 25.00	0.21	0.09	0 – 4.00	0.14	0.03	0 – 0.77
2007	9.02	0.90	1 – 23.00	0.09	0.03	0 – 1.00	0.19	0.04	0 – 1.00

Table 1 – Number of visits per site and number of feces and hair samples collected per site per visit from river otter latrine sites in Yellowstone Lake from the end of May to the end of August 2002, 2003, 2006, and 2007.

DNA analyses - Prior to DNA extraction, each fecal sample was sieved through fine-mesh stainless steel, autoclavable sieves to ensure the removal of all hard parts of prey material. This is an important step for improving the quality and quantity of extractable DNA through reducing the extraction and amplification of non-target DNA. Sieving also helps avoid the problem of the uneven distribution of cells shed through the intestinal lining as documented by Kohn et al. (1995). Excess EtOH was evaporated from each sample after sieving in a closed hood. Following the sieving a 200 µl sub-sample was used to extract DNA with a QIAamp DNA Mini Kit (QIAGEN Inc, Valencia, CA; Hansen et al. 2008). We used QIAGEN DNeasy tissue extraction kit (QIAGEN Inc, Valencia, CA) to extract DNA from hair. All feces and hair samples collected in 2002-2003 and 2006-2007 were extracted. We will use similar methods to extract DNA from samples collected in 2008.

DNA amplifications (PCR) are currently under way. PCR are performed using a PTC-0200 DNA Engine Peltier Thermal Cycler (MJ Research, Inc., Waltham, MA). Primers RIO-01, RIO-05, RIO-17, and RIO-19 developed for river otters (Beheler et al. 2004, 2005), and LUT-701, LUT-733, LUT-801, and LUT-829 developed for Eurasian otters (*Lutra lutra*; Dallas and Piertney 1998) are used in PCR reactions. Positive (blood samples from river otters with known genotypes) and negative (PCR blanks) controls are included with each PCR run in order to ensure the reliability of PCRs and monitor contamination (Hansen et al. 2008). PCR products are resolved on an ABI 3130xl Automated Sequencer (Applied Biosystems Foster City, CA; ABI) with formamide-LIZ ladder, as an internal size standard in each lane. The data will be sized in base pairs and analyzed using ABI software GeneMapper v4 at the Nucleic Acid Exploration Facility at the University of Wyoming.

A consensus genotype will be obtained from positive PCRs with identifiable alleles that have sufficient replication (Goossens et al. 2000). In order to reduce genotyping error and time spent trying to amplify poor quality samples, each sample that does not amplify after four PCR runs with the most reliable marker (RIO-19) will be discarded (Morin et al. 2001, Paetkau 2003). Genotypes will be evaluated after two initial runs (Frantz et al. 2003). Loci that amplify the same heterozygous individual twice will be recorded, and homozygote genotypes will be accepted on a provisional basis after a stepwise amplification approach of up to seven PCRs. In the case that an allele amplifies only once to yield one heterozygote genotype in seven runs with the other six runs resulting in the same homozygous genotype, the allele will be designated as constituting a half-genotype (Miller et al. 2002, Frantz et al. 2003, 2004).

Estimating abundance, density, and survival of otters - To ensure that the number of loci used is sufficient for individual identification, the probability of identity (P_{ID}; the probability that two individuals from a population share the same genotype) will be calculated using the program GIMLET v.1.3.2 (Valiére 2002). We will calculate both the lower limit, $P_{ID\text{-}unbiased}$, which includes a sample-size correction, and assumes a randomly mating population of unrelated individuals in Hardy-Weinberg equilibrium (Paetkeau 2003), as well as the upper limit, $P_{ID\text{-}sib}$, which assumes the population only to be composed of siblings (Waits et al. 2001).

To estimate abundance of river otters in Yellowstone Lake, we will develop capture histories for individual river otters based on DNA microsatellite profiles of hair and fecal samples. For example, preliminary analyses of river otter fecal samples collected in Victoria, British Columbia, identified 68 unique individuals that were recaptured between 0 and 6 times. These capture histories translated to an estimate of 72 otters (95% confidence interval: 53 – 105; Guertin et al. *in prep*.). Similarly,

using capture histories of genotyped individuals, we will employ robust design models in the program MARK (White and Burnham 1999) to estimate the apparent survival and capture probabilities for the 2002-2003 and 2006-2008 time periods (Pollock 1982, Amstrup et al. 2005). Models will be ranked using Akaike Information Criteria corrected for small sample size (AICc; Burnham and Anderson 2002) and evaluated for validity of parameter estimates. Population size will be derived post-hoc based on total number of captures and capture probabilities (Williams et al. 2002a).

Otter densities for each time period will be calculated by dividing the estimated abundance of otters by the length of the shoreline surveyed. Because river otters rarely travel more than a 100m from shore (Bowyer et al. 2003), shoreline length represents a better measure of otter distribution than area (Blundell et al. 2001). To compare the estimates of abundance and densities between the two time periods (2002-2003 and 2006-2007), we will use a *t*-test corrected for repeated samples (Zar 1999).

To evaluate temporal changes in reproductive success, we will estimate relatedness of individuals with the program KINSHIP (Queller and Goodnight 1989). We will then compare values of relatedness using a two-tailed Mann-Whitney test with a Monte Carlo estimation of probability (10,000 replications) following Fabiani et al. (2006).

Modeling the relation between river otter densities and survival and cutthroat trout decline - To establish the degree to which numbers of river otters have declined following the decline of cutthroat trout in Yellowstone Lake, we will use an individual-based bioenergetic model (Grimm and Railsback 2005) to infer supportable otter population sizes in relation to estimates of the availability of cutthroat trout. First, we will estimate the economics of foraging for individual otters, as a function of food availability. Data exist in the literature on energetic costs and duration of foraging (Ben-David et al. 2000, Williams et al. 2002b, Kruuk 2006). National Park Service data on the densities of potential prey fish will be combined with historic size class distributions to infer the average energetic return from a captured fish (Derby and Lovvorn 1997, Ruzycki et al. 2003). We will then calculate the number of foraging bouts required per day and infer a threshold prey density, below which an individual otter will be unable to meet energetic requirements and will either emigrate or die. Once a threshold is established, we will use an individual-based, depletion modeling approach (Grimm and Railsback 2005, Sutherland 2005) to estimate the "carrying capacity" of otters as a function of food availability. The model will be spatially and temporally explicit, and upper limits on otter density will be set by estimates of habitat availability, minimum tolerable home range sizes and group formation (Bowyer et al. 2003, Ben-David et al. 2005, Crait and Ben-David 2007). The final model will be compared with data on historical prey abundance to provide estimates of otter population size, both currently and during recent decades.

✦ LITERATURE CITED

Amstrup, S.C., T.L. McDonald, and B.F.J. Manly. *Eds.* 2005. Handbook of capture-recapture analysis. Princeton University Press. Princeton, New Jersey.

Banchero, N., and R.F. Grover. 1972. Effect of different levels of simulated altitude on O_2 transport in llama and sheep. American Journal of Physiology 222: 1239-1245.

Beheler, A.S., J.A. Fike, G. Dharmarajan, O.E. Rhodes, and T.L. Serfass. 2005. Ten new polymorphic microsatellite loci for North American river otters (*Lontra canadensis*) and their utility in related mustelids. Molecular Ecology Notes 5: 602-604.

Beheler, A.S., J.A. Fike, L.M. Murfitt, O.E. Rhodes Jr., T.L. Serfass. 2004. Development of polymorphic microsatellite loci for North American river otters (*Lontra canadensis*) and amplification in related mustelids. Molecular Ecology Notes 4: 56-58.

Ben-David, M., G.M. Blundell, J.W. Kern, J.A.K. Maier, E.D. Brown, and S.C. Jewett. 2005. Communication in river otters: creation of variable resource sheds for terrestrial communities. Ecology 86:1331-1345.

Ben-David, M., T.M. Williams, and O.A. Ormseth. 2000. Effects of oiling on exercise physiology and diving behavior in river otters: a captive study. Canadian Journal of Zoology 78:1380-1390.

Blundell, G.M., J.A.K. Maier, and E.M. Debevec. 2001. Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. Ecological Monographs 71:469-489.

Bowyer, R. T., G. M. Blundell, M. Ben-David, S. C. Jewett, T. A. Dean, and L. K. Duffy. 2003. Effects of the *Exxon Valdez* oil spill on river otters: injury and recovery of a sentinel species. Wildlife Monographs 153: 1-53.

Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer, New York.

Crait, J.R., and M. Ben-David. 2006. River otters in Yellowstone Lake depend on a declining cutthroat trout population. Journal of Mammalogy 87:485-494.

Crait, J. R., and M. Ben-David. 2007. Effects of river otter activity on terrestrial plants in trophically altered Yellowstone Lake. Ecology 88:1040-1052.

Crait, J.R., G.M. Blundell, K.E. Ott, J.K. Herreman, and M. Ben-David. 2006. Late seasonal breeding of river otters in Yellowstone National Park. American Midland Naturalist 156:189-192.

Crait, J.R., H. D. Prange, N. Marshall, H.J. Harlow, and M. Ben-David. *in prep*. High altitude diving adaptations of river otters in Yellowstone National Park. Journal of Experimental Biology.

Dallas, J.F., and S.B. Piertney. 1998. Microsatellite primers for the Eurasian otter. Molecular Ecology 7: 1247-1251.

DePue, J.E., and M. Ben-David. 2007. Hair sampling techniques for river otters. Journal of Wildlife Management 71: 671-674.

Derby, C.E., and J.R. Lovvorn. 1997. Predation on fish by cormorants and pelicans in a cold-water river: a field and modeling study. Canadian Journal of Fisheries and Aquatic Sciences 54:1480-1493.

Fabiani, A., F. Galimberti, S. Sanvito, and R. Hoelzel. 2006. Relatedness and site fidelity at the southern elephant seal, Mirounga leonina, breeding colony in the Falkland Islands Animal Behaviour 72:617-626.

Frantz, A.C., L.C. Pope, P.J. Carpenter, T.J Roper, G J .Wilson, R.J .Delahay, and T.Burke. 2003. Reliable microsatellite genotyping of the Eurasian badger (*Meles meles*) using faecal DNA. Molecular Ecology 12: 1649-1661.

Frantz, A.C., M. Schaul, L.C. Pope, F. Frack, L. Schley, C.P. Muller, and T.J. Roper. 2004. Estimating population size by genotyping remotely plucked hair: the Eurasian badger. Journal of Applied Ecology 41:985-995.

Goossens, B., L. Chikhi, S.S. Utami, J. de Ruiter, and M.W. Bruford. 2000. A multi-samples, multi-extracts approach for microsatellite analysis of faecal samples in an arboreal ape. Conservation Genetics 1:157-162.

Grimm, V., and S.F. Railsback. 2005. Individual-based modeling and ecology. Princeton University Press, Princeton, NJ.

Guertin, D., A. Harestad, M. Ben-David, and J.E. Elliott. *in prep*. Fecal DNA fingerprinting reveals human-induced effects on densities and vital rates of coastal river otters in southwest British Columbia. Journal of Animal Ecology.

Hansen, H., M. Ben-David, and D.B. McDonald. 2008. Effects of genotyping protocols on success and errors in identifying individual river otters (*Lontra canadensis*) from their faeces. Molecular Ecology Resources 8:282-289.

Koel, T.M., P.E. Bigelow, P.D. Doepke, B.D. Ertel, and D.L. Mahony. 2005. Nonnative lake trout result in Yellowstone cutthroat trout decline and impacts to bears and anglers. Fisheries 30:10-19.

Kohn, M., F. Knauer, A. Stoffella, W. Schroder, and S. Paabo. 1995. Conservation genetics of the European brown bear – a study using excremental PCR of nuclear and mitochondrial sequences. Molecular Ecology 4:95-103.

Kooyman, G. L. 1989. Diverse divers: physiology and behavior. Springer-Verlag, Berlin.

Kruuk, H. 2006. Otters: ecology, behaviour and conservation. Oxford University Press, Oxford, UK.

Melquist, W. E., and M. G. Hornocker. 1983. Ecology of river otters in west central Idaho. Wildlife Monograph 83: 1-60.

Miller, C. R., P. Joyce, and L. P. Waits. 2002. Assessing allelic drop-out and genotype reliability using maximum likelihood. Genetics 160:357-366.

Morin, P.A., K.E. Chambers, C. Boesch, and L. Vigilant. 2001. Quantitative polymerase chain reaction analysis of DNA from noninvasive samples for accurate microsatellite genotyping of wild chimpanzees (*Pan troglodytes verus*). Molecular Ecology 10:1835-1844.

Paetkau, D. 2003. An empirical exploration of data quality in DNA-based population inventories. Molecular Ecology 12: 1375-1387.

Pfeiffer, P., and B.M. Culik. 1998. Energy metabolism of underwater swimming in river-otters (*Lutra lutra* L.). Journal of Comparative Physiology B 168:143-148.

Pollock, K.H. 1982. A capture-recapture design robust to unequal probability of capture. Journal of Wildlife Management 46:752-757.

Pomponi, M., E. Gavuzzo, C. Bertonati, A.E. Derocher, C. Lydersen, O. Wiig, and K. M. Kovacs. 2004. Hemoglobin, pH and DPG/chloride shifting. Biochimie 86:927-932.

Queller, D.C. and K.F. Goodnight. 1989. Estimating relatedness using genetic markers. Evolution 43:258-275.

Ruzycki, J.R., D.A. Beauchamp, and D.L. Yule. 2003. Effects of introduced lake trout on native cutthroat trout in Yellowstone Lake. Ecological Applications 13:23-37.

Storz, J.F. 2007. Hemoglobin function and physiological adaptation to hypoxia in high-altitude mammals. Journal of Mammalogy 88: 24-31.

Sutherland, W.J. 2005. From individual behaviour to population ecology. Oxford University Press, Oxford, UK.

Valière, N. 2002. GIMLET: a computer program for analysing genetic individual identification data. Molecular Ecology Notes 2: 377-379.

Waits, L.P., G. Luikart, and P. Taberlet. 2001 Estimating the probability of identity among genotypes in natural populations: cautions and guidelines. Molecular Ecology 10:249-256.

White, G.C., and K.P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120-S139.

Williams, B.K., J.D. Nichols, and M.J. Conroy. 2002a. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, San Diego.

Williams, T.M., M. Ben-David, S. Noren, M. Rutishauser, K. McDonald, and W. Heyward. 2002b. Running energetics of the North American river otter: do short legs necessarily reduce efficiency on land? Comparative Biochemistry and Physiology A 133:203-212.

Zar, J.H. 1999. Biostatistical Analysis. New Jersey, Prentice-Hall, Inc. .

FIRE AND CARBON CYCLING IN THE SUBAPLINE FORESTS OF YELLOWSTONE NATIONAL PARK

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✦ INTRODUCTION

Our research group carried out two projects through UW-NPS and the AMK Ranch in 2007, a field study (project #1) and a workshop for managers (project #2).

In 2004 we had initiated a field study of carbon stocks along a replicated chronosequence of stands in Yellowstone National Park that had burned at varying times from ca. 1700 AD through 1988. In each stand we measured all of the major carbon pools (including live biomass, dead biomass, and soil carbon) to characterize changes over time in net ecosystem production (the net balance between carbon uptake and loss from an ecosystem). These empirical data were then used to evaluate the potential effects of changing climate and changing fire frequency on how the Yellowstone landscape as a whole functions as either a carbon sink or a carbon source in the global carbon cycle.

After analyzing the data from our initial field season, we discovered an apparent anomaly in our results: total carbon stocks in the recently burned stands (1988) were substantially lower than predicted. This could have resulted from a sampling error, or could indicate that the stands in our sample selection were not representative of recently burned stands throughout the landscape. Therefore, we returned to the field in 2007 to conduct additional sampling to distinguish between these two explanations. Details are provided below under project #1, field studies.

In addition to the field study, we hosted a workshop on fire and carbon storage at the AMK Ranch for land managers. The purpose of the workshop was to provide a synthesis and summary of our field and modeling studies of the previous three years, as well as an update on current issues and thinking about the roles of forests and fires in global carbon dynamics. This workshop is described below under project #2, workshop for managers.

Project #1: Field Study – Testing Results from Previous Year's Sampling

A three-week field season at the AMK was used in 2007 to field check some of the data collected in 2004-07 in Yellowstone National Park as part of a study examining effects of fire on carbon cycling (funded by the Joint Fire Sciences Program). This work included a 8-person field crew, consisted of three undergraduates and one technician from Wayne State University, two recent graduates from Colorado State University, and Brandon and Janice Corcoran, all supervised by Dan Kashian and Mike Ryan during the first week of field work.

Our initial objective was to re-sample and re-quantify dead coarse wood originally sampled in our chronosequence that measured changes in carbon storage with increasing stand age. The original data suggested that far less carbon is stored in recently burned stands (< 25 years old) than in older stands. This is problematical, as similar amounts of carbon should be present in all stand ages because most killed biomass (and thus carbon) remains after the fire. Our youngest age class had similar amounts of dead biomass as our oldest age class, when we expected to find approximately 50% *more* based on the likely amount of biomass killed by the fire (Figure 1).

Live biomass in young stands was significantly less than that in older stands, consistent with our data, and we therefore hypothesized that our sampling underrepresented the amount of dead biomass in the younger stands.

During the first week of the field season we re-sampled all 15 of the stands in our youngest age class using alternative methods of line intercept sampling that both increased the length of the transects and altered their orientation to avoid any bias in the predominant direction of the downfall. Surprisingly, our re-sampling revealed estimates of dead biomass within < 5% of our original estimates. We therefore hypothesized that the 15 sampled young stands, or some significant subset of them, were not representative of typical values of dead biomass found in recently burned stands in Yellowstone.

We employed a set of random samples of biomass across the subalpine plateaus of Yellowstone National Park as an attempt to quantify the "average" basal area of burned and unburned stands for comparison to our own chronosequence stands. We were also interested in quantifying the amount of dead biomass prior to the last fire (using separate measurements of charred vs. un-charred coarse wood) to ensure that pre-disturbance dead biomass was not biasing the estimates. We randomly sampled basal area of dead biomass in 40 burned stands using line transects and 40 unburned stands using prism sampling. Burned stands were sampled 200 meters from the roads and were spaced at least 2.5 miles apart; unburned stands were also sampled 200 meters from the roads and were at least 1.5 miles apart. Unburned stands were sampled for standing trees only, and thus estimates of dead biomass in unburned stands are inherently low because they do not include fallen dead wood.

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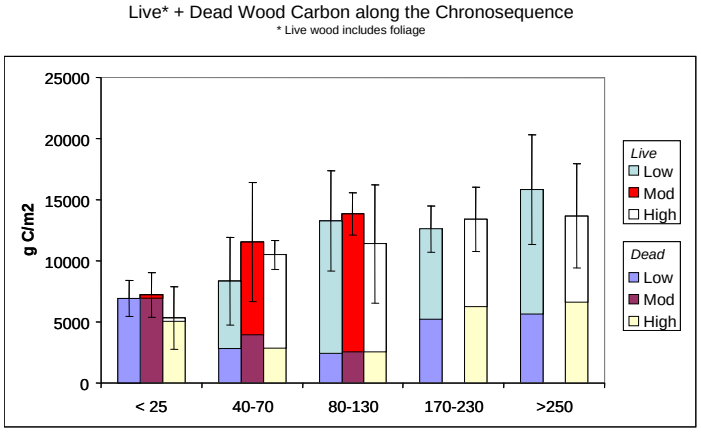

Figure 1: Mean carbon in live and dead pools across a chronosequence of 77 lodgepole pine stands sampled in Yellowstone National Park (preliminary results – please do not distribute).

We found that the 15 stands sampled as part of our chronosequence have likely underestimated typical values of dead biomass. Total biomass of our young stands is lower (though variable) than that of the randomly sapmpled unburned stands (Figure 2). Total biomass of random burned and unburned stands was approximately equal, as we expected, and biomass in the random unburned stands approximates that of the older stands in the chronosequence.

Project #2: Workshop for Managers – Fire and Carbon Storage in Forests

We held a one-day workshop entitled (Fire and Carbon Storage in Forests" on May 30, 2007, from 9am-5pm, in the Berol Lodge at the AMK Ranch. The purpose of the workshop was to inform land managers and to have discussion and feedback about the background and new developments in:

- **Forests in the regional carbon cycle**
- **Forest potential for carbon sequestration**
- **Fire and carbon cycling – short and long-term effects**
- **Remote sensing of forest disturbance**

- Presenters included: **Mike Ryan**, USDA Forest Service; **Bill Romme**, Colorado State University; **Mark Harmon**, Oregon State University; and **Jeff Hicke**, University of Idaho.

- Attending the workshop were managers from Grand Teton National Park and surrounding national forests.

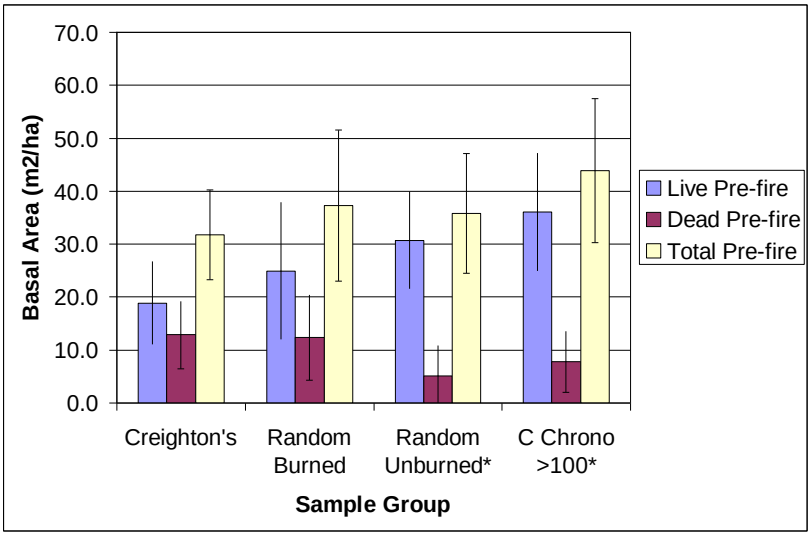

Figure 2: Mean live and dead basal area for lodgepole pine stands sampled randomly and within a chronosequence in Yellowstone National Park (preliminary results – please do not distribute).

ALTERATIONS IN YELLOWSTONE LAKE NITROGEN CYCLING DUE TO INTRODUCED LAKE TROUT AND SUBSEQUENT DECLINE OF YELLOWSTONE CUTTHROAT TROUT

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✦ ABSTRACT

Invasive species may alter processes by indirectly affecting other species in the ecosystem, but indirect affects are difficult to measure and often pre-invasion data were not collected. However, models may be used with empirical relationships and available past data to reconstruct past processes. The introduction of lake trout (*Salvelinus namaycush*) in Yellowstone Lake may have indirect effects on nitrogen cycling and provide an opportunity to study the effects of an invasive species on lake processes. To estimate how lake trout altered nitrogen cycling in Yellowstone Lake, we measured ammonium (NH_4^+) uptake by phytoplankton in 2005 and estimate past NH_4^+ uptake using empirical relationships and past data. Using ^{15}N, we measured phytoplankton uptake in 4 areas of Yellowstone Lake. Phytoplankton demanded 4.9 mg N m^{-2} hr^{-1} during the ice-free season of 2005. Uptake was higher at warmer water temperatures and shallower Secchi disk depths (measure of phytoplankton biomass). Using relationships among uptake, water temperature, and Secchi disk depth, we estimated phytoplankton uptake in the past based on historical Secchi disk depths and water temperatures. Water temperatures have increased 0.29˚C/decade and Secchi disk depths became 0.53 m/decade deeper over the past 30 years. Using our multiple regression model, phytoplankton uptake did not change between 1976 and 2006. The interaction between warmer water temperatures and deeper Secchi disk depths (a sparser algal assemblage) cancelled out resulting in no changed in modeled uptake. Therefore, when estimating past processes, we should use multiple predictors.

✦ INTRODUCTION

The introduction of invasive species and climate change threaten to alter ecosystems around the globe; however, many times their effects on ecosystems are unknown, but potentially large. Invasive species threaten to homogenize biota (Rahel 2000), alter biodiversity (Lonsdale 1999, Randall 2000), change interactions among species (Ruzycki et al. 2003), and modify ecosystem structure and function (Tronstad 2008). Climate change was single handedly responsible for changes in species ranges (Parmesan and Yohe 2003), earlier annual events (Winder and Schindler 2004), and temperatures (Walther et al. 2002). However, the combined effects of invasive species and climate changed have rarely been investigated.

Of particular concern is the interaction between climate change and invasive species (Dukes and Mooney 1999, Stachowicz et al. 2002). Predicting the response of ecosystems to a single stressor is complicated, and invasive species and climate change may interact in

surprising ways. Together invasive species and climate change may be additive or multiplicative; however, the answer remains largely uninvestigated (Dukes and Mooney 1999). One exception is Stachowicz et al. (2002) who found that the growth rate and recruitment of invasive sessile marine invertebrates was higher than native invertebrates at higher temperatures, suggesting that climate change facilitated invasive species introductions. Our study investigated how climate change and invasive species simultaneously affected nutrient uptake in Yellowstone Lake.

Ideally, time series data are used to tease apart the effects of invasive species and climate change; however, often data were not collected through time. To estimate how invasive species and climate change interact, we can use models. Models do not replace historical data, but they can be useful to estimate changes.

The introduction of lake trout (*Salvelinus namaycush*) in Yellowstone Lake provided an opportunity to investigate the combined effect of invasive species and climate change. Previous studies demonstrated that lake trout indirectly altered phytoplankton biomass in Yellowstone Lake (Tronstad 2008). However, the indirect effect of lake trout on phytoplankton uptake was unknown. Phytoplankton uptake had not previously been measured in Yellowstone Lake, therefore, past nitrogen demand by phytoplankton is unknown. However, using empirical relationships, and past water temperature and Secchi disk depths (measure of phytoplankton biomass), we estimated past phytoplankton uptake. Our objective was to quantify current phytoplankton uptake of nitrogen and estimate uptake in the past.

Study Site

Yellowstone Lake is located on the Yellowstone Plateau, Wyoming, which has a cold, continental climate with short summers and long winters (Felicetti et al. 2003). Yellowstone Lake is partially located within the Yellowstone caldera, an active silicic volcano (Morgan et al. 2003). Geology of the lake and surrounding basin is mainly rhyolite, with northern and eastern areas composed of andesite (Finn and Morgan 2002). Yellowstone Lake is mesotrophic (Kilham et al. 1996) and ice-covered from December through May (Gresswell and Varley 1988). Yellowstone Lake is the largest high-elevation (2357 m) lake in North America (Gresswell et al. 1997), with a surface area of 341 km^2, shoreline length of 239 km, and average depth of 43 m (Kaplinksi 1991). The lake is dimictic with summer stratification occurring from mid-July to mid-September with a deep (~20 m) epilimnion. During the ice-free season, surface water temperatures vary between 3˚C after ice-off and 18˚C in mid-summer, dissolved oxygen ranges between 7 and 11 mg/L, slightly basic pH (7.2 to 8.3), and low water electrical conductivity (69 to 96 µS/cm; J. Arnold, unpublished data).

Yellowstone Lake contained the largest remaining lacustrine population of Yellowstone cutthroat trout (Varley and Gresswell 1988), but their abundance fluctuated through time. The number of spawning cutthroat trout was low in the 1940s and 1950s due to egg-taking and liberal creel limits; however, the cutthroat trout population recovered after egg-taking ceased and stringent creel limits were imposed. The number of spawning cutthroat trout was high in the 1970s and 1980s, averaging 48,000 fish spawning annually in Clear Creek, a tributary stream on the east side of Yellowstone Lake. The number of cutthroat trout peaked in 1978 when 70,105 fish spawned in Clear Creek. However, the abundance of cutthroat trout declined by 60% in Yellowstone Lake and 99% in Clear Creek since 1990 (Koel et al. 2005). Presently, indices of cutthroat trout abundance are the lowest on record.

Several fish species have been introduced in Yellowstone Lake, and longnose sucker (*Catostomus catostomus*), redside shiner (*Richardsonius balteatus*), lake chub (*Couesius plumbeus*), and lake trout (*Salvelinus namaycush*) have reproducing populations (Gresswell and Varley 1988, Gresswell et al. 1997). Lake trout are the only piscivorous fish in Yellowstone Lake. Even as young fish, only a small proportion of lake trout diet is zooplankton (Ruzycki et al. 2003) Lake trout were illegally introduced into Yellowstone Lake (Kaeding et al. 1996) in ~1985 (Munro et al. 2005) and they eat ~41 cutthroat trout per year (Ruzycki et al. 2003). Lake trout are found throughout the water column after ice-out, but live primarily in the depths of Yellowstone Lake during summer. In fall, these fish spawn in shallow areas of Yellowstone Lake. The National Park Service (NPS) actively remove lake trout using gill nets, electrofishing, and a must kill angler restriction to reduce predation on native cutthroat trout

(Koel et al. 2005). Between 1994 and 2006, the NPS removed >198,000 lake trout from the lake (Koel et al. 2007).

Other threats to cutthroat trout include whirling disease and drought. Whirling disease was discovered in 1998 and mainly affects young of the year cutthroat trout in certain spawning streams (Koel et al. 2006). For example, whirling disease has decimated the spawning run to Pelican Creek, a tributary with organic substrates that is preferred by the tubificid host, *Tubifex tubifex* (Krueger et al. 2006). Only 11% of cutthroat trout in Yellowstone Lake were infected with whirling disease (Koel et al. 2006). However, the number of spawning cutthroat trout has drastically declined in streams not affected by whirling disease. Therefore, we attributed the decline of cutthroat trout primarily to lake trout predation. On-going drought also affects young of the year cutthroat trout in small tributary streams by stranding individuals (Koel et al. 2005).

✦ METHODS

To quantify the current demand for NH_4^+ in Yellowstone Lake, we measured NH_4^+ uptake by pelagic microbes (i.e., algae and bacteria). We estimated microbial NH_4^+ uptake by incubating $^{15}NH_4Cl$ in 2.5 L Nalgene polycarbonate bottles for 3 hours in early June, late July, and early October 2005. We collected water at 5, 10, and 15 m depths from 4 areas (South Arm, Southeast Arm, east of Stevenson Island, and West Thumb) of Yellowstone Lake (2 to 3 bottles per depth per site) and incubated bottles at their respective depths in northern Yellowstone Lake. To minimize uptake after incubations, we kept water samples dark and on ice. We collected phytoplankton by filtering 1.2 L of water through ashed 25-mm PALL type A/E glass fiber filters (~1 µm pore size) at 3 stages in the experiment: before adding $^{15}NH_4^+$ (ambient), immediately after adding $^{15}NH_4^+$ (t = 0) and after 3 hours of incubating (t = 3 hr). Filters were rinsed with 60-mL of deionized water after filtering microbes to remove excess ^{15}N from filter. Samples were analyzed for $\delta^{15}N$ (‰) and the mass of N (µg) using Thermo-Finnigan Delta^{plus} Advantage gas isotope-ratio mass spectrometer (Waltham, MA) interfaced with a Costech Analytical ECS4010 elemental analyzer (Valencia, California) at the Colorado Plateau Stable Isotopes Laboratory in Flagstaff, Arizona.

To estimate NH_4^+ uptake by phytoplankton, we calculated the fraction of ^{15}N in each sample (^{15}N/total N; atomic fraction; AF). The amount of ^{15}N taken up during the incubation was calculated as the difference in *AF*:

$$AF_{xs} = AF_{t=3hr} - AF_{t=0}$$

where AF_{xs} is the *AF* excess, $AF_{t=3hr}$ is the AF after 3 hours of incubating, and $AF_{t=0}$ is the *AF* at time zero (sample taken immediately after ^{15}N was added). Total ^{15}N taken up ($^{15}N_{TU}$; µg N L^{-1} hr^{-1}) was calculated by:

$$^{15}N_{TU} = \frac{N_{filter} \times AF_{xs}}{t \times v}$$

where N_{filter} is the amount of N on the filter (µg), *t* is the incubation time (hr), and *v* is the volume of water filtered (L). The mass of ^{15}N taken up (M_{TU}; µg N/L) by microbes was calculated as:

$$M_{TU} = {}^{15}N_{TU} \times t$$

Mean concentration of ^{15}N excess in the bottle ($\overline{C}_{^{15}N}$; µg ^{15}N/L) was calculated as:

$$\overline{C}_{^{15}N} = \frac{0.2 - (0.2 - M_{TU})}{2}$$

where 0.2 µg ^{15}N/L is the concentration added to each bottle. To calculate the turnover time for an NH_4^+ molecule (TT; hr^{-1}), we used:

$$TT = \frac{^{15}N_{TU}}{\overline{C}_{^{15}N}}$$

We calculated phytoplankton NH_4^+ uptake (µg N m^{-3} hr^{-1}) by:

$$U = TT \times C_A \times 1000$$

where C_A is the ambient concentration of NH_4^+ (µg N/L) in Yellowstone Lake water. In addition to microbial uptake, we measured Secchi disk depths (m) at each site and water temperature (˚C) at the incubation site.

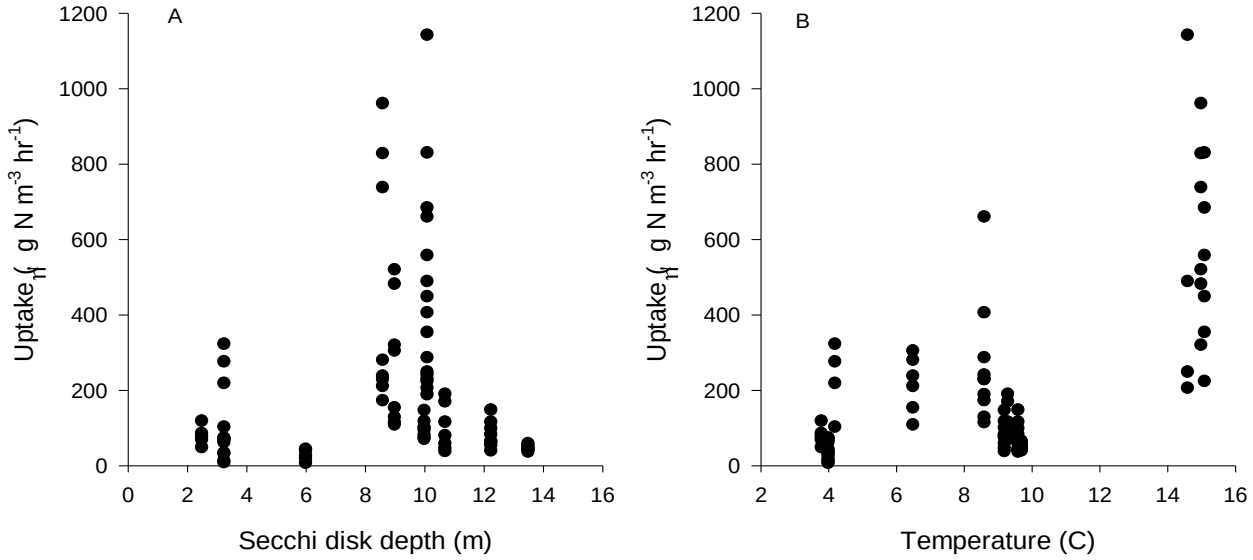

Fig. 1. A. Phytoplankton uptake (μg N m^{-3} hr^{-1}) was lower at deeper Secchi disk depths (m)
Fig. 1. B) Cooler water temperatures (˚C).

To estimate changes in past NH_4^+ uptake in Yellowstone Lake, we modeled uptake using past Secchi disk depths and water temperatures recorded since 1976 using multiple regression. Secchi disk depths are an index of phytoplankton biomass in Yellowstone Lake (Tronstad 2008) and cutthroat trout indirectly affect phytoplankton biomass through cascading trophic interactions (Tronstad 2008). Temperature represented the effects of climate change on Yellowstone Lake. Because long-term data were available for these variables, we created relationships among Seechi disk depths, water temperature, and NH_4^+ uptake from our 2005 measurements. To estimate past NH_4^+ uptake, we used historical Seechi disk depths and water temperatures with our empirical relationships from 2005.

✦ RESULTS

Pelagic microbes took up more NH_4^+ in July (8.1 ± 1.9 mg N m^{-2} hr^{-1}; 405 ± 93 μg N m^{-3} hr^{-1}), than June (1.6 ± 0.7 mg N m^{-2} hr^{-1}; 81 ± 34 μg N m^{-3} hr^{-1}) or October (1.6 ± 0.29 mg N m^{-2} hr^{-1}; 82 ± 15 μg N m^{-3} hr^{-1}; Tukey's: $p < 0.05$) in 2005. Ammonium residence time was shortest in June (9.7 ± 3.9 hr) and July (3 ± 0.6 hr), and longest in October (38 ± 5.8 hr; Tukey's: $p < 0.05$). Because Secchi disk depths and water temperatures were collected in Yellowstone Lake since 1976, we formed empirical relationships between these variables and NH_4^+ uptake in 2005. In 2005, deeper Secchi disk depths (SD; m) indicated lower NH_4^+ uptake (Fig. 1A). Conversely, higher water temperatures (T; ˚C) suggested higher NH_4^+ uptake (Fig. 1B). Together, Secchi disk depth and water temperature explained 73% of the variation in NH_4^+ uptake (N_{TU}; μg N m^{-3} hr^{-1}) measured in 2005

($\ln N_{TU} = 3.68 + 0.29T - 0.18SD$, t_T = 11.6, t_{SD} = -5.8, $P < 0.0001$, df = 51).

We predicted past NH_4^+ uptake using the empirical relationship from 2005, and past surface water temperatures and Secchi disk depths (Theriot et. al. 1997; Jeff Arnold, unpublished data). Secchi disk depths have become 1.6 m deeper since 1976 (Fig. 2A), indicating lower phytoplankton biomass (Tronstad 2008). Lake temperatures increased 0.29° C/decade during the past 30 years (Fig. 2 B):

$$T = -40 + 0.029y - 0.18a - 0.86I + 0.056a \times I$$

where y is year (e.g., 1976), a is days since August 10th, I is an indicator variable where 0 is on or before August 10th and 1 is after August 10th;
r^2 = 0.87, df = 213, t_y = 3.0, t_a = -33, t_I = -2.1, $t_{I \times a}$ = 5.7, $p < 0.001$). Water temperature in Yellowstone Lake increased from ice-off to August 10th and decreased thereafter, thus, we regressed inter-annual variation in water

temperature as days since August 10th. Using these past data, the multiple regression model suggested that microbial uptake in Yellowstone Lake was similar from 1976 to 2005 ($t = -0.06$, $df = 215$, $r^2 = 0$, $p = 0.95$; Fig. 2C).

Ammonium uptake in Yellowstone Lake was comparable to NH_4^+ uptake in oligotrophic Flathead Lake, Montana (12.6 to 240 µg N m^{-3} hr^{-1}; (Dodds et al. 1991). Pelagic microbes in Yellowstone Lake demanded less NH_4^+ than an eutrophic Alaskan Lake (140 to 51,700 µg N m^{-3} hr^{-1}; (Gu and Alexander 1993), and eutrophic Lake Balaton, Hungary (110 to 1560 µg N m^{-3} hr^{-1}; (Presing et al. 2001).

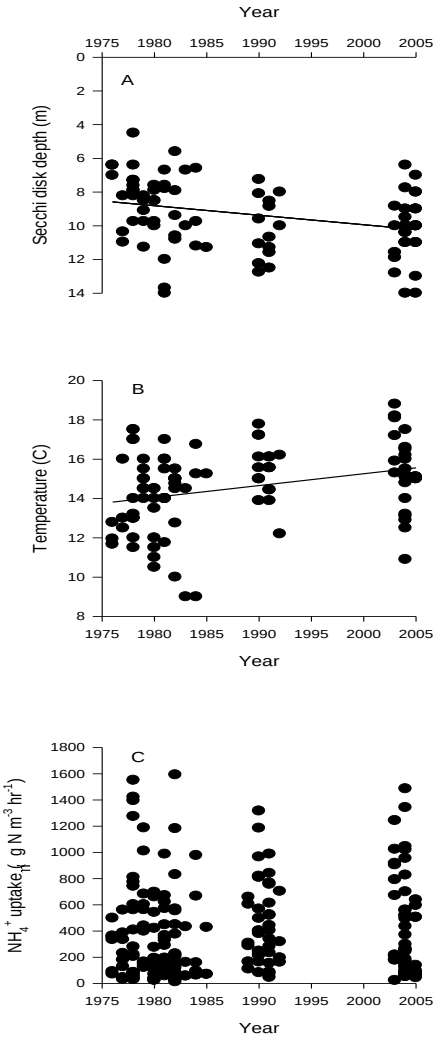

Fig. 2. A.) Secchi disk depths became 0.53 m/decade deeper and B.) water temperatures became 0.29 ºC/decade warmer between 1976 and 2006. C.) Using the relationships in Fig. 1 and past data in A and B, our model suggested that phytoplankton uptake has not changed during the past 30 years.

✦ DISCUSSION

Zooplankton excretion supplied the majority of NH_4^+ demanded by phytoplankton in Yellowstone Lake; however, cutthroat trout excretion supplied a fraction of demand. In Yellowstone Lake, zooplankton excretion supplied 86% of the NH_4^+ demanded by phytoplankton currently (Tronstad 2008). Our model suggested that phytoplankton uptake was similar between 1976 and 2006, thus zooplankton would have supplied ~100% of the NH_4^+ demanded in the past. Cutthroat trout excretion supplied 0.23% of current demand. Assuming demand has not changed, cutthroat trout supplied 0.45% of past demand. Thus, comparing animal fluxes to nutrient demand is useful when estimating the importance of fluxes within the ecosystem.

The indirect effect of lake trout on phytoplankton was probably greater than their direct effect through changes in excretion fluxes. The introduction of lake trout facilitated a trophic cascade that lowered phytoplankton biomass (Tronstad 2008). Despite changes in excretion fluxes, native cutthroat trout excretion was a minor part of nutrient cycling in Yellowstone Lake. Our results were contrary to Glaholt and Vanni (2005) who reported that the direct effect of blue gill (*Lepomis macrochirus*) excretion was greater than their indirect effect on phytoplankton. Phytoplankton biomass indirectly decreased by ½ to $^1/_9$ after the introduction of lake trout resulting in 1.6 m deeper Secchi disk measurements in Yellowstone Lake (Tronstad 2008). Similar to other lakes (e.g., Winder and Schindler 2004), climate changed increased water temperature by 0.29˚C/decade in Yellowstone Lake. In our model, warmer water temperatures cancelled the effect of decreased phytoplankton biomass resulting in no change in modeled NH_4^+ uptake in Yellowstone Lake. If we used temperature or Secchi disk depth alone to predict changes in uptake, we would have predicted higher and lower uptake, respectively.

✦ CONCLUSIONS

Climate change and invasive species can interact in surprising ways. Here, climate change and invasive species interacted additively resulting in no change in modeled NH_4^+ uptake.

Warmer water temperatures cancelled the effect of a sparser phytoplankton assemblage induced by invasive lake trout.

✦ LITERATURE CITED

Dodds, W.K., J.C. Priscu and B.K. Ellis. 1991. Seasonal uptake and regeneration of inorganic nitrogen and phosphorus in a large oligotrophic lake: size-fractionation and antibiotic treatment. Journal of Plankton Research 13:1339-1358.

Dukes, J. S. and H.A. Mooney. 1999. Does global change increase the success of biological invaders? Trends in Ecology & Evolution 14:135-139.

Felicetti, L.A., C.C. Schwartz, R.O. Rye, M.A. Haroldson, K. A. Gunther, D. L. Philips and C. T. Robbins. 2003. Use of sulfur and nitrogen stable isotopes to determine the importance of whitebark pine nuts to Yellowstone grizzly bears. Canadian Journal of Zoology 81:763-770.

Finn, C., and L.A. Morgan. 2002. High-resolution aeromagnetic mapping of volcanic terrain, Yellowstone National Park. Journal of Volcanology and Geothermal Research 115:207-231.

Glaholt, S.P. and M.J. Vanni. 2005. Ecological responses to simulated benthic-derived nutrient subsidies mediated by omnivorous fish. Freshwater Biology 50:1864-1881.

Gresswell, R.E., W.J. Liss, G.L. Larson and P.J. Bartlein. 1997. Influence of basin-scale physical variables on life history characteristics of cutthroat trout in Yellowstone Lake. North American Journal of Fisheries Management 17:1046-1064.

Gresswell, R.E. and J.D. Varley. 1988. Effects of a century of human influence on the cutthroat trout of Yellowstone Lake. American Fisheries Society Symposium 4:45-52.

Gu, B., and V. Alexander. 1993. Seasonal variations in dissolved inorganic nitrogen utilization in a subartic Alaskan lake. Archiv Fur Hydrobiologie 126:273-288.

Kaeding, L.R., G.D. Boltz and D.G. Carty. 1996. Lake trout discovery in Yellowstone Lake threaten native cutthroat trout. Fisheries 21:16-20.

Kaplinksi, M.A. 1991. Geomorphology and geology of Yellowstone Lake, Yellowstone National Park, Wyoming. Master's thesis. Northern Arizona University, Flagstaff.

Kilham, S. S., E.C. Theriot, and S.C. Fritz. 1996. Linking planktonic diatoms and climate change in the large lakes of the Yellowstone ecosystem using resource theory. Limnology and Oceanography 41:1052-1062.

Koel, T. M., J. L. Arnold, P. Bigelow, P. D. Doepke, B. D. Ertel and M. E. Ruhl. 2007. Yellowstone Fisheries and Aquatic Sciences Annual Report for 2006. YCR-2007-04, National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming.

Koel, T. M., P. Bigelow, P. D. Doepke, B. D. Ertel and D. L. Mahony. 2005. Nonnative lake trout result in Yellowstone cutthroat trout decline and impacts to bears and anglers. Fisheries 30:10-19.

Koel, T.M., D.L. Mahony, K.L. Kinnan, C. Rasmussen, C.J. Hudson, S. Murcia and B.L. Kerans. 2006. *Myxobolus cerebralis* in native cutthroat trout of the Yellowstone Lake ecosystem. Journal of Aquatic Animal Health 18:157-175.

Krueger, R.C., B.L. Kerans, E.R. Vincent and C. Rasmussen. 2006. Risk of *Myxobolus cerebralis* infection to rainbow trout in the Madison River, Montana, USA. Ecological Applications.

Lonsdale, W.M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522-1536.

Morgan, L.A., W.C. Shanks, D. Lovalvo, S.Y. Johnson, W.J. Stephenson, K.L. Pierce, S.S. Harlan, C.A. Finn, G. Lee, M. Webring, B. Schulze, J. Duhn, R. Sweeney and L. Balistrieri. 2003. Exploration and discovery in Yellowstone Lake: results from high-resolution sonar imaging, seismic reflection profiling, and submersible studies. Journal of Volcanology and Geothermal Research 122:221-242.

Munro, A.R., T.E. McMahon and J.R. Ruzycki. 2005. Natural chemical markers identify source and date of introduction of an exotic species: lake trout (*Salvelinus namaycush*) in Yellowstone Lake. Canadian Journal of Fisheries and Aquatic Sciences 62:79-87.

Parmesan, C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37-42.

Presing, M., S. Herodek, T. Preston and L. Voros. 2001. Nitrogen uptake and the importance of internal nitrogen loading in Lake Balaton. Freshwater Biology 46:125-139.

Rahel, F.J. 2000. Homogenization of fish faunas across the United States. Science 288:854-856.

Randall, J.M. 2000. Improving management of nonnative invasive plants in wilderness and other natural areas. USDA Forest Service Proceedings 5:64-73.

Ruzycki, J.R., D.A. Beauchamp and D. L. Yule. 2003. Effects of introduced lake trout on native cutthroat trout in Yellowstone Lake. Ecological Applications 13:23-37.

Stachowicz, J.J., J.R. Terwin, R.B. Whitlatch and R.W. Osman. 2002. Linking climate change and biological invasions: ocean warming facilitates nonindigenous species invasions. Proceedings of the National Academy of Science 99:15497-15500.

Theriot, E.C., S.C. Fritz and R.E. Gresswell. 1997. Long-term limnological data from the larger lakes of Yellowstone National Park, Wyoming, U.S.A. Artic and Alpine Research 29:304-314.

Tronstad, L. M. 2008. Ecosystem consequences of declining Yellowstone cutthroat trout on Yellowstone Lake and tributary spawning streams. Dissertation. University of Wyoming, Laramie.

Varley, J.D. and R.E. Gresswell. 1988. Ecology, status, and management of the Yellowstone cutthroat trout. American Fisheries Society Symposium 4:13-24.

Walther, G.R., E. Post, P. Convey, A. Menzel, C. Parmesan, T.J.C. Beebee, J.M. Fromentin, O. Hoegh-Guldberg and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389-395.

Winder, M. and D. E. Schindler. 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. Ecology 85:2100-2106.

GREATER YELLOWSTONE ECOSYSTEM

LEAD TOXICOSIS IN SCAVENGING SPECIES WITHIN THE SOUTHERN GREATER YELLOWSTONE ECOSYSTEM

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✦ INTRODUCTION

Lead toxicosis in terrestrial birds has been receiving much attention in recent years (for review, see Fisher et al. 2006). Particularly, much of this attention has been focused around the critically endangered California Condors (*Gymnogyps californianus*) because of the large percentage of free-flying condors that are exhibiting and dying from lead poisoning (Parish et al. 2007). Church et al. (2006) has found that the majority of lead ingested by the condors originates from spent rifle ammunition in offal and big game not retrieved by hunters, thus substantiating the suppositions by Pattee et al. (1990), Miller et al. (1998), and Hunt et al. (2005) that the majority of lead poisoning in condors came from hunting practices. However, condors may not be the only scavenging species at risk from ingesting offal and rifle shot carrion.

There are several studies that describe lead fragmentation of rifle bullets in the carcasses and offal of ground squirrels (*Spermophilus richardsonii*), prairie dogs (*Cynomys ludovicianus*), deer (*Odocioleus* spp.), and elk (*Cervus canadensis*) and make the argument that these fragments pose a hazard to any potentially scavenging species (Knopper 2005, Pauli et al. 2007, Hunt et al. 2005, and Craighead and Bedrosian 2008). We have recently gathered data to substantiate that claim by finding that Common Ravens (*Corvus corax*) have significantly higher blood lead levels during the big game hunting seasons in Wyoming than non-hunting periods and nestling controls (Craighead and Bedrosian, 2008).

There have been increasing studies of lead exposure in eagles in recent years also. Kramer and Redig (1997) found that the incidence of lead ingestion in both bald and golden eagles did not change after the ban of lead shot for waterfowl hunting. Further, Miller et al. (1998) and Wayland et al. (2003) both found high incidence of lead poisoning in eagles and found that the times and areas of high exposure were not correlated to waterfowl hunting for both the western US and Great Plains. Both studies suggested that big game hunting may be a significant source of lead exposure for eagles. Conversely, Wayland and Bollinger (1999) found a greater prevalence of lead exposure in bald eagles in areas of high waterfowl hunting in the Canadian prairie provinces, but did not find a similar relationship for golden eagles. Pattee et al. (1990) found that the blood lead levels of golden eagles in California increased from September – December and suggested that the increase could have been from deer hunting in the area. All of the studies on lead poisoning and eagles concur that big game hunting could be a cause of lead exposure for those species.

Not only does lead ingestion occur in avian species, but there is a potential for lead ingestion through offal in mammalian species as well. Coyotes (*Canis latrans*), wolves (*C. lupis*), cougars (*Puma concolor*), and fox (*Vulpes vulpes*) have all been documented to scavenge in the Greater Yellowstone Ecosystem (Wilmers et al. 2003, pers. obs). While coyotes may ingest a larger percentage of offal and un-recovered, hunter shot carcasses than wolves and cougars,

the potential for lead to occur in the diets of the latter two species still exists.

We investigated the potential correlation between big game hunting and lead exposure in scavengers in the "protected" landscape of Grand Teton National Park, WY, and the southern Greater Yellowstone Ecosystem. We sampled blood lead levels of eagles during and after an annual big game hunt and sampled nestling bald eagles within this area as a control. Further, we tested blood and tissues of cougars, coyotes and wolves to document potential lead ingestion.

✦ METHODS

Eagles were captured within the southern Greater Yellowstone Ecosystem (GYE) (43º91'N, 110º40'W). The southern GYE is comprised of mainly public land encompassing Grand Teton National Park, the National Elk Refuge and 3 wilderness areas in the surrounding 4 national forests. Elk (Cervus canadesis), deer (*Odocioleus* spp.), pronghorn antelope (*Antilocapra americana*) and bison (*Bison bison*) hunting annually occurs within the valley, and most hunters leave offal from their kills in the field (see Craighead and Bedrosian 2008, for a detailed description of habitat and hunting practices).

Eagles were captured during the winter months of 2005-2006. All but one capture was performed with a net launcher (CODA Ent. Mesa, AZ) using road-killed carrion as bait. The other capture was performed with a modified whoosh net. Eagles were baited with road-killed carrion that was determined not to have been shot. Blood samples from nestlings were taken in cooperation with Grand Teton National Park and Montana State University (A. Harmata) and were sampled from nests within the southern GYE. Once captured, each eagle received a USGS band, was aged, and a 2.0 cc of blood was drawn from the brachial vein for lead analysis and placed in EDTA collection tubes (Becton, Dickinson, and Company, Kranklin Lakes, NJ). Bald eagles were aged based on McCullough (1989), golden eagles were aged based on primary molt patterns (Pyle 2005), and gender was determined for bald and golden eagles by Bortolotti (1984) and Edwards and Kochert (1986), respectively.

We collected blood samples from the femoral vein of cougars captured during the winter months from 2005-2007. All cougars were live-captured using hounds to tree the individuals and we used rhohimbine to anesthetize the cougar before lowering them from the tree. Cougars received a radio collar, an ear tag, tattoo, and were aged. We obtained tissue samples from two moribund cougars that were later diagnosed with plague. All cougars sampled exhibited home ranges within the southern GYE during sample collection (unpubl. data). Blood samples extracted from coyotes were obtained from Utah State University (J. Burghardt). Coyotes were live-captured using snare traps, a radio collar was placed on each individual and a blood sample was taken from the femoral vein. We took a liver sample from one road-killed coyote. We obtained blood samples from wolves captured within Grand Teton National Park by the USFWS (M. Jimenez). Liver samples were collected from wolves that had been lethally controlled by the USFWS and AHPIS in the west-central side of the GYE. We took tissue samples as far from the shot trajectory as possible to reduce the potential for contamination from the shotgun shot. Finally, we obtained a liver sample from one road-killed fox.

Most mammalian blood samples were placed in LiHeparin storage tubes (Becton, Dickinson, and Company, Kranklin Lakes, NJ) and tested for BLL using a Leadcare® portable blood lead analyzer (ESA Biosciences Inc., Chelmsford, MA) and recorded in µg/dL. Each Leadcare® sample was tested within 24 h after collection. Bovine controls were tested periodically to confirm accuracy of the tester and to check for contamination. We also tested wolf blood samples placed in EDTA storage tubes.

Blood samples from eagles and wolves placed in EDTA storage tubes were analyzed for blood lead levels (BLL) by inductively coupled plasma mass spectrometry (ICMPS). These blood samples and all tissues were sent to the Diagnostic Center for Population and Animal Health (Michigan State University, Lansing, MI)

for ICMPS testing. Each sample was tested for arsenic, cadmium, lead, mercury, selenium and thallium levels. Leadcare® and ICPMS testing are directly comparable using the equation Leadcare = 0.7404(ICPMS) – 0.4067 (Craighead and Bedrosian2008).

Blood samples from recaptured eagles (n = 1) collected at least two weeks apart were considered independent samples because the lead depuration rate for birds is approximately two weeks (Fry and Maurer 2003, Craighead and Bedrosian 2008). Because of this depuration rate, we did not sample any eagles from 15 December 2006 though 8 January 2007 so we could compare blood lead levels from the hunting and post-hunting seasons. Also, we considered any blood samples taken within the 2 weeks after the end date of the hunting season to be potentially under the influence of the hunt and included them in the "hunt" sample for analysis.

We first tested for differences between blood lead levels of bald and golden eagles using Mann-Whitney because the data were not normally distributed and could not be adequately transformed. We tested for differences in blood lead levels between the hunting and non-hunting season samples using Mann-Whitney and a Kruskall-Wallis test was employed to determine if age was a factor in determining BLLs. Finally, we used chi-square tests to reveal potential differences in the proportion of eagles with clinical lead exposure (≥60 ug/dL) in the hunt versus non-hunt, and to test for differences in the proportion of eagles with sub-clinical exposure (20≤ BLL <60) and background levels (<20) between the two seasons. We also tested for a correlation between body condition of bald eagles and blood lead levels using a regression analysis. We obtained the body condition index using the residuals of a regression analysis between mass (minus estimated crop weight) and a structural body measurement (bill depth).

✦ RESULTS

Eagles

We captured and tested samples for blood lead levels from a total of 40 eagles, including one recapture 48 d after initial capture that was considered an independent sample (33 bald eagle and 7 golden eagle samples). From the total sample, we found no difference in the median BLLs between bald and golden eagles (P = 0.109, W = 722.0; Table 1). However, we did find some evidence to suggest during the hunting season bald eagles exhibited higher BLLs than golden eagles (P = 0.077, W = 426.0), but sample size for golden eagles was very limited (n = 2). There was no difference in BLLs between species during the non-hunting season (P = 0.315, W = 30.0). We found that age was not a factor in determining BLLs (P = 0.603, H = 3.64). We therefore decided to pool the data for the subsequent analysis.

We found evidence to suggest that the median BLL during the hunting season was larger than the non-hunt (P = 0.051; Figure 1). We found significantly more eagles with acute lead exposure during the hunting season (P = 0.011, χ^2 = 6.502), but there was no difference between season for sub-clinical exposure (P = 0.736, χ^2 = 0.113). We found no relationship between body condition index and BLL for bald eagles (P = 0.75). Based on the exposure level criterion defined by Redig (1984), we found 85% of birds tested had been exposed to lead (Table 2). Further, we found 10% to have acute lead poisoning and all were sampled during the hunting season. It also appeared that the magnitude of acute poisoning levels increased with the duration of the hunting season (Figure 1).

We tested nine cougars for BLLs using the Leadcare® system (Table 3). Median BLL for the combined samples was 1.2 µg/dL (range = 0.6 – 1.5; S.D. = 0.26). The median BLL for coyotes was 1.5 µg/dL (*n* = 4; range = 0.0 – 2.0; S.D. = 1.0). The one wolf tested did not exhibit elevated BLL (Table 3). We tested seven wolf blood samples using ICMPS (5 yearlings and 2 adults). All had BLL <1.0 ug/dL (range = 0.4-0.9; median = 0.8; S.D. = 0.21). All liver tissue samples were below detectible limits for lead (0.5 ppm).

	n	median	SD	range
All Captures				
All Birds	40	40.9	99.4	11.6 - 458.0
Bald Eagle	33	52	107.5	11.6 - 458.0
Golden Eagle	7	32.7	11.7	14.1 - 43.8
Hunting Season				
All Birds	29	55.9	113.3	14.1 - 458.0
Bald Eagle	27	56	115.9	14.4 - 458.0
Golden Eagle	2	19.8	8.6	14.1 - 25.5
Non-Hunting Season				
All Birds	11	30.2	12.3	11.6 - 53.3
Bald Eagle	6	27.7	13.9	11.6 - 53.3
Golden Eagle	5	39.3	10.3	18.1 - 48.3

Table 1. Blood lead level (µg/dL) descriptive statistics for Bald Eagles and Golden Eagles captured from November – January in Jackson Hole, Wyoming.

Blood lead level	n	mean	SD
<20	6	15.3	2.4
20-59	22	37.3	12.3
60-100	8	69.8	12.9
>100	4	352.1	84.1

Table 2. Mean blood lead levels (µg/dL) of Bald and Golden Eagles captured between November – January in Jackson Hole, Wyoming by exposure levels. Blood lead levels <20 µg/dL = background, 20-59 µg/dL = exposed, 60-99 µg/dL = clinically affected, and >100 = acute lead poisoning (guidelines based on Redig 1984).

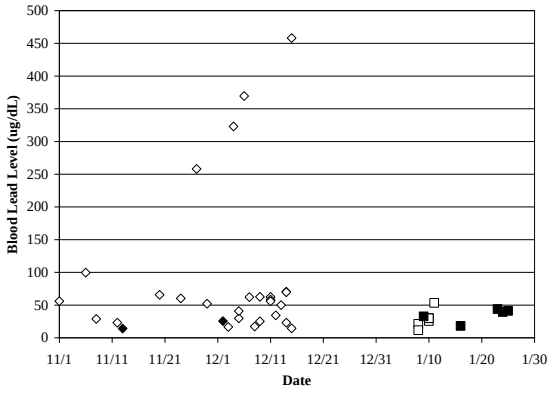

Figure 1. Blood lead levels (µg/dL) of bald eagles (open symbols) and golden eagles (closed symbols) tested during the months of November – January in Jackson Hole Wyoming.

Mammals

We tested nine cougars for BLLs using the Leadcare® system (Table 3). Median BLL for the combined samples was 1.2 µg/dL (range = 0.6 – 1.5; S.D. = 0.26). The median BLL for coyotes was 1.5 µg/dL (*n* = 4; range = 0.0 – 2.0; S.D. = 1.0). The one wolf tested did not exhibit elevated BLL (Table 3). We tested seven wolf blood samples using ICMPS (5 yearlings and 2 adults). All had BLL <1.0 ug/dL (range = 0.4-0.9; median = 0.8; S.D. = 0.21). All liver tissue samples were below detectible limits for lead (0.5 ppm).

Species	Date Sampled	Age*	Blood Lead (ug/dL)
Cougar	11/5/2005	1	1.1
Cougar	1/24/2005	2	1.3
Cougar	3/22/2005	3	1.5
Cougar	11/13/2006	3	1.4
Cougar	11/24/2006	2	0.6
Cougar	12/3/2006	2	1.2
Cougar	12/11/2006	2	1.2
Cougar	2/23/2007	3	1.2
Cougar	2/24/2007	3	1.0
Coyote	8/17/2006	3	1.0
Coyote	8/25/2006	3	0.0
Coyote	9/29/2006	3	2.0
Coyote	2/18/2007	3	2.0
Wolf	6/8/2006	3	0.8

* Kitten = 1, Sub-adult = 2, Adult = 3.

Table 3. Blood lead levels of mammals tested within the southern Greater Yellowstone Ecosystem tested with a Leadcare®, portable lead tester.

✦ DISCUSSION

We found evidence to support the supposition that eagles are ingesting higher amounts of lead during the hunting season in the southern Yellowstone ecosystem. The clearest sign of increased lead ingestion during the hunt was the proportion of eagles that had both clinical exposure and acute lead poisoning during the hunt (20% and 10%, respectively). No eagle tested exhibited BLLs >53.3 µg/dL during the non-hunting season (Figure 1). Differences

between bald and golden eagle BLLs during the hunt is likely an artifact of sample size. We also found no relationship between age and lead exposure, indicating that this phenomenon affects potentially all eagles within this area.

* Kitten = 1, Sub-adult = 2, Adult = 3.
Table 3. Blood lead levels of mammals tested within the southern Greater Yellowstone Ecosystem tested with a Leadcare®, portable lead tester.

A large proportion of eagles tested during the non-hunting season had elevated lead levels (82%). This is similar to what we observed during the hunting season (86%), suggesting that eagles in this area are ingesting lead from a source other than hunter provided carrion. There was a similar proportion of individuals of both bald and golden eagles that exhibited elevated lead levels during the non-hunt (83% and 80%, respectively), suggesting that both species are being exposed from similar sources (e.g., not dietary fish). While the source has yet to be identified, it is likely not carrion, because the ravens within this area exhibit no elevated blood lead levels post-hunt (Craighead and Bedrosian 2008).

We found no evidence to support the supposition that mammals are ingesting unnatural sources or amounts of lead within the GYE. Even after the Leadcare® results had been adjusted to correspond to ICMPS results, the highest BLL we detected was only 2.6 ug/dL, which is well below the elevated BLL threshold. Even though 57% of the blood samples tested with Leadcare® were collected during the hunting season (Table 3), we found no evidence of acute lead exposure in mammals in the GYE. We also found no evidence to support the notion that mammals in the GYE have had any exposure during their lifetimes. Liver lead levels indicate chronic, lifetime exposure and were all below detectible limits.

A large amount of lead is annually deposited across the nation in the form of very small lead particles in offal and un-retrieved big game (Hunt et al. 2005, Craighead and Bedrosian 2008). A wide variety of scavenging species utilizes this offal for food in the GYE (Wilmers et al. 2003) and, thus, may be vulnerable to lead toxicosis. While our data indicate that lead ingestion may be a serious issue for eagles, mammals may not be at high risk. This difference may be due to different amounts of lead ingested (mammals may utilize food resources other than offal) or differences in lead absorption rates between the classes. Regardless, the amount and severity of the lead ingestion by eagles warrants concern and further investigation.

✦ LITERATURE CITED

Bortolotti, G.R. 1984. Sexual size dimorphism and age-related size variation in Bald Eagles. Journal of Wildlife Management. 48:72-81.

Church, M.E., R. Gwiazda, R.W. Risebrough, K. Sorenson, C.P. Chamberlain, S. Farry, W. Heinrich, B.A. Rideout, and D.R. Smith. 2006. Ammunition is the principal source of lead accumulated by California Condors re-introduced to the wild. Environmental Science and Technology 40: 6143-6150.

Craighead, D. and B. Bedrosian. 2008. Blood lead levels of common ravens with access to big game offal. Journal of Wildlife Management.72(1):240-245.

Edwards, T. C., Jr. and M.N. Kochert. 1986. Use of body weight and length of footpad as predictors of sex in golden eagles. Journal of Field Ornithology. 57:317-319.

Fisher, I.J., D.J. Pain, V.G. Thomas. 2006. A review of lead poisoning from ammunition sources in terrestrial birds. Biological Conservation. V131; 3; P 421-432.

Hunt, W. G., W. Burnham, C. Parish, K. Burnham, B. Mutch, and J.L. Oaks. 2005. Bullet fragments in deer remains: implications for lead exposure in avian scavengers. Wildlife Society Bulletin 33: 167-170.

Fry, D.M. and J.R. Maurer. 2003. Assessment of lead contamination sources exposing

California Condors. Report of California Department of Fish and Game.

Knopper, L., P. Mineau, A. Scheuhammer, D. Bond, D. McKinnon. 2006. Carcasses of shot Richardson's ground squirrels may pose lead hazards to scavenging hawks. Journal of Wildlife Management 70: 295-299.

Kramer, J.L. and P.T. Redig. 1997. Sixteen years of lead poisoning in eagles, 1980-1995: an epizootiologic view. Journal of Raptor Research 31: 327-332.

McCullough. M.A. 1989. Moulting sequence and aging of bald eagles. Wilson Bulletin. 101:1-10.

Miller. M.J.R., M. Restani, A. R. Harmata, G. R. Bortolotti, and M. E. Wayland. 1998. A comparison of blood lead levels in bald eagles from two regions on the plains of North America. Journal of Wildlife Diseases 34: 704-714.

Parish, C.N., W.R. Heinrich, and W.G. Hunt. 2007. Five years of lead exposure among California condors released in Arizona. Pages__*In* A. Mee, L. S. Hall., and J. Grantham, *eds*. California Condors in the 21st Century. American Ornithologists' Union and Nuttall Ornithological Club. In press. at www.peregrinefund.org).

Pattee, O.H., S.N. Wienmeyer, B.M. Mulhern, L. Sileo, and J.W. Carpenter. 1981. Experimental lead-shot poisoning in bald eagles. Journal of Wildlife Management 45: 806-810.

Pauli, J.N., and S.W. Buskirk. 2007. Recreational shooting of prairie dogs: a portal for lead entering wildlife food chains. Journal of Wildlife Management 71: 103-108.

Pyle. P. 2005. Remigial molt patterns in North American Falcomiformes as related to age, sex, breeding status, and life-history strategies. Condor. 107:823-834.

Redig, P.T. 1984. An investigation into the effects of lead poisoning on Bald Eagles and other raptors: final report. Minnesota Endangered Species Program Study 100A-100B. University of Minnesota, St. Paul.

Wayland, M. and T. Bollinger. 1999. Lead exposure and poisoning in bald eagles and golden eagles in the Canadian prairie provinces. Environmental Pollution 104: 341-350.

Wayland, M., L. K. Wilson, J. E. Elliot, M. J. R. Miller, T. Bollinger, M. McAdie, K. Langelier, J. Keating, and J. M. W. Froese. 2003. Mortality, morbidity, and lead poisoning of eagles in western Canada, 1986-98. Journal of Raptor Research. 37:8-18.

Wilmers, C.C., D.R. Stahler, R.L. Crabtree, D.W. Smith and W.M. Getz. 2003. Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. Ecology Letters 6: 996-1003.

DISTURBANCE INTERACTIONS: MOUNTAIN PINE BEETLE & BLISTER RUST IN WHITEBARK PINE

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✦ INTRODUCTION

Whitebark pine (*Pinus albicaulis* Englem.) is a keystone species of many high elevation ecosystems in the Greater Yellowstone Ecosystem (GYE) and directly influence watershed quality by regulating snow accumulation and retention, facilitating regeneration after a disturbance, and stabilizing soil and rock on steep, harsh sites.

Historically, the principle source of cyclic tree mortality in whitebark pine ecosystems was the mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopk.). Periodic epidemics of bark beetles result in widespread tree mortality and are an important component of stand dynamics. The current beetle activity in the Greater Yellowstone is at epidemic levels, driven by high densities of both susceptible host trees and beetles.

In contrast to the MPB, blister rust (*Cronartium ribicola* Fisch.) is an exotic pathogen and a continuous source of disturbance, rather than cyclic. Paramount to the influence of this fungus is a severe reduction in whitebark pine recruitment due to the loss of cone production and extensive damage to seedlings and saplings. Blister rust is continuing to spread throughout the GYE , and due to its perpetual presence, is considered the most damaging agent to whitebark pine.

Because the current decline of whitebark is unprecedented, my master's research seeks to quantify the interactions between blister rust and the MPB. It is not known how the following variables influence this species' susceptibility to the MPB: 1) presence of an alternate host, specifically lodgepole pine (*Pinus contorta* var. *latifolia*); 2) severity of white pine blister rust; or 3) variable whitebark pine density due to diffusion by non-alternate host species. An enhanced understanding of these questions could support successful preservation strategies for this critical and charismatic high elevation conifer.

✦ RESEARCH PROJECT

During the summer of 2006, I collected data from four study sites in the GYE with the help of two dedicated field assistants Michael Straw and Ryan Simms. Four sites were selected based on the presence of MPB and biophysical characteristics through the use of Forest Health Protection aerial surveys, personal field reconnaissance, and cooperation with National Forest and Park Service personnel.

At three of the four sites, two stand types were identified based on overstory conifer species composition. These different stand types assist in the determination of the roles tree density and a "diffusion-effect" by non-host species (*Abies lasiocarpa* Hook. and *Picea engelmanni* Parry.) play in the susceptibility of an individual whitebark pine to selection by the MPB within this sites. Blister rust was present on all three sites and in both stand types. The fourth study site, Sylvan Pass is dissimilar from

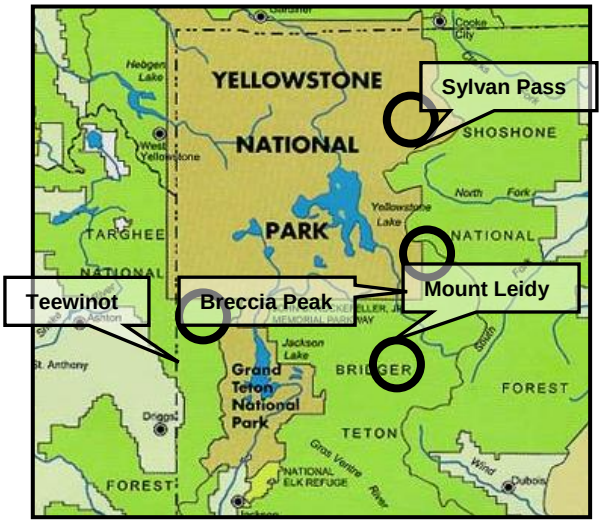

Figure 1. Map of collections sites in the Greater Yellowstone Ecosystem

the above three sites because blister rust is absent, and whitebark and lodgepole pine are growing in association as codominant canopy species. This site was examined to determine the role of host species in selection by the MPB.

At each stand, 24 temporary angle point sampling plots, using a metric basal area factor of 2.0, were systematically established to collect both tree and plot level data. Tree data collected included species, diameter at 1.3 meters, live or dead status, cone presence or absence, average number and size of pitch tubes, crown needle color, and blister rust severity (Six & Newcomb 2005). Plot data included location, elevation, slope, aspect, and topographic position.

Data analysis incorporates several statistical techniques. Non-parametric chi-square analyses were utilized to test the statistical significance of the differences in frequency of a given characteristic (such as tree diameter and blister rust severity) for bivariate tabular data (SAS Institute, 2006). Selection ratios provide a probability of use for a specified host characteristic, and are calculated by determining the frequency of occurrence of MPB in habitat A compared to the frequency in habitat B (Manly et al. 1993). In this case, dissimilar MPB habitats are defined by individual whitebark pine host characteristics. For example, selection by MPB for whitebark pine with heavy blister rust was compared to the selection of trees with light blister rust. Selection ratio analyses complimented the chi-square analyses by accounting for stand density, species composition, epidemic intensity, and temporal sequence of attack. Logistic regression was used to describe a dichotomous discrete response (selection by MPB or not) as a function of tree and stand variables (Minitab Release 14.1, 2007).

✦ PRELIMINARY FINDINGS

The overall condition of the whitebark stands sampled in this study provides a perspective on the severity of the disturbances currently impacting whitebark pine in the GYE. Roughly one half of the whitebark pine sampled in this study are dead, 70% have been attacked by MPB, and 85% have at least one blister rust symptom.

Our data provide evidence that at Sylvan Pass the MPB outbreak began in the whitebark pine, which were preferentially selected over lodgepole pine throughout the progression of the epidemic. In addition, beetle activity was greater in trees with greater blister rust severity. Therefore, we conclude that host tree species and blister rust severity influence individual tree selection by MPB.

✦ ACKNOWLEDGMENTS

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✦ LITERATURE CITED

Manly, B.F.J., L.L McDonald. & D.L. Thomas. 1993. Resource selection by animals. London: Chapman & Hall.

Minitab, 2007. State College, Pennsylvania. Version 14.1.SAS Institute, 2006. Cary North Carolina, Version. 9.3.1.

Six, D.L. & M. Newcomb. 2005. A rapid rating system for rating white pine blister rust incidence, severity and within-tree distribution in whitebark pine. Northwest Science, 79(2&3):189-195.

MONTANE MEADOW BUTTERFLY SPECIES DISTRIBUTIONS IN THE GREATER YELLOWSTONE ECOSYSTEM

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✦ ABSTRACT

The composition of butterfly communities is a good indicator of changing environmental conditions. Butterflies have tight associations with the plant community due to their dependence on plants throughout their life history. These associations make butterfly distributions predictable based on the plant communities. Butterfly abundance data have been collected annually since 1997 within montane meadow sites characterized along a hydrologic gradient within the Greater Yellowstone Ecosystem. From this research, community composition may be predictable relative to future climatic changes and key habitat constraints. Identifying such variables is important for butterfly conservation.

✦ INTRODUCTION AND OBJECTIVES

Butterfly communities have been established in the literature as well known indicators for environmental changes (Debinski and Brussard, 1994; Gutierrez and Menendez, 1998; Simonson et al., 2001; Dennis et al., 2006; Scalercio et al., 2006). Butterfly species richness can be predicted from models using landscape variables such as elevation and topographic heterogeneity (Nally et al., 2003) and plant richness (Field et al., 2006). Butterflies have been used to predict areas that represent hotspots of biological diversity (Simonson et al., 2001) and they may serve as good indicators of climate change (Debinski et al., 2000; Debinski et al., 2006; Parmesan, 2006). They are thought to be good indicators because they play important roles within different functional groups, including herbivores, pollinators, and prey and their distribution patterns are correlated with habitat diversity (Scalercio et al., 2006). Conservation concerns have been heightened by long-term studies in Europe that have shown butterfly communities to be declining (Thomas and Albery, 1995; Grill and Cleary, 2003; and Binzenhofer et al., 2005). Understanding what is causing this decline could lead the way to uncoupling the loss of species diversity and protecting the diversity of other taxa that share the butterfly habitat.

There are many factors that have been identified to have a negative effect on butterfly communities. Loss of suitable habitat is one of the most threatening factors for butterfly species persistence (Grill and Cleary, 2003). Changes in habitat suitability due to climatic variations can also affect butterfly abundance (Ockinger et al., 2006). The pristine nature and minimal human impacts in the Greater Yellowstone Ecosystem make it an ideal location for studying the effects of climate driven variation on butterfly communities.

In this study we hope to determine whether the butterfly communities in the Greater Yellowstone Ecosystem fluctuate predictably relative to alterations of climate driven changes along a hydrologic gradient in the landscape. Climate driven variables include temperature and precipitation fluctuations, and the effects of such changes on species of forbs that serve as host

plants and nectar resources for butterflies in this ecosystem. Shallow-rooted forbs are expected to be especially affected by an increase in temperature (Devalpine and Harte, 2001; and Saavedra et al., 2003; Cross and Harte, 2007) and a decrease in precipitation (Weaver, 1958) and we hypothesize that these changes will be reflected in butterfly abundance of the species that use these forbs for host plants or nectar. Stability in the butterfly community will be examined at different levels from a hierarchical perspective, including species presence and absences, abundance ranking, and absolute abundance (Pimm, 1984; Lawton and Gaston, 1989; Rahel, 1990). Groups of butterfly species using similar functional guilds of plants will be examined for correlated changes. Changes in floral resource cover and host plant percent cover will also be monitored to relate to changes in butterfly species abundance.

✦ METHODS

Study Area

The Greater Yellowstone Ecosystem was divided into two study regions for our project, which will be referred to as the Gallatin and the Teton regions. The Gallatin region includes 30 sites within the Gallatin National Forest and the northwestern portion of Yellowstone National Park in Montana. The Teton region has 25 sites within the Grand Teton National Park and Bridger Teton National Forest in Wyoming. The Gallatin and Teton regions are separated by 192 km, yet both have similar plant and butterfly communities (Su et al. 2004). The meadows selected for the surveys in both regions are approximately at the same elevation with homogenous topographic features. The average elevation for sites within the Gallatin region is 2098 m, and 2120 m in the Teton region. The meadows range from 1 – 7861 ha, with an average meadow patch of 500 ha. Six meadow types with distinct plant species were characterized, M1-M6, along a hydrologic gradient (hydric to xeric respectively) using satellite imagery (Jakubauskas et al., 1996). The Gallatin region has five replicates of each meadow type from M1-M6, and the Teton region has five replicates of each meadow type except meadows characterized as M4, which are not represented in the Teton region. The meadows were characterized as suitable for survey sites if they were within 8 km from a road or trail, a minimum of 100 m by 100 m and no more than 2 km on a side, as well as at least 500 m from another meadow site (Debinski et al., 2001).

Field Surveys

Field surveys were conducted during June through August for two week periods at each region, alternating between the two regions. Two surveys for each region were completed annually by early August. These surveys are part of a long-term study that was initiated in 1997 and continued through 2007. Sites were located in the field using written directions, topographic maps, and GPS coordinates to find the site marker stake within the meadow. In 1997, two randomly selected cardinal directions (NW, NE, etc.) were used for the placement of a 50 m x 50 m plot. This plot was annually measured and flagged so that every year the same area was sampled. Surveys were conducted on sunny days when the temperature is above 70^{o} F with low to moderate wind. The survey lasted for twenty minutes with two people surveying butterflies within the plot. Abundance data were collected by netting butterflies, collecting them in glassine envelopes, and finally releasing them at the end of the survey after individual butterflies were identified to the species level.

At each of the 55 study sites, vegetation was surveyed once per season in the middle of the growing season (July) in 20m x 20m plots which also had one corner of two cardinal directions located at the site marker stake. Cover estimates to 1% resolution were made for ten most dominant forb species in each plot. Nectar resources were quantified by counting the number of racemes for all flowering plant species along a 1 m wide transect positioned diagonally across the 50m x 50m butterfly survey plot and they were conducted on the same days as the butterfly surveys. To obtain climatic information we used two National Climate Weather Stations (240775: BigSky, and 486440: Moran 5WNW) to represent the GYE study regions. Daily precipitation and temperature data were obtained from these locations and summarized at an annual level. To detect trends in individual species over time, we will analyze the butterfly species for responses in both abundance and distribution across the hydrological gradient. Species with adequate sample sizes will be analyzed individually by meadow type using regressions to test for temporal trends and relationships with annual

climatic variables (e.g., average daily temperature, and precipitation) as well as host plant cover, and nectar resources.

✦ RESULTS

Here we provide an archive of some of these long-term data, including maps of the study sites (Figs. 1-2) with UTM locations, area, and elevation values for each site (Tables 1-2). We also include a report summarizing the overall abundance by species within each of the two study regions based upon data standardized to two surveys at each site per year across 5 years between 1997-2007 (Tables 3-4). Future reports will summarize the butterfly community trends relative to host plant, nectar, and environmental variables (temperature and precipitation).

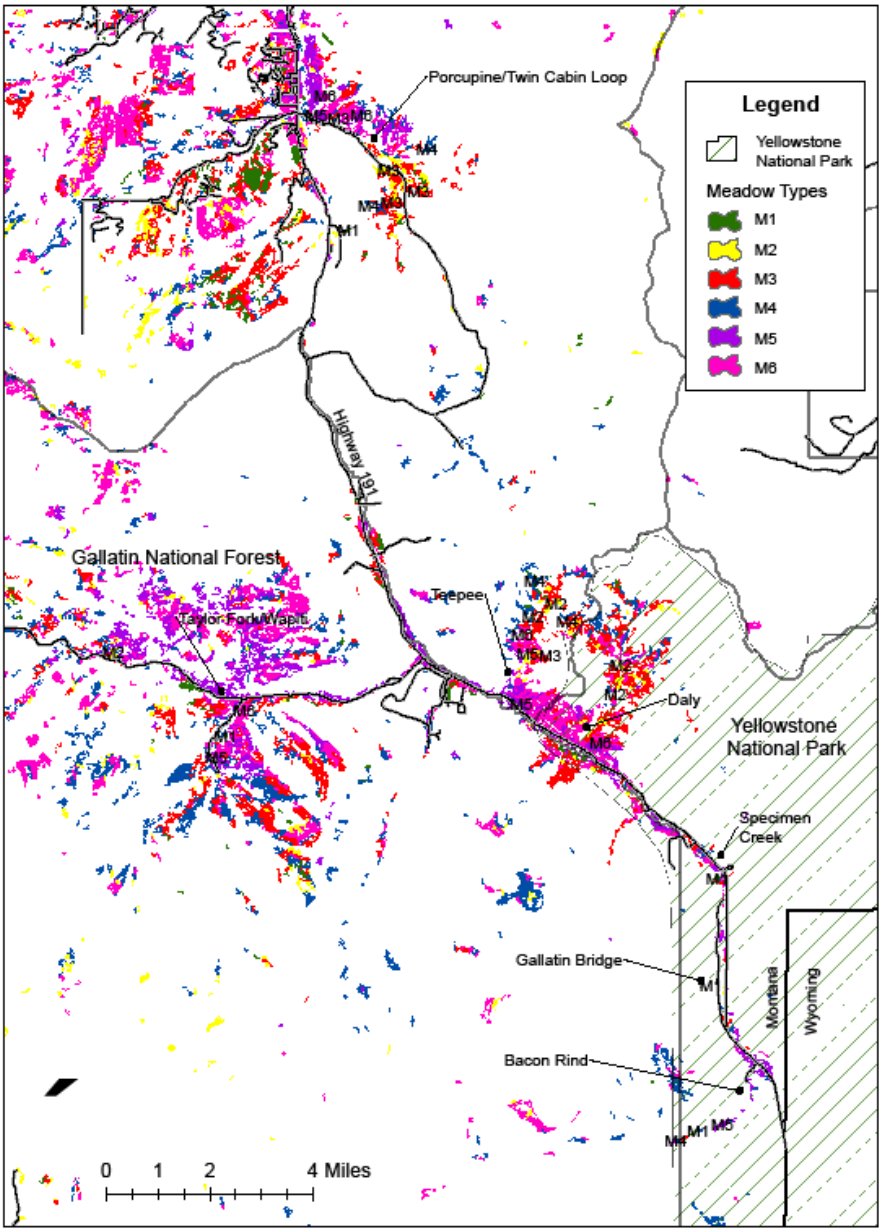

Figure 1. Gallatin Study Region including 30 long-term montane meadow survey sites. M1 meadows are hydric, M3 mesic and M6 meadows are xeric.

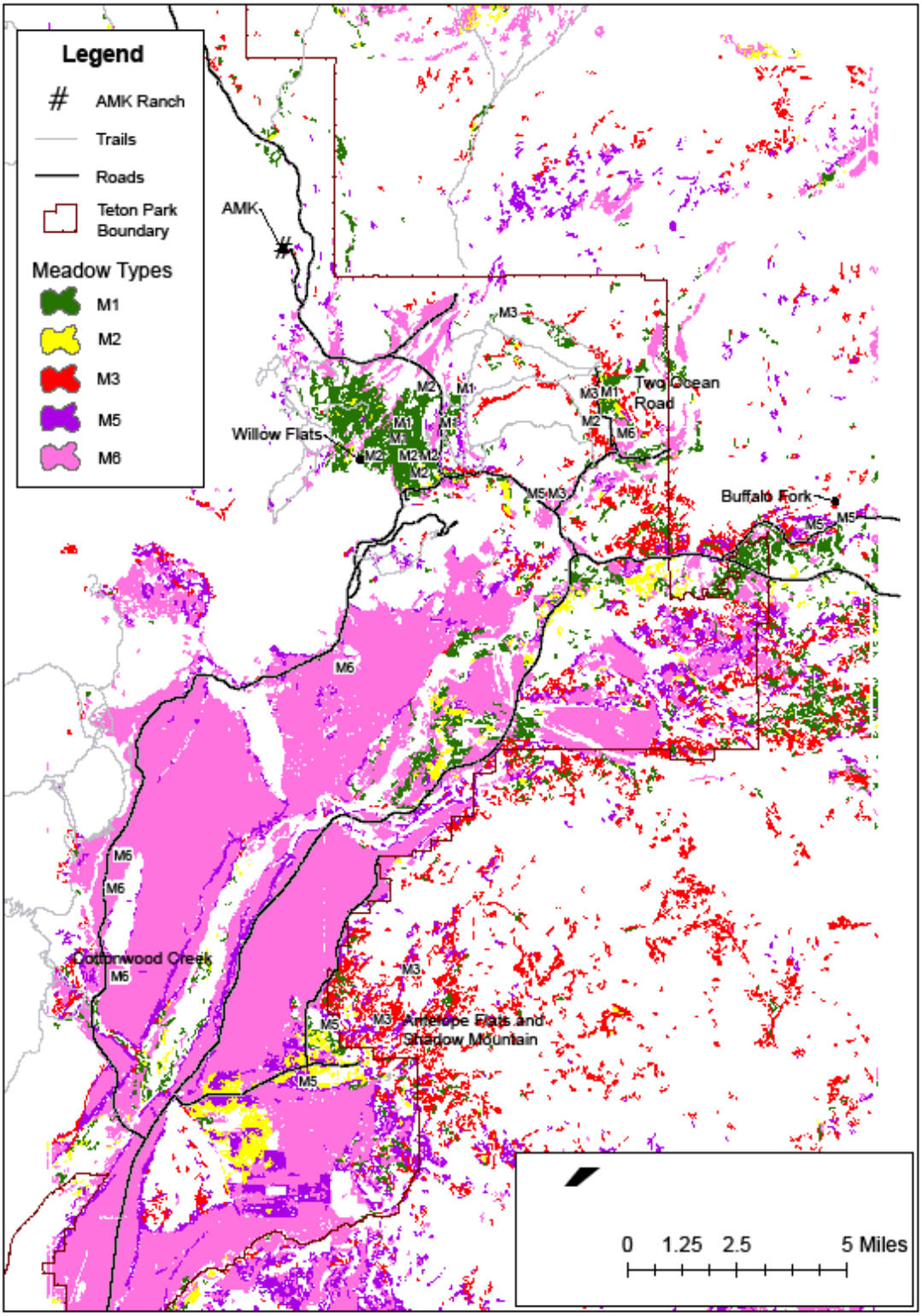

Figure 2. Teton Study Region including 25 long-term montane meadow survey sites. M1 meadows are hydric, M3 mesic and M6 meadows are xeric. M4 meadows are not present in the Teton region.

Region	Site #	Site Name	UTM Northing	UTM Easting	Elevation (ft)	Area (ha)
Gallatins	GM1A	Twin Cabin Willows	5004420	482077	6424	1.63
	GM1B	Bacon Rind	4975875	492784	7313	1.39
	GM1C	Specimen Creek	4983802	493514	6935	1.72
	GM1D	Wapiti (Taylor Fork)	4988439	478165	7050	1.05
	GM1E	Gallatin Bridge	4979476	493792	7060	~1.00**
	GM2A	Taylor Fork	4991010	474842	7080	4.00
	GM2B	Teepee Wet	4992350	488203	7152	3.97
	GM2C	Daly South	4990032	490471	7047	5.73
	GM2D	Figure 8	4992079	487750	7024	1.17
	GM2E	Daly North	4990504	490527	7109	3.02
	GM3A	Porcupine Exclosure	5007924	481627	6322	2.97
	GM3B	Black Bear Meadow	5004666	483472	7001	31.88
	GM3C	Porcupine/Twin Meadow	5005633	483988	6611	19.10
	GM3D	Porcupine Fork	5006304	483518	6400*	10.00
	GM3E	V Meadow Teepee Creek	4990795	488003	6998	15.10
	GM4A	Twin Cabin Pass	5004902	483106	6909	5.77
	GM4B	Porcupine 1.5 Creek	5006757	484573	6680	11.60
	GM4C	Teepee	4992771	487906	7237	11.65
	GM4D	Teepee East Feeder Stream	4991767	488234	7231	5.54
	GM4E	Bacon Rind	4975686	492264	7342	2.53
	GM5A	Bacon Rind M5	4976074	493441	7290	10.15
	GM5B	Porcupine M5	5007844	481033	6224	10.25
	GM5C	Wapiti Cabin	4987714	477806	7175	10.19
	GM5D	Teepee 191	4989358	487389	6722	19.11
	GM5E	Teepee Sage	4990752	487377	6883	2.48
	GM6A	Porcupine 3rd Creek	5007623	482059	6375	25.44
	GM6B	Wapiti Pond	4989242	478620	6942	55.87
	GM6C	Daly	4988125	489568	6800*	20.54
	GM6D	Teepee Burn	4991416	487553	7047	21.09
	GM6E	Gallatin Cabin	5008449	481177	6184	5.62

* Elevation taken from 7.5 min USGS map

** Estimated area value

Table 1. Study site locations and descriptions for the Gallatin region. UTM (Universal Transverse Mercator) coordinates as well as elevation and area of the meadow each site are listed for each site. Elevation and UTM data are based on readings from GPS (Magellan) during 2006 with accuracy within 20 meters.

Region	Site #	Site Name	UTM Northing	UTM Easting	Elevation (ft)	Area (ha)
Tetons	TM1A	Jackson Lodge Willow North	4859445	533499	6863	548.08*
	TM1B	Jackson Lodge Willow South	4858850	533656	6830	548.08*
	TM1C	Grand View	4859989	534803	6883	53.65
	TM1D	Two Ocean Road	4859500	540316	6909	77.85
	TM1E	Jackson Dam	4857743	532539	6811	548.08*
	TM2A	Willow Flats North	4857576	533684	6801	1.75
	TM2B	Willow Flats South	4857071	533741	6784	2.06
	TM2C	Two Ocean Road	4859177	539992	6988	5.82
	TM2D	Christian Pond	4858777	534780	6853	1.64
	TM2E	Cygnet Pond	4860372	530345	6880	1.08
	TM3A	Two Ocean Lake	4862882	536736	6958	7.74
	TM3B	Two Ocean Road	4859928	540060	6991	35.54
	TM3C	Lozier Hill	4856601	538763	6837	12.45
	TM3D	Shadow Mountain Hairpin	4838220	532801	7851	119.62
	TM3E	Sound Of Music	4839404	533446	8175	3.32
	TM5A	Lozier Hill	4856428	537905	6853	13.38
	TM5B	Buffalo Fork West	4855233	548289	7048	54.47
	TM5C	Buffalo Fork East	4855564	549366	6952	6.91
	TM5D	Antelope Flats	4835685	528705	6745	76.03
	TM5E	Shadow Mountain Base	4837479	530133	6801	23.71
	TM6A	Two Ocean Road	4858336	540888	6886	65.78
	TM6B	Cow Lake	4851603	532596	6926	2805.39
	TM6C	Timbered Island Northwest	4838381	522773	6801	4801.85**
	TM6D	Timbered Island Southwest	4841752	522279	6801	4801.85**
	TM6E	Cottonwood Creek	4838382	522770	6673	4801.85**

* One M1 meadow

** One M6 meadow

Table 2. Study site locations and descriptions for the Teton Region. UTM (Universal Transverse Mercator) coordinates as well as elevation and area of the meadow each site are listed for each site. Elevation and UTM data are based on readings from GPS (Magellan) during 2006 with accuracy within 20 meters.

Table 3. Abundance for each butterfly species observed in the Gallatin Region for the years: 1997, 1998, 2000, 2001, 2006, and 2007 totaled over all years, sites and replicates.

Species Latin Names	Species Common Names	Total Abundance
Agriades glandon	Arctic Blue	39
Anthocharis sara stella	Stella Sara Orangetip	18
*Boloria freija**	Freija Fritillary	2
Boloria frigga	Frigga Fritillary	4
Boloria kriemhild	Relict Fritillary	97
*Boloria montinus**	Purplish Fritillary	1
Boloria selene	Silver-bordered Fritillary	39
Callophrys sheridanii	Sheridan's Hairstreak	2
Cercyonis oetus	Small Wood-Nymph	592
Cercyonis sthenele	Great Basin Wood-Nymph	1
Chlosyne palla	Northern Checkerspot	36
Coenonympha haydenii	Hayden's Ringlet	1579
Coenonympha tullia inornata	Inornate Common Ringlet	93
Colias alexandra	Queen Alexandra's Sulphur	2
Colias christina	Christina's Sulphur	11
Colias eurytheme	Orange Sulphur	1
Colias gigantea	Giant Sulphur	17
Colias pelidne	Pelidne Sulphur	22
Colias philodice	Clouded Sulphur	61
Danaus plexippus	Monarch	2
Erebia epipsodea	Common Alpine	659
Euchloe ausonides	Large Marble	126
Euphilotes enoptes ancilla	Dotted Blue	27
Euphydryas chalcedona	Variable Checkerspot	20
Euphydryas editha	Edith's Checkerspot	17
Euphydryas gillettii	Gillett's Checkerspot	18
Glaucopsyche lygdamus	Silvery Blue	216
Glaucopsyche piasus	Arrowhead Blue	3
Limenitis weidemeyerii	Weidemeyer's Admiral	2
Lycaeides idas	Northern Blue	18
Lycaeides melissa	Melissa Blue	92
Lycaena cupreus	Lustrous Copper	1
*Lycaena dione**	Gray Copper	1
Lycaena editha	Edith's Copper	105
Lycaena helloides	Purplish Copper	488
Lycaena heteronea	Blue Copper	160
Lycaena hyllus	Bronze Copper	2
Lycaena mariposa	Mariposa Copper	9
Lycaena nivalis	Lilac-bordered Copper	7
Nymphalis antiopa	Mourning Cloak	4
Nymphalis californica	California Tortoiseshell	2
Nymphalis milberti	Milbert's Tortoiseshell	3
Oeneis chryxus chryxus	Brown Chryxus Arctic	29
Oeneis uhleri	Uhler's Arctic	1

Table 3. (continued)

Species Latin Names	Species Common Names	Total Abundance
Papilio eurymedon	Pale Swallowtail	1
*Papilio machaon**	Old World Swallowtail	5
Papilio rutulus	Western Tiger Swallowtail	2
Papilio zelicaon	Anise Swallowtail	21
Parnassius clodius	Clodius Parnassian	53
Parnassius phoebus smintheus	Rocky Mountan Phoebus Parnassian	121
Phyciodes campestris	Field Crescent	504
*Phyciodes mylitta**	Mylitta Crescent	107
Phyciodes selenis	Northern Crescent	27
Phyciodes tharos	Pearl Crescent	13
Pieris napi marginalis	Margined Mustard White	83
Pieris napi oleracea	Mustard White	27
Pieris rapae	Cabbage White	3
Plebejus icarioides	Boisduval's Blue	726
Plebejus lupini	Lupine Blue	40
Plebejus saepiolus	Greenish Blue	366
Plebejus shasta	Shasta Blue	13
*Polygonia faunus**	Green Comma	4
*Polygonia gracilis**	Hoary Comma	2
*Polygonia satyrus**	Satyr Comma	1
Pontia beckerii	Becker's White	9
Pontia occidentalis	Western White	7
Pontia protodice	Checkered White	19
*Satyrium titus**	Coral Hairstreak	1
Speyeria atlantis hesperis	Hesperis Atlantis Fritillary	95
Speyeria callippe	Callippe Fritillary	37
Speyeria cybele	Great Spangled Fritillary	1
Speyeria egleis	Great Basin Fritillary	15
Speyeria hydaspe	Hydaspe Fritillary	8
Speyeria mormonia	Mormon Fritillary	879
Speyeria zerene	Zerene Fritillary	21
Vanessa cardui	Painted Lady	98

* Butterfly Species only found only in Gallatin Region butterfly surveys.

Table 4. Abundance for each butterfly species observed in the Teton Region for the years: 1997, 1998, 2000, 2001, 2003-2007 totaled over all years, sites and two replicates.

Species Latin Names	Species Common Names	Total Abundance
Agriades glandon	Arctic Blue	45
Anthocharis sara stella	Stella Sara Orangetip	10
Boloria frigga	Frigga Fritillary	67
Boloria kriemhild	Relict Fritillary	74
Boloria selene	Silver-bordered Fritillary	167
*Callophrys dumetorum***	Bramble Hairstreak	18
Callophrys sheridanii	Sheridan's Hairstreak	13
Cercyonis oetus	Small Wood-Nymph	492
*Cercyonis pegala***	Common Wood-Nymph	2
Chlosyne palla	Northern Checkerspot	55
Coenonympha haydenii	Hayden's Ringlet	692
Coenonympha tullia inornata	Inornate Common Ringlet	593
Colias alexandra	Queen Alexandra's Sulphur	6
Colias christina	Christina's Sulphur	4
Colias eurytheme	Orange Sulphur	2
Colias gigantea	Giant Sulphur	69
*Colias interior***	Pink-Edged Sulphur	17
Colias pelidne	Pelidne Sulphur	26
Colias philodice	Clouded Sulphur	42
Erebia epipsodea	Common Alpine	605
Euchloe ausonides	Large Marble	80
Euphilotes enoptes ancilla	Dotted Blue	73
Euphydryas chalcedona	Variable Checkerspot	45
Euphydryas editha	Edith's Checkerspot	24
Euphydryas gillettii	Gillett's Checkerspot	6
*Euptoieta claudia**	Variegated Fritillary	1
Glaucopsyche lygdamus	Silvery Blue	101
Glaucopsyche piasus	Arrowhead Blue	29
Limenitis weidemeyerii	Weidemeyer's Admiral	12
Lycaeides idas	Northern Blue	56
Lycaeides melissa	Melissa Blue	62
Lycaena cupreus	Lustrous Copper	13
Lycaena editha	Edith's Copper	81
Lycaena helloides	Purplish Copper	239
Lycaena heteronea	Blue Copper	475
Lycaena hyllus	Bronze Copper	37
Lycaena nivalis	Lilac-bordered Copper	68
*Lycaena phlaeas***	American Copper	1
*Lycaena rubidus***	Ruddy Copper	1
Nymphalis antiopa	Mourning Cloak	7
Nymphalis californica	California Tortoiseshell	1
Nymphalis milberti	Milbert's Tortoiseshell	7
Oeneis chryxus chryxus	Brown Chryxus Arctic	12
*Oeneis jutta***	Jutta Arctic	3

Table 4. (continued)

Species Latin Names	Species Common Names	Total Abundance
Oeneis uhleri	Uhler's Arctic	1
*Papilio canadensis***	Canadian Tiger Swallowtail	7
Papilio eurymedon	Pale Swallowtail	3
Papilio rutulus	Western Tiger Swallowtail	21
Papilio zelicaon	Anise Swallowtail	27
Parnassius clodius	Clodius Parnassian	38
Parnassius phoebus smintheus	Rocky Mountan Phoebus Parnassian	9
Phyciodes campestris	Field Crescent	79
Phyciodes selenis	Northern Crescent	266
Phyciodes tharos	Pearl Crescent	5
Pieris napi marginalis	Margined Mustard White	42
Pieris napi oleracea	Mustard White	7
Pieris rapae	Cabbage White	5
Plebejus icarioides	Boisduval's Blue	1305
Plebejus lupini	Lupine Blue	202
Plebejus saepiolus	Greenish Blue	827
Plebejus shasta	Shasta Blue	21
Pontia beckerii	Becker's White	3
Pontia occidentalis	Western White	5
Pontia protodice	Checkered White	17
Satyrium sylvinus	Coral Hairstreak	1
Speyeria atlantis hesperis	Hesperis Atlantis Fritillary	6
Speyeria callippe	Callippe Fritillary	126
Speyeria cybele	Great Spangled Fritillary	41
*Speyeria edwardsii***	Edwards's Fritillary	3
Speyeria egleis	Great Basin Fritillary	10
Speyeria hydaspe	Hydaspe Fritillary	8
Speyeria mormonia	Mormon Fritillary	596
Speyeria zerene	Zerene Fritillary	28
*Vanessa annabella***	West Coast Lady	1
*Vanessa atalanta***	Red Admiral	2
Vanessa cardui	Painted Lady	74

** Butterfly Species only found only in Teton Region butterfly surveys.

✦ CONCLUSIONS

The benefits of a long-term data set increase our probability of detecting climate driven population fluctuations. Many studies on butterfly populations only observe the communities for two to three years and extrapolate trends with little assurance that their observed patterns identify community patterns (Hill et al., 1995; Spitzer et al., 1997; Gutierrez and Menendez, 1998). Previous work in the GYE system has shown that the different meadow types have distinct plant communities (Jakubauskas et al., 2001; Kindscher et al., 1998) as well as predictable butterfly communities that associate with each of these meadows established along a hydrologic gradient (Debinski et al., 2002). Recent analysis of the plant community in our study sites shows that the forb cover in many of the meadow types has decreased from 1997 to 2007 (Debinski, unpublished data), particularly in the mesic to xeric meadow types. Butterfly communities may also be showing shifts (Debinski, unpublished data). Our next steps

will be to analyze butterfly trends with respect to changes in both the plant cover and abiotic data such as temperature and precipitation. Understanding climatic influences on butterfly communities will provide a window into understanding larger ecosystem responses to long-term drought in the GYE

✦ LITERATURE CITED

Binzenhofer, B., B. Schroder, B. Strauss, R. Biedermann and J. Settele. 2005. Habitat models and habitat connectivity analysis for butterflies and burnet moths – the example of *Zygaena carniolica* and *Coenonympha arcania*. Biological Conservation 126: 247-259.

Cross-Smith, M. and J. Hart. 2007. Compensatory responses to loss of warming-sensitive plant species. Ecology 88:740-748.

Debinksi, D. M., C. Ray and E.H. Saveraid. 2001. Species diversity and the scale of the landscape mosaic:do scales of movement and patch size affect diversity? Biological Conservation 98:179-190.

Debinski, D. M. and Brussard, P.F. 1994. Using biodiversity data to asses species-habitat relationships in Glacier National Park, Montana. Ecological Applications 4: 833-843.

Debinski, D.M., M.E. Jakubauskas and K. Kindscher. 2000. Montane meadows as indicators of environmental change. Environmental Monitoring and Assessment 64: 213-225.

Debinski, D.M., R.E. VanNimwegen and M.E. Jakubauskas. 2006. Quantifying relationships between bird and butterfly community shifts and environmental change. Ecological Applications 16 (1): 380-393.

Debinski, D.M., M.E. Jakubauskas, K. Kindscher, E.H. Saveraid and M. Borgognone. 2002. Predicting meadow communities and species occurrences in the Greater Yellowstone Ecosystem. P. 499-506. *In* Predicting Species Occurrences: Issues of Scale and Accuracy (Scott, J.M., P.J. Heglund, M. Morrison, M. Raphael, J. Haufler, B. Wall, editors). Island Press. Covello, CA.

Dennis, R.L.H., T.G. Shreeve, N.J.B. Isaac, P.B. Hard, R. Fox and J. Asher. 2006. The effects of visual apparency on bias in butterfly recording and monitoring. Biological Conservation 128: 486-492.

DeValpine, P. and J. Harte. 2001. Plant response to experimental warming in a mountain meadow. Ecology 82: 637-648.

Field, R.G., T. Gardiner, C.F. Mason, and J. Hill. 2006. Countryside stewardship scheme and butterflies: a study of plant and butterfly species richness. Biodiversity and Conservation 15:443-452.

Grill, A. and D.F.R. Cleary. 2003. Diversity patterns in butterfly communities of the Greek native reserve Dadia. Biological Conservation 114: 427-436.

Gutierrez, D. and R. Menendez. 1998. Stability of butterfly assemblages in relation to the level of numerical resolution and altitude. Biodiversity and Conservation 7: 967-979.

Hill, J. K., C. Hamer, L.A. Lace and W.M.T. Bunham. 1995. Effects of selective logging on tropical forest butterflies on Buru Indoneisa. Journal of Applied Ecology 32: 754-760.

Kindscher K., A. Fraser, M.E Jakubauskas, and D.M. Debinski. 1998. Identifying wetland meadows in Grand Teton National Park using remote sensing and average wetland values. Wetlands Ecology and Management 5:265-273.

Jakubauskas, M.E., D.M. Debinski and K. Kindscher. 1996. Integration of multispectral and ecological data for characterizing montane meadow communities in the Greater Yellowstone Ecosystem. IEEE 2300-2302.

Jakubauskas, P., K. Kindscher, and D.M. Debinski. 2001 Hyperspectral remote sensing of nonforested montane vegetation communities. Third International

Conference on Geospatial Information in Agriculture and Forestry. Denver, Co. Nov 5-7.

Lawton, J.H. and K.J. Gaston 1989. Temporal patterns to the herbivorous insects of bracken: a test of community predictability. Journal of Animal Ecology 58: 1021-1034.

Nally, R.M., E. Fleishman, J.P. Fay and D.D. Murphy. 2003. Modeling butterfly species richness using mesoscale environmental variables: model construction and validation for mountain ranges in the Great Basin in Western North America. Biological Conservation 110: 21-31.

Ockinger, E., 0. Hammerstedt, S.G. Nilsson and H.G. Smith. 2006. The relationship between local extinctions of grassland butterflies and increased soil nitrogen levels. Biological Conservation 128: 564-573.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecological. Systematics. 37: 637-669.

Pimm, S.L. 1984. Complexity and stability of ecosystems. Nature 307: 321-326.

Rahel, F.J. 1990. The hierarchical nature of community persistence: a problem of scale. American Naturalist 136: 328-344.

Saavedra, F., D.W. Inouye., M.V. Price and J. Harte. 2003 Changes in flowering and abundance of *Delphinium nuttallianum* (Ranunculaceae) in response to a subalpine climate warming experiment. Global Change Biology 9: 885-894.

Scalercio, S.R. Pizzollotto and P. Brandmayr. 2007. Multi-scale analysis of butterfly diversity in a Mediterranean mountain landscape: mapping and evaluation of community vulnerability. Biodiversity and Conservation 16(12): 3463-3479.

Simonson, S.E., P.A. Opler, T.J. Stohlgren and G.W. Chong. 2001. Rapid assessment of butterfly diversity in a montane landscape. Biodiversity and Conservation 10: 1369-1386.

Spitzer, K.,J. Jaros, J. Havelka, and J. Leps. 1997. Effects of small-scale disturbance on butterfly communities of an Indochinese montane rainforest. Biological Conservation 80: 9-15.

Su, J.C., D.M. Debinski and K. Kindscher. 2004. Beyond species richness: Community similarity as a measure of cross taxon congruence for Coarse-Filter Conservation. Conservation Biology 18: 167-173.

Thomas, C.D. and I.S.G. Abery. 1995. Estimating rates of butterfly decline from distribution maps: the effects of scale. Biological Conservation 73: 57-65.

Weaver, J.E. 1958. Classification of root systems of forbs of grassland and a consideration of their significance. Ecology 39 (3): 393-401.

QUANTIFYING EARLY INDICATORS OF GLOBAL CLIMATE CHANGE

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✦ RESEARCH SUMMARY

One of the more significant voids remaining in our scientific understanding of global climate change is the relationship between climate change and the resulting changes expected in ecological communities. Because a large proportion of the North American landscape has been modified by human activities, it is difficult to assess whether ecological changes are being caused by human activities or climate change. Thus, we must look to landscapes where the modification has been less severe. One of the most pristine landscapes in North America where scientists can study natural processes is that of the Greater Yellowstone Ecosystem. Within this system some of the more sensitive habitats are the montane meadows. These habitats exist along a continuum from very dry (xeric) sagebrush meadows, to flowering (mesic) meadows, to wet (hydric) sedge meadows. Because of the relatively short growing season, species in these meadows can exhibit quick changes in distribution and abundance relative to climatic changes. My research uses satellite images and field surveys to evaluate how meadow habitats and their associated species respond to interannual changes in precipitation and soil moisture. I am examining the plant and butterfly communities to measure the response. Over 100 species of butterflies occur in this area and many are closely associated with specific types of meadows. This research is significant because it will provide an early warning system for assessing the effects of climate change. Documenting changes in montane meadows will assist in understanding how climate change may affect more highly managed areas of the globe.

The research sites include 55 relatively low elevation (2000-2500m) montane meadows arrayed along a hydrological gradient (M1-M6). We focused our work on low elevation meadows (2000-2500 m), to maximize replication by meadow type and to avoid introducing another environmental gradient (elevation) into our analysis. M1 meadows are hydric with willow (*Salix* spp.) thickets. M2 meadows are sedge (*Carex* spp.) marshes. M3 – M4 meadows are mesic and characterized by a forb-grass coverage. M5 meadows have a mixture of sagebrush (*Artemisia tridentata*) and herbaceous vegetation. M6 meadows are the most xeric in our hydrological gradient, and sagebrush and bare ground are dominant components of cover. We established 55 core sampling sites (minimum of 1 ha in size and the selected sites were as flat as possible to avoid introducing the influence of slope or aspect as a variable); 30 sites were located in the Gallatin region (Gallatin National Forest and the northwest section of Yellowstone National Park - 5 of each of 6 meadow types), and 25 sites were located in the Teton region (Grand Teton National Park and Bridger Teton National Forest - 5 of each meadow type except for M4 meadows, which are not found there). Sites were located a minimum of 500 m apart. These "core sites" were sampled annually for plants, butterflies, and birds from 1997-2001. During 2002-2005, we sampled only the bird and butterfly communities in the 25 Teton sites due to limited funding. NSF LTREB funding supported field research focused on the plant and butterfly community during 2006. Below is a summary of the research goals and objectives and some of the preliminary results.

✦ PROJECT GOAL

My goal is to determine how interannual variability in precipitation and soil moisture affects montane meadow communities of plants and butterflies. The *central hypothesis* for the research is that meadow type and species distribution patterns are particularly sensitive to climate variations (e.g., precipitation, soil moisture) at a local level. Thus, the combination of changes in remotely sensed imagery, soil moisture and species composition may provide us with short-term indications (at the level of 1-3 years) of how climatic variation is manifested in this extreme environment. These short-term indicators can then be used to track longer-term changes. I have formulated this hypothesis based upon preliminary findings suggesting that montane meadows exhibit variations in remotely sensed classification as a response to interannual variability of climate. The *rationale* for the proposed research is that I will be able to determine whether climate variability is affecting ecological communities. I am testing this central hypothesis via the following objectives and associated working hypotheses:

Objective 1: Conduct a pilot test to assess the soil moisture in a subset of each of the meadow types along the hydrological gradient. Variation in soil moisture is the mechanism that I hypothesize is driving changes in this landscape. During 2006, field-based soil moisture probes were tested for assessing differences in soil moisture across the meadow gradient. *Working hypothesis 1: Interannual variations in precipitation are capable of causing significant changes in local soil moisture.*

Objective 2: Identify plant species that show sensitivity to climate variability as manifested as changes in their distribution and abundance. I am using data from 1997-2006 to examine how interannual climate variability affects plant communities. *Working hypothesis 2: Plant species will show interannual shifts in percent cover that are correlated with changes in soil moisture.* Because the plant community within each of the meadow types contains a mixture of species with different tolerances for moisture, there is potential for short-term change in perennial plant communities based on the vigor of each of the species. Annual species existing in the seed bank will also have the potential to either flourish or become desiccated depending upon their moisture tolerances and the underlying soil moisture.

Objective 3: Identify butterfly species that show sensitivity to climate variability as manifested as changes in their distribution and abundance. The changes in the plant community will be reflected in the butterfly community based upon species-specific changes in habitat utilization. Because butterflies move freely throughout the landscape, they can focus on important sites for nectar or host plants. As changes occur in the plant community, butterflies will move within the landscape mosaic among meadow types. *Working hypothesis 3: Butterfly species will show interannual shifts in distribution and abundance along the hydrological gradient that are correlated with changes in soil moisture.* For example, xeric species may move into more mesic sites in a drier year.

✦ METHODS

Regional Weather Data: We will quantify broad-scale changes in precipitation and temperature over time using two national climate weather stations (240775: Big Sky and 486440: Moran 5WNW) to represent the two GYE study regions.

Soil Moisture assessment: Soil moisture meters were installed at one meadow of each type within each sampling region (for a total of 11 sites) in 2006. These meters were monitored and soil samples were taken from each site to calibrate the meters, but there were several problems with animals digging up and disturbing the meters.

Vegetation and Nectar Surveys: Vegetation was surveyed once per season in the middle of the growing season (July) using the 20x20m long-term survey plots. Cover estimates were made to 1% resolution for the 10 most predominant forb species and woody plant by genus. Grasses, rushes, and sedges (graminoids) were surveyed as a group. Plants will be analyzed for changes in percent cover within

each of the following functional groups: shallow-rooted forbs, deep-rooted forbs, graminoids, and shrubs. Nectar resources will be quantified by counting the number of racemes for all nectar species along a 1 m wide transect positioned diagonally across the 50x50m butterfly survey plot on the day of the butterfly survey.

Butterfly Species Characterization in Sample Sites: Abundance data were collected annually for butterflies in each of the sampling sites from June to early-August. Butterflies were surveyed twice/season at each of these sites and sampling was temporally spaced to cover the two major emergence periods within the summer. Surveys occurred between 0930-1630 hrs with two people netting for 20 minutes in 50x50 m plots at each sampling site. Surveys were limited to times when temperature was above 70 F, wind was less than 16 km/hr. Vouchers were pinned where necessary for ID.

✦ PRELIMINARY RESULTS

We have hypothesized that soil moisture is a major environmental driver in the montane meadow system, and we expect that changes in soil moisture will be differentially reflected across the moisture gradient of meadows and their associated plant and insect communities. We expect that with drying trends, forbs and grasses, which use water from higher in the soil horizon, will decrease in cover whereas woody plants will increase. Our data appear to support this hypothesis (Debinski, unpublished data). We are now in the process of analyzing the butterfly abundance trends over 1997-2006 by host plant preferences. We expect that those butterfly species associated with forbs and grasses will be more significantly affected by drought conditions and changes in percent host plant cover than those associated with woody species and may show greater interannual variance in abundance patterns. Thus, we expect asymmetric and potentially compensatory responses across the soil-plant-insect system. Our hierarchical framework will allow us to predict plant and insect species that may be especially sensitive to changes.

Our research thus far has shown that mesic montane meadows have the highest percent cover and diversity of forbs and exhibit the highest levels of variation of remotely sensed imagery both seasonally and interannually (Debinski *et al.* 2000; 2002). Remotely sensed data are correlated with variations in both soil moisture and vegetative biomass. During the past ten years (which is considered a time of drought) we have identified several important trends in our meadow plant communities. The butterfly community in hydric to mesic meadows showed changes in distributional patterns towards a state indicative of drier meadows (Debinski *et al.* 2006). Further, two hydric meadow species were missing from the Teton sites in 2004 (i.e., they were not seen in any of the 25 sites): *Boloria frigga*, and *Euphydryas gillettii*, a rare wetland habitat associate. Both species had been observed annually in these sites since 1997 and returned in 2005 and 2006. Such changes may be the random variations observed within one year, but they reinforce the importance of long-term data.

✦ LITERATURE CITED

Debinski, D.M., M.E. Jakubauskas and K. Kindscher. 2000. Montane meadows as indicators of environmental change. Environmental Monitoring and Assessment. 64:213-225.

Debinski, D.M., M.E. Jakubauskas, K. Kindscher, E.H. Saveraid and M. Borgognone. 2002. Predicting meadow communities and species occurrences in the Greater Yellowstone Ecosystem. Pp. 499-506 In: Scott, J.M., P.J. Heglund, M. Morrison, M. Raphael, J. Haufler, B. Wall, (ed.) Predicting Species Occurrences: Issues of Scale and Accuracy. Island Press. Covello, CA.

Debinski, D.M., R.E. VanNimwegen and M.E. Jakubauskas. 2006. Quantifying relationships between bird and butterfly community shifts and environmental change. Ecological Applications 16(1):380-39

GENERAL FLORISTIC SURVEY OF GRAND TETON NATIONAL PARK AND VICINITY, WYOMING

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✦ INTRODUCTION

A broad-scale floristic inventory of all vascular plants was proposed for Grand Teton National Park and the John D. Rockefeller Jr. Memorial Parkway (JDR) primarily to document the extant flora in remote backcountry areas. The Teton Mountains are floristically important because of the unique habitats which they contain, because their relatively undisturbed (human disturbance) condition, and because of their proximity to the Yellowstone Plateau, a floristically unique area of Wyoming. Many studies have explored these lands for purposes of vegetation characterization (Cogan et al. 2005, McCloskey 2006) though an explicit and complete plant inventory parkwide had never been undertaken.

We first examined the vascular plant specimen holdings of the Rocky Mountain Herbarium (RM) to assess spatially where the previous records were obtained. It was observed that some townships (36 square miles) within the Park had as little as 8 voucher collections and one partial township (8 square miles) had zero vouchers. This information again reinforced our focus on backcountry areas; we also chose to collect in frontcountry areas to document introduced plants and for sampling completeness. This report serves as the final product of this project yet the full species list is not included for space limitations.

✦ METHODS

A landscape-scale floristic inventory was conducted on Grand Teton National Park and the JDR, wholly within Teton County, Wyoming. The collection localities were often reached by hiking long distances from the trailhead. When the desired habitat was reached, geographic coordinates were recorded, then all vascular plants exhibiting fruits or flowers were collected. From such a starting point, we continued along the collecting path and collecting was designed to encompass the bulk of nearby plant habitats, often with a distant plant habitat as target. Target habitats were often chosen because of the high likelihood of rare or unusual plants they might contain (Hartman and Nelson 2005). Examples of target habitats in the project area were: alpine elevations, limestone substrates, neoglacial deposits, montane ponds, thermal areas, and wetlands. In the meander search/collecting path method described here, the highest number habitats are thought to be encountered for the unit time in the field.

About half of the collecting paths were in frontcountry areas or along trails. When covering these areas, an ample representation of introduced plants along with the native flora was expected. Nearly all of the rest of the collecting routes were off-trail in areas infrequently or never visited by humans.

Collected plants were pressed and dried for scientific vouchering and they were identified by Dave Scott at the Rocky Mountain Herbarium, Laramie, WY. The herbarium environment is conducive to correct identifications due to the availability of authenticated specimens and other taxonomic resources easily referenced there. Identifications for the families Apiaceae and Caryophyllaceae were verified by Ron Hartman, specialist in both families for western North American taxa. B. Ernie Nelson, RM manager verified all other important collections: 1) Wyoming Natural Diversity Database (WYNDD) sensitive species, 2) Teton County records (plants first documented in Teton County) and, 3) some taxa first documented in the Park under this project.

Each voucher includes associated scientific name and authority, plant habitat information, collector, date, (often) GPS coordinates, elevation, and land ownership fields. This information was produced for specimen labels in a Microsoft Access database and was conveyed to Grand Teton National Park, Science and Resource Management personnel upon completion.

✦ RESULTS

Overall, floristic diversity was captured by the high number of specimens collected across the Park and JDR in two field seasons during summers 2006 and 2007. Figure 1 illustrates the spatial extent of collections by displaying the 277 collection localities. The total number of herbarium quality collections was 5851 vouchers. As expected, multiple collections of certain taxa were obtained and for these common plants a better understanding of their distribution was attained. The total number of species documented was 869, and 912 taxa (includes subspecies/variety taxonomic level) were documented. A full set of vouchers now reside at the RM (on loan from the Park) for all taxa reported here. The USDA PLANTS database (Version 15 May 2008) was considered the taxonomic authority for the species list. As well as a full list of vascular plants collected, new populations of WYNDD taxa were revealed and newly documented WYNDD taxa previously unknown to the area were collected. Likewise, contributions of this study are 20 County records, and introduced species locations. A synopsis of these results follows.

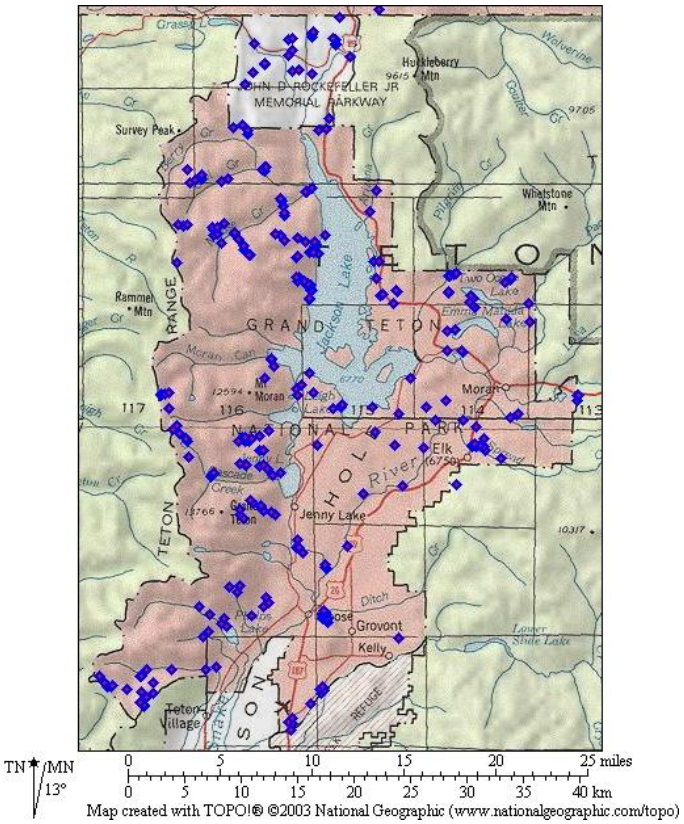

Figure 1. Collection localities from the floristic inventory of Grand Teton National Park and John D. Rockefeller Jr. Memorial Parkway. The diamond symbol indicates each locality; 277 unique GPS coordinates were recorded. Taxa either currently or historically tracked by WYNDD numbered 44 species (Table 1). The 2003 list was considered because it represented WYNDD species of conservation concern at the time we started this project. Further, the 2007 WYNDD list was produced using data from this project prior to its publication. Subsequently, it is useful to take into account both lists as they provide a context to judge species trajectories through time. Nine WYNDD taxa we collected were previously unknown to Grand Teton National Park or the JDR (Table 1).

Scientific name	Common name	2003 list	2007 list	2007 Heritage Rank	New to GRTE
Agrostis mertensii	Northern bentgrass	listed	listed	G5/S2	x
Antennaria aromatica	Aromatic pussytoes	potential concern	potential concern	G3G4/S3	
Aquilegia formosa	Crimson columbine	listed	listed	G5T5/SH	
Aspidotis densa	Pod-fern	listed	listed	G5/S1	
Asplenium trichomanes-ramosum	Green spleenwort	listed	listed	G4S2	
Astragalus shultziorum	Shultz's milkvetch	potential concern	potential concern	G3S3	
Astragalus terminalis	Railhead milkvetch	listed	listed	G3/S1	
Athyrium americanum	American alpine lady fern	listed	listed	G4G5T4T5/S2	
Botrychium minganense	Mingan moonwort	listed	listed	G4/S1	x
Botrychium multifidum	Leathery grape-fern	listed	deleted	G5/S3	
Carex cusickii	Cusick's sedge	listed	listed	G5/S2	
Carex echinata ssp. *echinata*	Little prickly sedge	listed	listed	G5/S1	
Carex incurviformis var. danaensis	Incurved sedge	listed	listed	G4G5T3/S2	x
Carex leptalea	Bristly-stalk sedge	listed	listed	G5/S2	
Carex limosa	Mud sedge	listed	listed	G5/S2	x
Carex livida	Livid sedge	listed	listed	G5/S2	x
Carex proposita	Smoky Mountain Sedge	listed	listed	G4/SH	x
Descurainia pinnata ssp. paysonii	Payson's tansymustard	listed	listed	G5T3?/S2	
Draba crassa	Thick-leaf Whitlow-grass	potential concern	potential concern	G3/S3	
Draba fladnizensis var. *pattersonii*	White arctic whitlow-grass	listed	listed	G4T2T3/S2	
Drosera anglica	English sundew	listed	listed	G5/S2	
Eleocharis flavescens var. *thermalis*	Warm springs spikerush	listed	listed	G5T2T3Q/S2	
Gentianopsis simplex	Hiker's gentian	listed	listed	G5/S1	x
Gymnocarpium disjunctum	Oak fern	listed	listed	G5/S2	
Huperzia haleakalae	Fir clubmoss	listed	listed	G4G5/S1	
Juncus filiformis	Thread rush	listed	listed	G5/S2	
Kelloggia galioides	Milk kelloggia	listed	listed	G5/S1	
Lesquerella carinata var. *carinata*	Keeled bladderpod	listed	listed	G3G4T3T4/S2	
Lesquerella paysonii	Payson's bladderpod	potential concern	potential concern	G3/S3	
Listera convallarioides	Broad-leaved twayblade	listed	listed	G5/S2	
Luzula glabrata var. *hitchcockii*	Smooth wood-rush	listed	listed	G5T4/S1	
Minuartia macrantha [*Minuartia filiorum*]	House's stitchwort	listed	listed	G3G4/S1	
Myriophyllum verticillatum	Whorled water-milfoil	listed	listed	G5/S1	x
Parnassia kotzebuei	Kotzebuei grass-of-parnassus	listed	listed	G5/S2	
Porterella carnosula	Western porterella	listed	listed	G4S1	
Sanicula graveolens	Sierra sanicle	listed	listed	G4G5/S2	x
Scirpus americanus	American bulrush	listed	listed	G5/S2	
Spirodela polyrhiza	Common water-flaxseed	listed	listed	G5/S1	
Stellaria crispa	Crimped stitchwort	listed	listed	G5/S1	
Utricularia minor	Lesser bladderwort	listed	listed	G5/S2	
Viola orbiculata	Western rough-leaved violet	listed	deleted	G5/S2	
Viola renifolia	Kidney leaf white violet	listed	listed	G5T5/S1	
Xerophyllum tenax	Western beargrass	listed	listed	G4G5/S1	

Table 1. Sensitive taxa tracked by Wyoming Natural Diversity Database (WYNDD) and encountered during the inventory. Taxa shown according to WYNDD Wyoming Plant and Animal Species of Concern list 2003 version (Keinath, et al.) and 2007 Wyoming Plant Species of Concern list (Heidel 2007).

Heritage Rank: WYNDD uses a standardized ranking system originally developed by The Nature Conservancy and its network of natural heritage programs (now coordinated by NatureServe [Arlington Virginia]) to indicate the probability of extinction, at both the global and state scales, of each plant and animal taxon. The following letters denote the spatial scale at which a taxon's status is scored:
G = Global rank: refers to the range-wide probability of extinction for a species
T = Trinomial rank: refers to the range-wide probability of extinction for a subspecies or variety
S = State rank: refers to probability of extinction from WY for a given taxon
These letters are each followed by a numeric, 1-5 score:
1 = Critically imperiled because of extreme rarity (often <5 extant occurrences) or because some factor makes it highly vulnerable to extinction
2 = Imperiled because of rarity (often 6-20 extant occurrences) or because of factors making it vulnerable to extinction
3 = Rare or local throughout its range or found locally in a restricted range (often 21-100 known occurrences)
4 = Apparently secure, although it may be quite rare in parts of its range, especially at the periphery
5 = Demonstrably secure, although it may be rare in parts of its range, especially at the periphery
Some 81 taxa were collected on Grand Teton National park or the JDR which had not been previously documented. This number includes the 9 WYNDD taxa mentioned above.

✦ DISCUSSION

Two State records were collected in Grand Teton National Park. One, *Achillea ptarmica* is an introduced cultivar found to be naturalized in irrigation ditches near the historical Whitegrass Ranch. These plants were found to be flowering in late summer (August) at only this single locality thus we recommended here that a more complete inventory of this species be carried out. This rhizomatous perennial indeed has potential to spread from the current habitat of irrigation ditches to natural riparian corridors.

A second species new to Wyoming is the native sedge, *Carex atrosquama*. It is not surprising to document this species because it has been collected in nearby Colorado, Idaho, Montana, and Utah. Western Wyoming, however, may be the eastern extent of this species' distribution. Habitat recorded for *Carex atrosquama* was a montane area in the lower South Fork of Granite Canyon. Though this is the first collection of this species in Wyoming, it may be more common than the lack of records indicate because sedges are often cryptic and repeatedly get overlooked.

Introduced plants comprised only 7.5% of the total taxa documented here. In fact most were already known from the Park, but we assert 9 new introduced taxa now documented due to this inventory. A few insidious species were: *Linaria vulgaris*, *Cirsium arvense*, and *Carduus nutans*, where the first two were often observed in montane backcountry areas. These two species probably represent the most invasive weeds in backcountry areas. Less invasive introduced taxa commonly observed in backcountry areas were: *Poa annua* on trails, *Crepis tectorum* in scoured streambeds, moist meadows or burned areas. Also, *Phleum pratense* was seen in a diversity of backcountry habitats and *Cerastium fontanum* ssp. *vulgare* was collected in remote riparian areas.

A biodiversity hotspot was observed near the Huckleberry Hot Springs in the JDR. Several native plants were exclusively collected there, though a significant suite of introduced plants were also found at that locality. The introduced species appear to be associated with walking paths adjacent the springs and should be controlled in the future, given their proximity to the thermal springs habitat that does provide for native biodiversity. Related to this topic is the exceptional native plant diversity of the JDR wetlands in general. Several species were only collected in these habitats and these areas display affinities to the flora of the Yellowstone Plateau (to the north), which is different than much of the flora of Grand Teton National Park.

✦ LITERATURE CITED

Cogan, D. and K. Varga, G. Kittel, K. McCloskey, D. Abendroth, J. Gremer, C. Bolen. 2005. Grand Teton National Park 2002-2005 vegetation mapping project final report. NPS-USGS Vegetation Mapping Program. U.S. Department of the Interior, Denver, CO.

Hartman, R.L. and B.E. Nelson 2005. General information for floristics proposals. Online:http://www.rmh.uwyo.edu/research/GeneralInformationforFloristicsProposals.pdf

Heidel, B. 2007. Wyoming plant species of concern list. Unpublished document. Wyoming Natural Diversity Database, Laramie, WY.

Keinath, D., and B. Heidel, G. Beauvais. 2003. Wyoming plant and animal species of concern. Unpublished document. Wyoming Natural Diversity Database, Laramie, WY.

McCloskey, K. J. 2006. Vascular plant species richness and distribution in a heterogeneous landscape. Ph. D dissertation, Utah State University, Logan.

GRAZING EFFECTS OF THE INVASIVE MUDSNAIL, *Potamopyrgus antipodarum* AND TWO NATIVE INVERTEBRATES

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✦ INTRODUCTION

Although many efforts are being made to address ecological impacts of invasive species, very little effort has been made to address the evolutionary impacts of biological invasions (Sakai *et al.* 2001, Cox 2004). Yet these impacts are likely to be widespread; invasive species have been shown to alter patterns of natural selection or gene flow (Parker *et al*. 1999), and many of the best examples of rapid evolution involve invasive species interacting with native species (Reznick and Ghalambor 2001, Strauss *et al.* 2006). Hence, I am addressing both the ecological and the potential evolutionary consequences of the invasive New Zealand mud snail, *Potamopyrgus antipodarum* on native benthic macroinvertebrates in the Greater Yellowstone Area (GYA).

Several characteristics of *Potamopyrgus antipodarum* make it a likely selective agent on native invertebrates. First, it has achieved very high densities in the invasive range (500,000/m^2 in some areas of the Greater Yellowstone Ecosystem; Hall *et al*. 2003) and dominates these communities (Kerans *et al.* 2005, Hall *et al.* 2006), suggesting *P. antipodarum* have a strong impact on the biotic and abiotic environment. In fact, Hall and colleagues (2003) showed that *P. antipodarum* consumed 75% of gross primary productivity, and Riley et al (*in review*) showed that they reduce periphyton biomass (the microscopic algae, fungi, and bacteria on substrata). Because the growth of individuals and populations of algivores can be limited by the abundance of algae (reviewed in Lamberti 1996), this consumption of the majority of resources by *P. antipodarum* is likely to have a negative effect on other benthic herbivores. Second, studies have shown either direct (Riley *et al*. *in review*, Krist and Dybdahl *in prep.*) or indirect (Kerans *et al.* 2005) evidence that *P. antipodarum* is competing with native invertebrates. These detrimental consequences to the fitness of native invertebrates may either reduce their population sizes or, with sufficient time and genetic variation, lead to evolutionary change in populations of natives.

In July 2006, I conducted a grazing experiment to determine which native species are most likely affected by *P. antipodarum*. I chose the native species based on availability and on recent studies that 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 *in review*, Krist and Dybdahl, *in prep*.). 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 Greater Yellowstone Ecosystem (Kerans *et al.* 2005).

In the experiment, I allowed grazers to consume periphyton on tiles that had been

colonized in the stream. By examining the periphyton remaining on the tiles after grazing and comparing it to the ungrazed control tiles, I could determine the extent of overlap in diet between *P. antipodarum* and the native species. Species with the greatest overlap in diet with *P. antipodarum* are the most likely to be affected by the invasion.

✦ METHODS

To obtain periphyton for our experiment, I placed unglazed tiles (23.5 cm^2 area) in Polecat Creek in early July 2006. Periphyton is a layer of algae, bacteria, and fungus in a non-living matrix that covers rocks and plants in freshwater. The tiles were attached to platforms that excluded benthic grazers (Lamberti and Feminella 1996). All platforms were placed in unshaded areas with similar flow regimes. The tiles were colonized with periphyton for 18 days.

In late July 2006, I collected *P. antipodarum*, a native snail *Fossaria sp.*, and the caddisfly *Brachycentrus* sp.. In each experimental unit, I placed a single tile with individuals of one of the species of grazers. The number of animals differed by species because I placed an equivalent amount of ash free dry mass in each chamber. I used length-mass regressions (Hall *et al*. 2006, Riley unpublished, Benke *et al.* 1999) to convert body length to ash free dry mass. I measured random samples of 20-30 individuals of each species to obtain a mean length for these regressions. I used the same biomass of *P. antipodarum* that had been shown to significantly depress biomass and chlorophyll *a* in a similar study (Winterbourn and Fegley 1989), but adjusted for the tile size and duration of the current experiment.

In addition to the three species, I included ungrazed controls containing a single tile and no animals. There were eight replicates for each treatment. I placed the experimental chambers in the stream and allowed the animals to graze for 48 hours. The chambers were placed at a depth that covered the animals and the tile but allowed some air at the top of the cage. The air pocket is required for the air-breathing snail *Fossaria* sp.

Experimental chambers were constructed from 156. 25 cm^2 square plastic storage containers. The plastic was removed from each side and top and replaced with nylon window screening (1.2 mm size pores). The screen allowed fresh water to flow through the chambers. I attached the chambers to a single brick by threading a 14 cm long bolt through a hole in the bottom of the chamber and attaching nuts and washers to the bottom of the brick to secure the two together.

At the end of the experiment, my field assistants and I removed all of the animals from each cage and scrubbed the remaining periphyton off of the tiles with brushes. I used the slurry to measure algal assemblage, chlorophyll *a*, and ash free dry mass (AFDM). We preserved 1 ml of the slurry in glutareldehyde to determine algal assemblage. I used vacuum filtration to concentrate 5 ml of the slurry onto a glass fiber filter (Pall A/E, 25 mm) to measure chlorophyll *a* and the remaining slurry onto a glass filter to measure AFDM.

I obtained pheophyton-corrected measures of chlorophyll *a* by extracting the chlorophyll *a* from the filters using buffered ethanol. Then, I measured absorbance with a flourometer before and after the addition of HCl. I measured AFDM of each sample as the difference between the dry mass (24 hours at 60° C) and the mass after ashing (1 hour at 500° C).

To determine algal assemblage, I made two kinds of slides. One type was used to identify non-diatom algae and the second type was used to identify diatoms. I diluted the solution to 4 ml with distilled water. To make the first type of slide, I used vacuum filtration to place a 3 ml sample onto a metrical membrane filter (Pall GN-6 grid, 25 mm) and mounted the filters on glass microscope slides using 2-hydroxypropyl methacrylate (HPMA) resin. Permanent mounts were made by drying the resin (24 hr at 60° C), mounting cover slips with additional resin and drying again (48 hrs at 60° C). To make the slides for identifying diatoms, I "cleaned" a subsample of the algal assemblage with bleach to remove all organic matter. This process empties the diatom exoskeleton (frustule) of organic matter, leaving the structure easier to observe. To identify the diatoms to genus, I made a few permanent slides of samples from each treatment. I added naphrax to a drop of the cleaned diatom sample, placed a coverslip over the solution and heated until bubbly. Diatom counts of the cleaned samples were made

in a Palmer Maloney cell. Diatoms were identified using several keys and references (Patrick and Reimer 1966; Prescott 1978; Lowe and Laliberti 1996).

To determine whether each species significantly reduced the concentration of chlorophyll *a* or biomass (AFDM), I used Welch's two sample t-tests to compare values for each species (treatment) to the controls. I used a Bonferroni correction for the p value because of multiple tests (p = 0.017).

✦ RESULTS

I found that all three species significantly reduced the amount of chlorophyll *a* (Figure 1). However, only the caddisfly *Brachycentrus* sp. marginally reduced the biomass of periphyton (Figure 2). Comparisons were made against the controls for each species with a Welch's two sample t-test.

After learning to identify and differentiate diatom genera, my student Caroline Charles counted two of the eight replicates per treatment. Preliminary analysis of these diatom assemblages revealed that the variance among samples was extremely high (e.g., Figure 3). Based on this initial analysis, I decided not to count the remaining six replicates per treatment (total 24 samples), and to repeat this study in the summer of 2007 with increased replication.

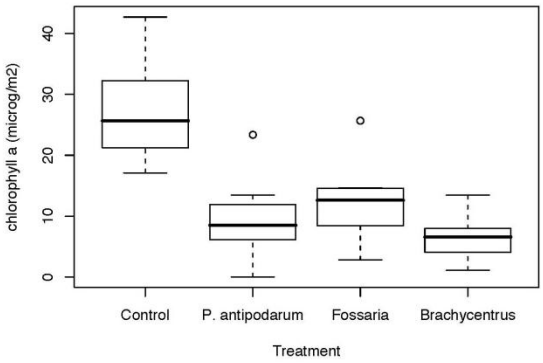

Figure 1. Concentration of chlorophyll a (μg/m2) on tiles measured among treatments of the experiment. Grazers were absent in the controls. Concentration of chlorophyll a was significantly lower than controls on tiles grazed by the invasive snail *P. antipodarum* (t = 4.00, df = 11.9, p = 0.002) the native snail *Fossaria* sp.(t = 3.90, df = 13.4, p = 0.002), and the caddisfly *Brachycentrus* sp.(t = 6.43, df = 9.7, p < 0.001).

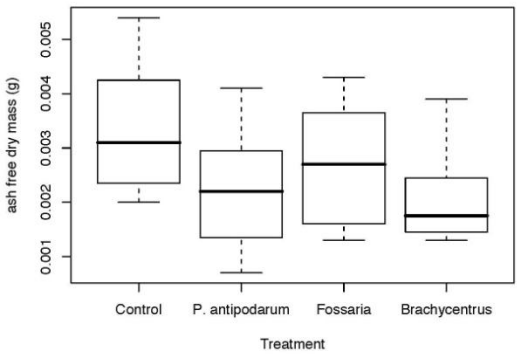

Figure 2. Ash free dry mass (g) on tiles measured among treatments of the experiment. Grazers were absent in the controls. Biomass was not significantly lower than controls for the invasive snail *P. antipodarum* (t = 1.80, df = 12.69, p = 0.096), and the native snail *Fossaria* sp.(t = 1.11, df = 14.0, p = 0.285), but was marginally decreased by the caddisfly *Brachycentrus* sp.(t = 2.46, df = 12.8, p = 0.029). I used a Bonferroni correction for the p value because of multiple tests (p = 0.017).

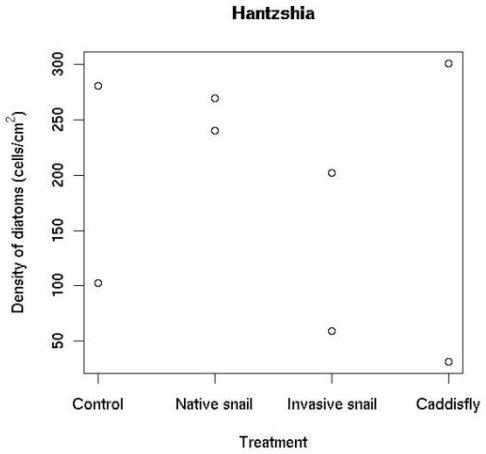

Figure 3. Density (cells/cm^2) of the diatom *Hantzshia* among treatments of the experiment. Grazers were absent in the controls. Each dot represents the density of one sample; only two samples are shown for each treatment. The native snail is *Fossaria* sp. and the exotic snail is the New Zealand mudsnail *P. antipodarum*.

✦ DISCUSSION

I estimated benthic algal biomass by measuring chlorophyll *a* and ash free dry mass (AFDM). Interestingly, chlorophyll *a* was reduced by each of the grazing species but biomass (AFDM) was not significantly decreased by either snail species and was only

marginally decreased by the caddisflies. This incongruence in the results may reflect what chlorophyll *a* and AFDM measure. Chlorophyll *a* only measures the algal portion of periphyton because this pigment is specific to algae. Additionally, our measure of chlorophyll *a* only includes living cells (concentration of chlorophyll *a* is pheophyton-corrected). In contrast, AFDM includes inorganic matter and living and non-living non-algal organic matter such as fungi, bacteria, and detritus (Stevenson 1996). Hence, a significant reduction of chlorophyll *a* and not AFDM suggests that the grazers may be preferentially feeding on the living algal cells and leaving behind the dead and non-algal matter. Also, algal biomass may not be reduced if large, slow growing diatoms are grazed and replaced by small, fast growing diatoms species (Steinman 1996). However, this explanation is unlikely because it would not lead to the reductions in chlorophyll *a* in the grazed tiles that I observed.

The algal assemblage on the tiles grazed by each species should reveal the types of algae eaten and the relative amounts of each species compared to the controls. Comparisons of algal assemblage between the invasive mudsnail and the native species should reveal the extent of dietary overlap. Native invertebrates with the greatest overlap in diet are the most likely to be negatively affected by the invasive *P. antipodarum*. However, we did not collect all of the data on algal assemblage, so conclusions about algal assemblage are pending analysis of the data from the 2007 grazing experiment.

In the few samples that my student Caroline Charles counted, certain species of diatoms had higher frequencies in the grazed tiles than in the controls. This unexpected result may be caused by increased replication rates when competitors were eliminated by grazing. This result may also be caused by increased light or other nutrients for understory diatoms as overstory diatoms were removed by grazing (Steinman 1996).

From these preliminary and incomplete results, we can conclude that the invasive *P. antipodarum* and the two native species are all consuming periphyton. Hence, the two native species are likely to be affected by the invasive snail. Ongoing analysis of algal assemblage from the more recent experiment will reveal the extent of dietary overlap and hence the species which are most likely to be affected by the invasive mudsnail, *P.antipodarum.*

Possible affects of the mudsnail on natives include reduced population sizes and possibly extirpation caused by reduced fitness of natives. Additionally, native species may grow more slowly under depleted resources, resulting in plastic changes in body size and life histories. Plastic responses might include smaller size at metamorphosis and, since adult insects do not grow, smaller adult sizes. Size is positively correlated to fecundity in most invertebrates, so smaller adult sizes should further decrease fitness. Finally, with sufficient time and genetic variation, decreased fitness from reduced resources may lead to significant evolutionary change in populations of native competitors.

✦ LITERATURE CITED

Benke, A.C. , A.D. Huryn, L.A. Smock, and J.B. Wallace. 1999. Length-mass relationships for freshwater invertebrates in North America with particular reference to the southeastern United Sates. Journal North American Benthological Society. 18: 308-343.

Cox, G.W. 2004. Alien Species and Evolution: The evolutionary ecology of exotic plants, animals, microbes, and interacting native species. Island Press, Washington, D.C., USA.

Hall, R.O. Jr., J.L. Tank, M.F. Dybdahl. 2003. Exotic snails dominate nitrogen and carbon cycling in a highly productive stream. Frontiers in Ecology and the Environment. 1:407-411.

Hall, R.O., M.F. Dybdahl, and M.C. VanderLoop. 2006. Invasive species and energy flow: Extremely high secondary production of introduced snails in rivers. Ecological Applications. In Press

Kerans, B.L., M.F. Dybdahl, M.M. Gangloff, and J.E. Jannot. 2005. *Potamopyrgus antipodarum*: distribution, density, and effects on native macroinvertebrate assemblages in the Greater Yellowstone Ecosystem. Journal North American Benthological Society. 24:123-138.

Krist, A.C. and M.F. Dybdhal. *in prep.* The invasive New Zealand mud snail, *Potamopyrgus antipodarum,* reduces growth of the native snail, *Fossaria* sp.

Lamberti , G.A. 1996. The role of periphyton in benthic food webs. In *Algal Ecology: Freshwater Benthic Ecosystems* (Stevenson, R.J., Bothwell, M.L. and Lowe, R.L. eds). Academic Press, San Diego, USA.

Lamberti, G.A. and J.W. Feminella. 1996. Plant-Herbivore Interactions. In *Methods in Stream Ecology* (F.R. Hauer and G.A. Lamberti eds). Academic Press, San Diego, USA.

Lowe, R. L., and Laliberte, G. D. 1996. Benthic Stream Algae: Distribution and Structure. In: *Methods in Stream Ecology* (Hauer, F.R. and Lamberti, G.A., eds.). Academic Press Inc. pp. 269-293.

Parker, I.M., D. Simberloff, W.M. Lonsdale, K. Goodell, M. Wonham, P.M. Kareiva, M.H. Williamson, B. Von Holle, P.B. Moye, J.E. Byers, and L. Goldwasser. 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biological Invasions 1:3-19.

Patrick, R. and Reimer, C. W. 1966. The Diatoms of the United States. The Academy of Natural Sciences of Philadelphia, PA.

Prescott, G.W. 1978. How to Know the Freshwater Algae. Wm. C. Brown Company Publishers, IA.

Reznick, D.N. and C.K. Ghalambor. 2001. The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. Genetica 112-113:183-198.

Riley, L.A., M.F. Dybdahl, R.O Hall, Jr. *in review.* Grazing and competition interaction strengths match patterns of introduced species dominance. Biological Invasions.

Sakai, A.K., F.W. Allendorf, J.S. Holt, D.M. Lodge, J. Molofsky, K.A. With, S. Baughman, R.J. Cabin, J.E. Cohen, N.C. Ellstrand, D.E. McCauley, P. O'Neil, I.M. Parker, J.N. Thompson, S.G. Weller. 2001. The Population Biology of Invasive Species. Annual Review of Ecology and Systematics. 32:305-32.

Steinman, A. D. 1996. Effects of grazers on freshwater benthic algae. In *Algal Ecology: Freshwater Benthic Ecosystems* (Stevenson, R.J., Bothwell, M.L. and Lowe, R.L. eds). Academic Press, San Diego, USA.

Stevenson, R.J. 1996. An introduction to algal ecology in freshwater benthic habitats. In *Algal Ecology: Freshwater Benthic Ecosystems* (Stevenson, R.J., Bothwell, M.L. and Lowe, R.L. eds). Academic Press, San Diego, USA.

Strauss, S.Y., J.A. Lau, and S.P. Carroll. 2006. Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? Ecology Letters 9:357-374.

Winterbourn, M.J. and A. Fegley. 1989. Effects of nutrient enrichment and grazing on periphyton assemblages in some spring-fed, south island streams. New Zealand Natural Sciences. 16:57-65.

HYBRIDIZATION OF SNAKE RIVER CUTTHROAT IN THE LOWER GROS VENTRE RIVER

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✦ INTRODUCTION

The cutthroat trout *Oncorhynchus clarki* is Wyoming's only native trout. The Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) is designated as a "species of special concern" by a number of agencies and conservation groups. Although the Yellowstone cutthroat trout has recently avoided federal listing because of robust headwater populations (USFWS 2006), they face continued threats across their range. The fine-spotted Snake River native trout is a morphologically divergent ecotype of the Yellowstone subspecies, although it is not genetically distinguishable (Allendorf and Leary 1988, Novak et al. 2005). The Gros Ventre, an important tributary of the Snake River located partially in Grand Teton National Park, historically supported robust populations of fine-spotted Snake River cutthroat trout. Principal threats to Gros Ventre native trout, especially in the lower end of the drainage within the park boundaries, include both water diversions (loss of water and fish into irrigation ditches) and presence of exotic species.

As a result of the ubiquitous distributions of exotic fish that displace or hybridize with native trout, we are seeing an ever increasing number of case studies where conservation efforts that increase connectivity across the landscape result in exotic fish expansion and subsequent problems for native fish. In fact, conservation efforts to preserve genetically pure cutthroat trout populations include the placement of barriers to avoid the influence of exotic species (e.g., Novinger and Rahel 2003). Thus the benefits of increase in flow, habitat, and potential production of trout within the Gros Ventre system needs to be weighed against the potential expansion of exotic and hybrid fish into the larger Snake River system. An important component of this project is the potential for hybrid fish to move into the larger Snake River system with increased connection between the Gros Ventre and the Snake River. The presence of rainbow trout and rainbow x cutthroat trout hybrids has been documented in the Gros Ventre River system (Kiefling 1973, 1978, Novak et al. 2005). Hybrid fish were recently collected in samples above Slide Lake (Novak et al. 2005). The degree to which the Gros Ventre River above Slide Lake is connected to the Lower Gros Ventre is unknown. As we consider increased connection to the Snake River, we need to understand the degree to which the population in the Lower Gros Ventre is hybridized. This project allows us to evaluate whether hybrids are common in the lower Gros Ventre and understand where they occur.

Thus, connection to the large Snake River system could be detrimental to the genetically pure population of cutthroat trout found in the main Snake River system. Understanding the habitat use and movement corridors of cutthroat trout, rainbow trout, and hybrid cutthroat and rainbow trout is important for determining the best management practices for Snake River cutthroat in the Gros Ventre and the larger Snake River system. Native Yellowstone cutthroat trout have been extirpated from 70% of the perennial streams which currently support trout because of hybridization with rainbow trout and competition with brook

and brown trout (Kruse et al. 2000). Thus, prevention of the expansion of exotic species including hybrid fish is a serious concern for the system.

Objectives

(1) Examine the level of hybridization in the Lower Gros Ventre River system (from diversion survey, spring creek survey, and lower river survey).

(2) Check the visual assignment of fish (rainbow, hybrid and cutthroat) that will be radio-tagged to strengthen our inferences regarding movement and spawning locations for pure versus hybrid fish.

✦ METHODS

We used a variety of techniques including backpack electrofishing, river boat electrofishing in collaboration with Wyoming Game and Fish, as well as hook and line sampling. In the summer of 2007, we collected trout in major diversion ditches off of the Gros Ventre, two spring creeks (Spring Creek and Flat Creek), and in the Gros Ventre River below Slide Lake and near Kelly. In addition, we collected samples from two of the diversion ditches in the fall of 2007. For every trout, we performed a visual call for identification (cutthroat, hybrid, rainbow), measured the total length (mm) and removed a small sliver of the caudal fin for genetic analysis. We randomly subsampled from our catches to pick the samples to be analyzed. We have analyzed 25-28 fish from each spring creek (Spring and Flat Creeks), and 218 fish from the lower Gros Ventre including samples collected near Slide Lake, Kelly, Price Lucas, and Spring Gulch ditches. During the summer the entire river was diverted down Spring Gulch, therefore this was considered the lower extent of the study section. Finally, we analyzed 36 fish that had been radio-tagged in the lower Gros Ventre during the fall 2007.

Samples were stored in ethanol and returned to the Conservation Genetics Lab at The University of Montana for processing. We extracted DNA and used a Pronase solution to lyse cells. Protein precipitation was completed using PureGene. We amplified fourteen microsatellite loci diagnostic for hybridization between cutthroat and rainbow trout using fluorescently labeled primers in multiplex polymerase chain reactions (PCR). Microsatellite PCR product was visualized on an ABI 3130 sequencer. We scored allele sizes using Genemapper version 3.7.

We calculated both the proportion of individuals that had rainbow trout alleles present, as well as a hybrid index score (HIS). If any rainbow trout alleles were present in genotyping, we considered the individual a hybrid. The hybrid index score is the number of rainbow alleles divided by the number of total alleles at these diagnostic sites. Therefore, pure cutthroat trout would have a hybrid index score of 0 while a hybrid index score of 1 would be a pure rainbow trout.

✦ RESULTS

Hybridization in the Lower Gros Ventre

We detected hybridization between rainbow trout and cutthroat trout throughout the Lower Gros Ventre and its irrigation diversions. In the river system, approximately 23% of the individuals randomly sampled were hybridized. The overall hybrid index score for the Gros Ventre River was 0.072 with rainbow trout alleles being highly skewed towards Yellowstone cutthroat trout backcrosses. HIS's were widely distributed across individuals in the Gros Ventre, from pure cutthroat (HIS=0) to pure rainbow trout (HIS=1) (Figure 1). In comparison, there were few hybrids in the samples of the nearby spring creeks with only 4% of the sample (1 in sample of 28 - 30 fish) were hybrids. These few individuals from spring creeks also had very low HIS.

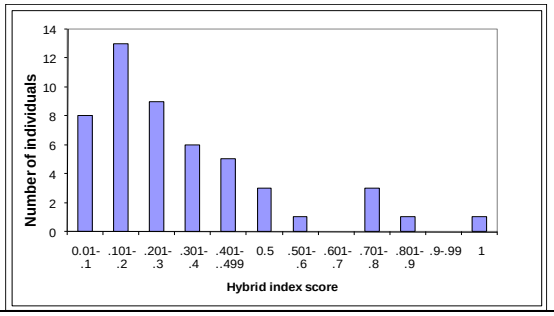

Figure 1. The frequency distribution of the HIS of hybrid fish in the lower Gros Ventre River. The majority (77%) of the fish captured were not hybrids (HIS=0); these fish are not shown in this figure.

The fact that we captured fish with very high HIS's implies a separation of heterospecific spawning populations, where pure (or almost pure) rainbow trout remain present in the system. Multiple genetic signals (including tests for Hardy-Weinberg equilibrium and Bayesian clustering) indicate there may be more than one hybridizing population within the Gros Ventre River.

Hybridization rates varied across the linear river gradient and temporally. Samples collected from downstream sites (i.e., Price Lucas and Spring Gulch) had higher proportions of hybrids in the sample than upstream sampling locations (Figure 2). Additionally in October, we captured fish in these downstream sites that had higher hybrid index scores than summertime samples. These differences in space and time associated with the capture of hybridized individuals indicate that hybrids may be moving around the system differently than the pure cutthroat trout. This will be further investigated by other efforts that will pit tag fish in the upcoming field season (UM) and the examination of movements of the radio-tagged fish that are being followed in a collaborative project. Jim Gregory (Gregory Aquatics) is contracted by Trout Unlimited and in collaboration with Wyoming Game and Fish has radio-tagged fish across a range of levels of hybridization to examine differences in habitat use and movement.

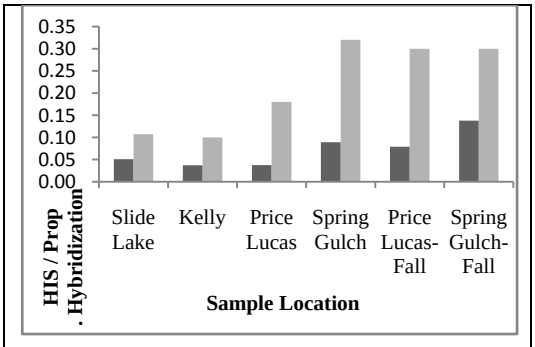

Figure 2. Average hybrid index score (HIS, white bars) and average proportion of the individuals that were hybridized in the samples (black bars). Slide Lake, Kelly, Price Lucas, and Spring Gulch were sampled in July. Price Lucas and Spring Gulch were sampled again in the fall (October/November) of 2007.

Assignment of radio-tagged fish

The second objective associated with this proposal was to check the assignment of the fish (pure cutthroat trout, hybrid, or rainbow trout) that were radio-tagged in the fall of 2007. This is an important component because it is difficult to properly visually identify cutthroat and rainbow hybrids. The genetic analysis with the visual identification is necessary to ensure that we are making appropriate inferences regarding the status of these individuals.

The visual calls were correct 86% of the time. All individuals miscategorized had relatively high HIS but were categorized as pure rainbow trout (Figure 3). In discussing this with Jim Gregory, he did know that some of the fish that were categorized as rainbow trout were likely hybridized fish. The radiotagged fish do demonstrate the entire range of the hybrid index scores. From previous studies, the fish that are most often incorrectly classified are cutthroat rainbow hybrid with relatively low HIS (Leary et al. 1996, Weigel et al. 2002). These fish are not in the radio-tagging study but do make up the majority of the hybrids in the Gros Ventre population are those that range from 0.01 to 0.4 HIS. Therefore, we will be examining the reliability of our visual calls for the random samples in the future.

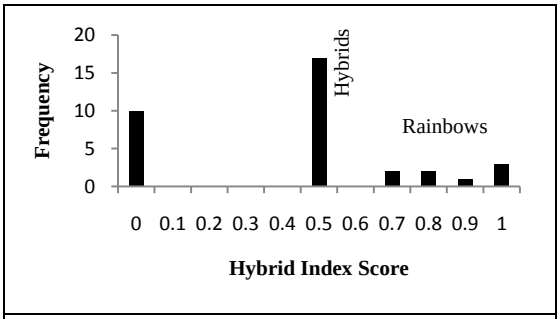

Figure 3. Hybrid index score compared with visual calls for the radio tagged fish. The groups for the visual calls are indicated in words on the frequency distribution graph.

✦ SUMMARY

The Gros Ventre River is a potential source of hybrids to the larger Snake River system. The Gros Ventre not only contained higher proportions of hybrids compared with nearby spring creeks, it also has fish with very high hybrid index scores, including some pure rainbow trout. Thus, examining the relative risks associated with the movement and dispersal of

hybrids should be considered in the management of this system. This project has provided evidence (through the bimodal distribution of HIS) that there are likely separate spawning populations of rainbow trout or fish that are primarily rainbow trout. Genetic analyses would predict at least two spawning aggregations of highly hybridized fish. Given these results, we would recommend examining the potential of suppressing these highly hybridized breeding populations to minimize their future impact on this important Snake River cutthroat conservation region. Finally, this project has described a pattern in the habitat use and/or movement (spatial and temporal patterns) of hybrids in this system that we hope will be elucidated further in the 2008 field season through both additional tagging by UM and continued collaboration with Jim Gregory, Gregory Aquatics.

✦ ACKNOWLEDGEMENTS

We could not have done this work without the field help and knowledge of the folks at Wyoming Game and Fish (Rob Gipson and crew), Trout Unlimited (Scott Yates and crew), Thomas Chandler, and Jim Gregory. In addition, Sally Painter, Steve Amish, and Matt Corsi (especially Sally!) were invaluable in helping with the laboratory procedures and genetics analyses. Finally, Ryan Kovach was partially funded by the MILES undergraduate research scholarship, Irene Evers research scholarship, and the Davidson Honor's College Research Scholarship.

✦ LITERATURE CITED

Allendorf, F. W., and R. F. Leary. 1988. Conservation and distribution of genetic variation in a polytypic: the cutthroat trout. Conservation Biology. 2:170-184.

Kiefling, J.W. 1973. Habitat evaluation of the Snake River and tributary streams. Part I Gros Ventre River Habitat Evaluation. Wyoming Game and Fish Commission Cooperative Research Project No. 4. Segment 6, Job 2, F-37-R-6. March 1973.

Kiefling, J.W. 1978. Studies on the ecology of the Snake River cutthroat trout. Wyoming Game and Fish Department Fisheries Technical Bulletin. 3:198pp.

Kruse, C.G., W.A. Hubert, F.J. Rahel. 2000. Status of Yellowstone cutthroat trout in Wyoming waters. North American Journal of Fisheries Management. 20:693-705.

Leary, R.F., W.R. Gould, and G.K. Sage. 1996. Success of basibranchial teeth in indicating pure populations of rainbow trout and failure to indicate pure populations of westslope cutthroat trout. North American Journal of Fisheries Management. 16:210-213.

Novak, M.A., J.L. Kershner, and K.E. Mock. 2005. Molecular genetic investigation of Yellowstone cutthroat trout and finespotted Snake River cutthroat trout. A report in partial fulfillment of: agreement #165/04 Wyoming Game and Fish Commission Grant. 48 pp.

Novinger, D.C. and F.J. Rahel. 2003. Isolation management with artificial barriers as a conservation strategy for cutthroat trout in headwater streams. Conservation Biology. 17:772-781.

USFWS (United States Fish and Wildlife Service). 2006. Status review: Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri*. U.S. Fish and Wildlife Service, Denver, Colorado.

Weigel, D.E., J.T. Peterson, and P.A. Spruell. 2002. Model Using Phenotypic Characteristics to Detect Introgressive Hybridization in Wild Westslope Cutthroat Trout and Rainbow Trout. Transactions of the American Fisheries Society. 131:389-403.

IMMUNOLOGICAL COSTS OF MATING TO MALE SAGEBRUSH CRICKETS

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✦ ABSTRACT

Male sagebrush crickets, *Cyphoderris strepitans*, offer an unusual nuptial food gift to females during mating: females chew on the ends of the males' fleshy hind wings and ingest hemolymph seeping from the wounds they inflict. Previous research has shown that once a male has mated, his probability of obtaining an additional copulation is reduced relative to that of a virgin male seeking to secure his first mating, a pattern known as the virgin-male mating advantage. One hypothesis that may explain this phenomenon is that mated males experience an energetically costly immune response via their wounds and therefore may be unable to sustain the costly acoustical signaling needed to attract additional females. To distinguish between the effects of mounting a costly immune response and the costs of producing a spermatophore, we mimicked a non-virgin mating status by injecting virgin males with bacterial lipopolysaccharides, a non-living elicitor of several immune pathways. After they had been treated, males were released in the field and recaptured over the course of the breeding season to monitor their mating success. Contrary to our prediction, LPS injected males did not take longer to secure matings than sham-injected virgin males. However, a companion study revealed that immunochallenged virgin males spent significantly less time calling (as assayed using time-lapse video photography) than sham-control virgin males. This confirms work in other cricket species showing a decline in mating effort following an immune challenge.

✦ INTRODCTION

The sagebrush cricket, *Cyphoderris strepitans*, is one of only seven extant species of a relatively unknown orthopteran family, the hump-winged grigs (Haglidae) (Kumala et al. 2005). *C. strepitans* occurs exclusively in high-altitude sagebrush meadows in mountainous areas of Colorado and Wyoming (Morris and Gwynne 1978). Mating occurs in the late spring after the snow melts. Males climb into sagebrush or lodegepole pine shortly after sunset to secure a perch, from where they emit acoustical signals that function to attract females (Snedden and Irazuzta 1994), and which appear to be the primary means of pair formation (Snedden and Sakaluk 1992). Copulation is initiated when a female climbs onto the dorsum of the male, at which time he attempts to transfer a spermatophore, a small gelatinous packet containing sperm. During copulation, the female feeds on the male's fleshy hind wings and the hemolymph that oozes from the wounds she inflicts. After the spermatophore has been transferred, the male actively pulls away from the female, terminating wing feeding (Eggert and Sakaluk 1994).

Virgin males secure more matings than their relative abundance in the wing tissue and hemolymph, they must also produce in the population would predict, a population wide pattern that has been described as the "virgin-male mating advantage" (Morris et al. 1989; Sakaluk and Ivy 1999; Snedden 1996). Mating appears to be costly to males: not only do they lose a significant portion of their hind wing

tissue and hemolymph, they must also produce another spermatophore if they are to mate again. Previous work has shown that non-virgin male calling time is reduced relative to virgin males (Sakaluk et al. 1987; Sakaluk and Snedden 1990).

One possible mechanism underlying the reduction in non-virgin male calling time is that a male's immune system is activated when his integument is breached via wing-feeding by females at mating, and that resources allocated to the ensuing immune response comes at the expense of the resources that would otherwise be devoted to acoustic signaling. While a number of studies have shown tradeoffs between investment in immune responses and the expression of secondary sexual characteristics (Sheldon and Verhulst 1996; Faivre et al. 2003), the present study would be the first to show, to the best of our knowledge, that mating itself can result in an immune response that constrains a male's future mating success. Of particular relevance to our study, recent work has shown that experimentally-induced immune responses in field crickets result in a reduction in male calling time (Jacot et al. 2004).

The objective of the present study was to determine the effects of an induced immune response on male sagebrush cricket mating success in a mark-recapture study. If the immune response resulting from female wing feeding during copulation is responsible for the decline in non-virgin male mating success, then virgin males subjected to a similar immunological challenge should exhibit a similar decline in the incidence of matings. This should occur because male calling time should be reduced via the mounting of an energetically costly immune response.

✦ METHODS

A mark-recapture study was conducted from May 21 to June 15, 2006 in Grand Teton National Park, Wyoming. A rectangular study plot of approximately 120 m X 80 m was established in sagebrush meadow habitat adjacent to the Snake River at Deadman's Bar. During the early portion of the breeding season, we attempted to capture and mark all of the virgin males present in the study plot. Males were found at night by orienting to their calls and using head lamps to determine their exact location within a sagebrush bush. The mating status of males was determined by examining their hind wings for the wounds inflicted by females; only virgin males, as evidenced by intact wings, were used in experimental treatments. Each virgin male was placed in a collecting vial, numbered to correspond with a surveyor's flag placed at the capture location, and transported to the University of Wyoming-National Park Service Research Center, approximately 30 km away, for processing.

Captured males were randomly assigned to one of two treatments: 1) males injected with 50 µg of bacterial lipopolysaccharides (LPS) in 10 µl of Grace's insect medium, and 2) sham-control males injected with 10 µl of Grace's insect Medium. LPS was chosen as it is the non-living, non-pathogenic portion of a gram negative bacterial cell wall which represents a common insect pathogen, *Serratia marcesens* (Adamo et al. 2001). Injections were administered ventrally between the third and fourth sternites using a 10-µl Hamilton syringe (Jacot et al 2004). Each male was marked individually with a numbered plastic tag secured to the pronotum with cyanoacrylic glue, and his femora painted with fluorescent model paint (Testors®) of a unique color that designated the treatment to which he had been assigned. Portable ultraviolet lanterns, the illumination of which caused the paint to fluoresce in the dark, were used to facilitate the capture of experimental individuals at night. The following evening at sunset, marked males were returned to their respective points of capture. We marked and released a total of 86 males (43 sham-control, 43 LPS-injected) over the course of five nights (May 21-May 25).

After experimental males had been released, males were recaptured and examined for evidence of mating activity regularly over the course of the breeding season, usually every second night, weather permitting. Mating activity was inferred by loss of hind wing material in all treatments. Wing wounds were classified as "fresh" (visibly wet wounds with no discoloration indicating that the male had mated on the night of capture) or "old" (dry, darkened wounds indicating that the male had mated at least one night previous to the night of capture).

A time-lapse video study took place concurrently with the field study in which we determined the effects of an induced immune

response on male calling effort. Two groups of virgin males were established in the same way as in the mark-recapture study, except that these males were collected from another population at Pacific Creek, approximately 20 km away from Dead Man's Bar. Each night of the study, males from each of the two treatments were paired with females at about 2000 h, and their mating activity monitored over a 5-hour period using time-lapse video photography. Nighttime recording was facilitated by the illumination provided by a 25-W red light bulb. Experimental pairs were confined in a Plexiglas viewing chamber (17 x 12 x 3.5 cm), divided into four equal compartments to prevent contact between crickets of different pairs, each of which contained a short stick to serve as a calling perch. Upon review of video recordings, we determined the time spent calling by each male during the trial, measured as the number of 5-min intervals in which stridulation occurred (one-zero sampling; Altmann 1974)

All data were analyzed using SAS (SAS Institute, 2004).

✦ RESULTS

Survival of experimental males was determined as the number of nights from the time a male was first captured to the night on which a male was last recaptured. We excluded from this calculation males that were never recovered following their initial release (see above) because these males may have lost their tags or immediately left the study area owing to the trauma of release. Males that were still alive on the last night of the study were treated as 'censored' observations. To compare survival across treatments, we employed failure time analysis (Fox 1993). Failure-time analysis accommodates censored data, observations in which an event such as a male's death or mating may not have occurred by the end of the study, as was the case here. Omission of such data, as is frequently done in behavioral studies, may lead to a serious bias in comparisons across treatments (Fox, 1993). There was no difference in male survival across treatments (Log-Rank χ^2 = 1.51, P = 0.22).

Time to mating was determined as the number of nights from the time a male was first released until he was captured as a non-virgin. Non-virgin males bearing fresh-wing wounds were assumed to have mated on the night they were captured. Non-virgin males bearing old-wing wounds were assumed to have mated at least one night previous to their capture or, if they had not been captured in the previous census, we recorded the night of mating as the mid-point of the earliest time they could have mated and the latest time they could have mated. Males that had still not mated by the time of their last capture were treated as 'censored' observations. We used failure time analysis to compare time to mating of sham control males with that of LPS injected males. LPS-injected males obtained matings at a lower rate than control males, but the difference was not quite statistically significant (Log-Rank χ^2 = 2.64, p = 0.104, Figure 1). We believe that this was due to a high percentage of censored observations (males that failed to secure a copulation over the duration of the study), because slightly more than half of the male population had already mated by the time we initiated the study because of an unseasonably warm early spring (Table 1).

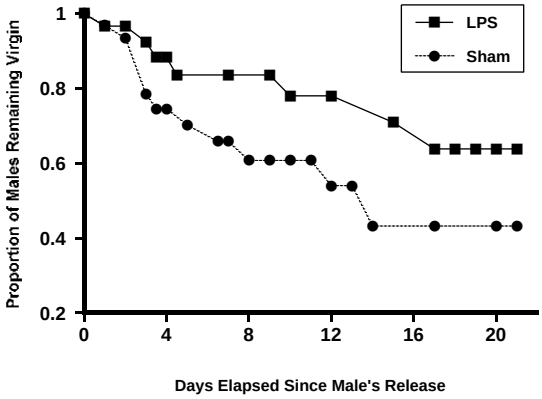

Figure 1. The proportion of male sagebrush crickets remaining unmated as a function of time elapsed since their initial release. LPS-males took longer to secure mating than control males, but the difference was not statistically significant (Log-Rank χ^2 = 2.64, p = 0.104).

Treatment	*N*	Mated	Unmated	% Censored
LPS injected	30	7	23	76.7
Sham control	31	12	19	61.3

Table 1. Number of males that mated and number of males that failed to mate by the end of the study (censored observations).

Calling data from the video study were analyzed using a repeated-measures ANOVA, with time (first night or second night of recording) entered as the repeated factor and treatment (LPS-injected or sham-control) entered as the other main effect. Control males called

significantly more than LPS-injected males (F = 5.08, P = 0.030). There was no significant difference in calling time across nights (F = 1.99, P = 0.17), and nor was there a significant time* treatment interaction (F = 0.32, P = 0.57; Figure 2)

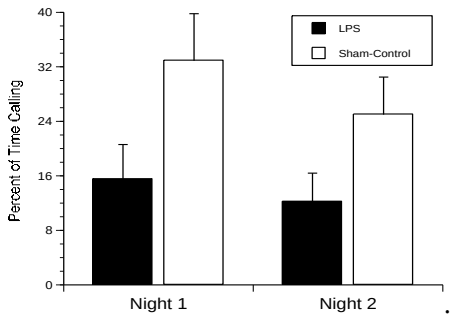

Figure 2. Mean percent of time spent calling (+ SE) by LPS-injected males and sham-control males over two consecutive nights.

✦ DISCUSSION

There was no significant difference between LPS-injected virgin males and control males, a result that is inconsistent with the hypothesis that the virgin male mating advantage occurs because males incur an energetically costly upregulation of the immune system as a result of the wing wounding they experience at mating. However, immunochallenged males spent significantly less time calling compared to control males. Because calling is vital to pair formation and hence, mating success (Snedden and Sakaluk 1992), this result provides evidence that supports the hypothesis. While a number of studies have shown tradeoffs between investment in immune responses and investment in secondary sexual characteristics (Sheldon and Verhulst 1996; Faivre et al. 2003; Jacot et al., 2004), no study has shown that mating itself can result in an immune response that compromises future mating success.

Even if LPS injected males were shown to secure fewer matings than sham injected males, more work would be necessary to understand the proximate underpinnings of this cost. Direct physiological evidence of a differential immune response of virgin males and non virgin males is required, and the specific correlates of immunocompetence remain to be identified (Adamo 2004). To that end, we will be conducting three kinds of laboratory-based immunoassays on field-collected virgin and non-virgin male *C. strepitans* in 2006 : 1) an encapsulation rate assay, 2) a phenoloxidase activity assay and 2) a lyoszyme-like activity assay.

✦ ACKNOWLEDGEMENTS

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✦ LITERATURE CITED

Adamo, S.A. 2004. How should behavioral ecologists interpret measures of immunity? Animal Behavior 68:1443-1449.

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227-267.

Eggert, A-K, S.K Sakaluk. 1994. Sexual cannibalism and its relation to male mating success in sagebrush crickets, *Cyphoderris strepitans* (Orthoptera: Haglidae). Animal Behavior. 47:1171-1177.

Faivre, B., A. Gregoire, M. Preault, F. Cezilly, G. Sorci**.** 2003. Immune activation rapidly mirrored in a secondary sexual trait. Science 300:103.

Fox, G.A. 1993. Failure-time analysis: emergence, flowering, survivorship and other waiting times. In: Design and analysis of ecological experiments, (Scheiner SM, Gurevitch J, eds). New York: Chapman & Hall. p. 253-289.

Jacot, A., H. Scheuber, M.W.G. Brinkhof. 2004. Costs of an induced immune response on sexual display and longevity in field crickets. Evolution 58:2280-2286.

Kumala, M., D.A. McLennan, D.R. Brooks, A.C. Mason. 2005. Phylogenetic relationships within hump-winged grigs, *Cyphoderris* (Insecta, Orthoptera, Tettigonioidea, Haglidae). Canadian Journal of Zoology 83:1003-1011.

Morris, G.K., D.T Gwynne. 1978. Geographical distribution and biological observations of *Cyphoderris* (Orthoptera: Haglidae) with a description of a new species. Psyche 85: 147-167.

Morris, G.K., D.T. Gwynne, D.E. Klimas, S.K. Sakaluk. 1989. Virgin male mating advantage in a primitive acoustic insect (Orthoptera: Haglidae). Journal of Insect Behavior 2:173-185.

Sakaluk, S.K., T.M. Ivy. 1999. Virgin-male mating advantage in sagebrush crickets: differential male competitiveness or non-independent female mate choice? Behaviour 136:1335-1346.

Sakaluk, S.K., W.A. Snedden. 1990. Nightly calling durations of male sagebrush crickets, *Cyphoderris strepitans*: size, mating and seasonal effects. Oikos 57:153-160.

Sakaluk, S.K., G.K. Morris, W.A. Snedden. 1987. Mating and its effect on acoustic signalling behavior in a primitive orthopteran, *Cyphoderris strepitans* (Haglidae): the cost of feeding females. Behavioral Ecology & Sociobiology 21:173-178. SAS Institute Inc. 2004. *SAS OnlineDoc® 9.1.3*. SAS Institute Inc: Cary, NC.

Sheldon, B.C., S. Verhulst. 1996. Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. Trends in Ecological Evolution. 11:317-321.

Snedden, W.A. 1996. Lifetime mating success in male sagebrush crickets: sexual selection constrained by a virgin male mating advantage. Animal Behavior. 51:1119-1125.

Snedden, W.A., S. Irazuzta. 1994. Attraction of female sagebrush crickets to male song: the importance of field bioassays. Journal Insect Behavior. 7:233-236.

Snedden, W.A., S.K. Sakaluk. 1992. Acoustical signalling and its relation to male mating success in sagebrush crickets. Animal Behavior. 44:633-639.

PREDICTING DISEASE SPREAD IN GREATER YELLOWSTONE UNGULATES USING PARASITE DNA MARKERS

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✦ INTRODUCTION

Infectious diseases are a serious threat to the viability of wildlife populations worldwide, including those in national parks and other protected areas where agricultural operations, development, and recreation are degrading and fragmenting habitat and increasing the potential for interactions between wildlife, domestic animals, and humans. The spread of infectious diseases and parasites is of particular concern in the greater Yellowstone area, which supports world-renowned herds of ungulates that provide significant visitor enjoyment and benefits to local economies through guiding and sport hunting. The high diversity, density, and co-mingling rates of ungulates in this area could facilitate the rapid emergence and spread of infectious diseases such as brucellosis, chronic wasting disease, and Johne's disease, with escalating disease threats to livestock and people along the public/private land interface.

A critical need is information on disease and parasite transmission pathways within and among species and through the greater Yellowstone area to help develop feasible strategies to minimize the adverse conservation, economic, and social effects of diseases. We began addressing this need by identifying informative, polymorphic DNA markers from parasite propagules shed in ungulate feces that can be used to non-invasively identify, track, and map transmission routes across the greater Yellowstone area. Similar analyses of DNA markers from microparasites (e.g., viruses, bacteria) and macroparasites (e.g., helminths) in other areas have been used to determine the rates and routes of movement and disease spread by diverse host species such as cougars, salmon, and cattle (Blouin et al. 1995, Monis et al. 2005, Criscione et al. 2005, 2006; Biek et al. 2006).

The objectives of our study were to: 1) analyze the prevalence of parasites in elk and other ungulates inhabiting the northern and west-central portions of Yellowstone National Park and Grand Teton National Park in Wyoming; 2) identify polymorphic nuclear and mtDNA loci for macro- and micro-parasites; and 3) estimate genetic differentiation and transmission rates within and between host species and populations from the three sampling locations. This information will help natural resource managers throughout the greater Yellowstone area to

understand and map routes of spread of environmentally transmitted diseases such as brucellosis and chronic wasting disease, and predict the risks and routes of transmission.

✦ METHODS

We collected 20 grams (e.g., 15-25 pellets) of fresh feces from elk, bighorn sheep, bison, pronghorn, and cattle from several geographic areas. Fecal samples were stored at 4^{o} C for <1 month until parasites were isolated in the laboratory. A sub-sample of each fecal sample was also immediately placed in 95% ETOH and/or frozen for recovery of micro-parasites or direct PCR-based DNA analysis.

Helminth larvae were recovered from host fecal samples at the University of Montana using a modified Baermann method (Foryet 2001, Ezenwa 2004*a*). Parasite prevalence was estimated as the proportion of host individuals with the parasite (Ezenwa 2003, 2004*b*). DNA was isolated from individual larvae using commercial kits (e.g., DNAeasy tissue kits, Qiagen). Primers for PCR amplification and sequencing of mtDNA were available for *Haemonchus* and *Dictyocaulus* (Blouin 2002, Hoglund et al. 2006). Primers for microsatellite genotyping and PCR-sequencing of many nuclear genes were also available (e.g., ITS-1, ITS-2; Blouin 2002, Wimmer et al. 2004).

To study a microparasite, *Brucella abortus*, we sampled 77 bison from slaughter houses (over ½ were seropositive for *Brucella*). We collaborated with other researchers and expect to obtain *Brucella* DNA isolates from an additional 50-100 bison, including animals migrating out of the northern and western boundaries of Yellowstone National Park. Also, we tested for *Yersinia enterocolitica* by culture from 30 bison feces from Grand Teton National Park. Isolation and culture of the bacteria was conducted in a commercial laboratory. DNA will be isolated from cultures (dead bacteria killed in 95% ETOH) or directly from fecal material using commercial kits (e.g., DNAeasy tissue kits, Qiagen). PCR primers for microsatellites and many nuclear genes are available for the bacteria species (e.g., Jourdan et al. 2000, Bricker and Ewaldt 2005, Sharma et al. 2006, Zheng et al. 2006).

DNA sequence analysis and estimation of polymorphism in each parasite species will be conducted using MEGA and Arlequin software (Luikart et al. 2001). Preliminary transmission rates will be estimated roughly as gene flow (i.e., migration) rates using population genetic distance statistics (e.g., F_{ST}) and models of population structure (e.g., island and stepping-stone models, using likelihood and Bayesian estimators; Beerli and Felsenstein 2001, Beerli 2006). Also, we will use assignment test approaches to directly identify recent transmissions without assumptions about population migration-mutation-drift equilibrium (e.g., Cornuet et al. 1999).

✦ RESULTS

We sampled feces from bison, elk, bighorn, pronghorn, and/or cattle from Grand Teton National Park, the northern range of Yellowstone, along with 24 elk from Idaho on the Sand Creek wintering grounds. Prevalence of helminth parasites in each host species and each location are provided in Table 1.

We identified and optimized mitochondrial DNA primers for the ITS and NAD genes. We will soon PCR amplify and sequence ITS for species identification of approximately 8 nematodes from each host animal sampled to identify nematodes to species and to establish prevalence data. For one or two helminth species that are most prevalent, we will sequence NAD for approximately 30 worms per host species (elk, bison, pronghorn, and cattle) in each geographic location. This will allow for preliminary estimates of parasite population genetic structure (and transmission rates) within verses between host species and geographic locations.

We developed a quantitative real-time PCR test for *Brucella* DNA to help identify infected bison and elk. This test will be applied to feces, urine, blood and tissue. We also are genotyping 10 HOOF-print VNTR (variable number of tandem repeat or microsatellites) in collaboration with researchers at the National Animal Disease Center in Ames, Iowa (G. Luikart, manuscript in preparation). This will allow for estimation of transmission rates within and between elk and bison populations.

Location	No. fecal samples	Host species	*Protostrongylus*	*Dictyocaulus*	G.I. nematodes
Grand Teton NP	38	elk	0	0.22	0.1*
	32	bison	0.08	0.28	0.44
	19	bighorn sheep	1.0	0.05	1.0
	35	cattle (Pinto Ranch)	0.03	0	0.15
Yellowstone NP	20	elk	likely zero	0.56	0.75
	15	pronghorn	0.87 (genus uncertain)		0.8
	41	bison	0.13	0.1	0.76
Northern Wyoming (outside YNP and GTNP)	22	cattle	0.09 (genus not certain)		0.53
	13	pronghorn	0.92 (genus uncertain)		0.91
Bench/Jewett Feed Grounds	20	elk	likely zero	0.58	0.08

Table 1. Prevalence of helminth parasites in ungulate host species from the greater Yellowstone area.

* These elk samples were rather old when analyzed, so prevalence estimates are likely biased low.

No *Yersinia* positives were identified in 30 bison feces from Grand Teton National Park. We currently are testing 120 more fecal samples from bison on their summer range and those consigned to slaughter from Yellowstone National Park, as well as samples from bison in Grand Teton National Park during winter. We will be testing these fecal samples, plus many fecal samples from elk, for *Yersinia enterocolitica* (strain 0:9) by PCR directly from feces and lymph node DNA isolates. Once PCR or culture identifies *Yersinina*, we intend to sequence a few gene fragments to identify polymorphisms for studying transmission, depending on funding availability.

✦ LITERATURE CITED

Beerli, P. 2006. Comparison of Bayesian and maximum likelihood inference of population genetic parameters. Bioinformatics 22:341-345.

Beerli, P., and J. Felsenstein. 2001. Maximum likelihood estimation of a migration matrix and effective population sizes in n subpopulations using a coalescent approach. Proceedings of the National Academy of Sciences USA 98:4563-4568.

Biek, R, A.J. Drummond, and M. Poss. 2006. A virus reveals population structure and recent demographic history of its carnivore host. Science 311:538-541.

Blouin, M.S. 2002. Molecular prospecting for cryptic species of nematodes: mitochondrial DNA versus internal transcribed spacer. International Journal for Parasitology 32:527–531.

Blouin, M.S., C.A. Yowell, C.H. Courtney, and J.B. Dame. 1995. Host movement and the genetic structure of populations of parasitic nematodes. Genetics 141:1007-1014.

Bricker, B.J., and D.R. Ewalt. 2005. Evaluation of the hoof-print assay for typing *Brucella abortus* strains isolated from cattle in the United States: results with four performance criteria. BMC Microbiology 5:37.

Cornuet J.M., S. Piry, G. Luikart, A. Estoup, and M. Solignac. 1999. New methods employing multilocus genotypes for selecting or excluding populations as origins of individuals. Genetics 153:1989-2000.

Criscione, C.D., R. Poulin and M.S. Blouin. 2005. Molecular ecology of parasites: elucidating ecological and microevolutionary processes. Molecular Ecology 14:2247-2257.

Criscione, C.D., B. Cooper, and M.S. Blouin. 2006. Parasite genotypes identify source populations of migratory fish more accurately than fish genotypes. Ecology 87:823-828.

Ezenwa, V.O. 2004*a*. Selective defecation and selective foraging: antiparasite behavior in wild ungulates? Ethology 110:851-862.

Ezenwa, V.O. 2004*b*. Host social behavior and parasitic infection: a multifactorial approach. Behavioral Ecology 15:446-454.

Foryet, W.J. 2001. Veterinary Parasitology Reference Manual, 5th Edition. Iowa State University Press, Ames.

Hoglund J., D.A. Morrison, J.G.Mattsson, A. Engstrom. 2006. Population genetics of the bovine/cattle lungworm (*Dictyocaulus viviparus*) based on mtDNA and AFLP marker techniques. Parasitology 133:89-99.

Jourdan A.D., S.C. Johnson, and I.V. Wesley. 2000. Development of a fluorogenic 5' nuclease PCR assay for detection of the ail gene of pathogenic *Yersinia enterocolitica*. Applied Environmental Microbiology 66:3750-3755.

Luikart G., L. Gielly, L. Excoffier, J.D. Vigne, J. Bouvet, and P. Taberlet. 2001. Multiple maternal origins and weak phylogeographic structure in domestic goats. Proceedings of the National Academy of Sciences USA 98:5927-5930.

Monis, P.T., S. Giglio, A.R. Keegan, and R.C. Andrew Thompson. 2005. Emerging technologies for the detection and genetic characterization of protozoan parasites. Trends in Parasitology 21:340-346.

Sharma, S., S. Mittal, S. Mallik, and J.S. Virdi. 2006. Molecular characterization of beta-lactamase genes blaA and blaB of *Yersinia enterocolitica* biovar 1A. FEMS Microbiology Letters 257:319-327.

Wimmer B, B.H. Craig, J.G. Pilkington, and J.M. Pemberton. 2004. Non-invasive assessment of parasitic nematode species diversity in wild Soay sheep using molecular markers. International Journal of Parasitology 34:625-631.

Zheng, H.X., M.J. Zhang, Y. Sun, and B. Jiang. 2006. Detection of *Yersinia enterocolitica* in diarrhea stool by real-time PCR. Zhonghua Yi Xue Za Zhi. 86:2281-2284.

MONITORING OF CONTAMINANTS IN NESTLING BALD EAGLES OF GRAND TETON NATIONAL PARK

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✦ ABSTRACT

We report on contaminants identified in nestling bald eagles of Grant Teton National Park (GTNP) and the Snake River Unit (SRU), Wyoming, during summers of 2006 and 2007.

We focus primarily on mercury (Hg), lead (Pb), and selenium (Se) because each was detected in all nestlings during both summers at moderate levels. Independent t-tests were performed both on the raw data and log-transformed data (using the natural logarithm) as a comparative analysis to investigate if contaminant loads had significantly increased from summer 2006 to summer 2007. Also, as a comparative analysis and alternative procedure, *nest site* was treated as the experimental unit and a repeated-measures analysis (longitudinal study) was conducted on the raw data to investigate if contaminant loads had significantly increased from summer 2006 to summer 2007.

Results of the analysis indicate that levels of Se essentially remained unchanged from summer 2006 to summer 2007 ($p=0.466$, log-transformed data). Levels of Pb in nestlings increased from summer 2006 to summer 2007 ($p=0.000$, log-transformed data). There was no difference in levels of Hg in nestlings from summer 2006 to summer 2007 ($p=0.058$, log-transformed data). The molar ratio (2.54ppm Se: 1ppm Hg) of Se to Hg did not change from 2006 to 2007 ($p=0.337$, raw data), although a 45% decrease in molar ratio was observed. Analyses of contaminants (using geometric means) in the blood of nestlings (from summer 2006 to 2007) showed a 64% increase in Hg, a five-fold increase in Pb (481%), and a 21% increase in Se. Potential localized sources of Pb contamination should be identified and removed from the proximity of any nest site(s) and the study area in general.

Advancing global climate change and associated desiccation and emolation of temperate and boreal forests, exacerbated by extensive clear-cutting may increase poisoning of aquatic ecosystems with high levels of contaminants, especially Hg, in the future. A monitoring program may be indicated to identify potential long-term changes within the GYE.

✦ INTRODUCTION

In the late 1980s, toxic elements and organochlorine pesticides were analyzed in blood and sera of bald eagles (*Haliaeetus leucocephalus*) captured along the Snake River in northwestern Wyoming (Harmata and Oakleaf 1992). From1985 -1992, 35% (n =146) of bald eagles tested had detectable levels of Pb, 91.4 % had detectable levels of Hg, and 100% had detectable levels of Se. At that time, survival and productivity of eagles did not appear affected. However, contaminant induced mortality was recorded in several eagles. Despite recommendations to monitor contaminants in nestling bald eagles at 5-year intervals (Harmata 1996), no follow-up analyses were conducted until summer 2006, after several bald eagles with Hg levels above the toxic threshold (≥0.4ppm wet weight, Burgess et al. 2005) were submitted to the Montana Raptor Conservation Center (MRCC), a raptor rehabilitation and education organization in Bozeman, Montana.

Since December 2005, approximately 15 bald eagles and one golden eagle (*Aquila chrysaetos*) were submitted for treatment to MRCC. Analysis revealed that eagles contained toxic levels of Hg in their blood. Six died, one was released, and the rest remain in treatment but most likely will not be releasable. Symptoms of Hg toxicity were expressed by at least three other eagles submitted prior to December 2005, but their blood was not analyzed specifically for this metal. We suspect that Hg poisoning may have emerged prior to December 2005, but was not diagnosed.

Since the summer of 2006, we have investigated contaminants in nestling, wintering and migrant bald eagles in southwestern Montana and northwestern Wyoming. Here we report on contaminants identified in nestling bald eagles of Grand Teton National Park (GTNP) and the Snake River Unit (SRU), Wyoming, during summers of 2006 and 2007.

✦ METHODS

Sampling was conducted at nest sites in GTNP and SRU (Table 1), along both lentic (Jackson Lake and Lower Slide Lake) and lotic systems (Snake River corridor from the Jackson Lake dam to the Elbow south of Hoback Junction).

In this study, we focused on Hg, Pb, and Se because each was detected in all nestlings during both summers at moderate levels and, due to their persistence in the environment, are of significant concern in the GYE (especially Hg). In addition, we tested six other soluble trace elements – antimony (Sb), arsenic (As), cadmium (Cd), chromium (Cr), nickel (Ni) and thallium (Tl) - in 2006-2007, and DDE (organochlorine metabolite of DDT) in eight nestlings in 2007. Blood samples were analyzed at Michigan State University, Veterinary Medical Center, Diagnostic Center for Population and Animal Health, Clinical Pathology Laboratory (DCPAH), A215, East Lansing, MI 48824-1314.

2006	2007
4LazyF Ranch (2)	4LazyF Ranch (3)
Elbow (1)	Elbow (2)
	Hoback Junction (1)
Lower Slide Lake (1)	Lower Slide Lake (2)
Moose (2)	Moose (1)
	Oxbow Bend (1)
Refuge (2)	Refuge (1)
	Spaulding Bay (2)
Triangle X Ranch (2)	Triangle X Ranch (2)

Table 1. Bald eagle nest sites sampled in the GYE, 2006-2007. (UTM locations available upon request from G.J. Montopoli). Number of nestlings in each nest is given in parentheses

Independent-sample t-tests were conducted to investigate if contaminant loads had increased from summer 2006 to summer 2007 (H_0: Levels of contaminants have not changed from 2006 to 2007; H_1: Levels of contaminants have increased from 2006 to 2007). Homogeneity of variance tests were performed to adjust for degrees of freedom if violations were present. All tests were conducted at the 0.05 level of significance.

Independent t-tests were performed both on the raw data and log-transformed data (using the natural logarithm) as a comparative analysis. The log-transformation is applicable to data expressed in ppm and uses the geometric mean (rather than the arithmetic mean) in the computation of the test statistic.

Also, as a comparative analysis and alternative procedure, *nest site* was treated as the experimental unit and a repeated-measures analysis (longitudinal study) was conducted on the raw data to investigate if contaminant loads had significantly increased from summer 2006 to summer 2007. If more than one nestling occurred at any given site, levels of contaminants were averaged over all nestlings at the site. Complete data for Hg, Pb, and Se over both summers only occurred for 6 nest sites.

✦ RESULTS

The main purpose of this study involves the investigation of the occurrence of Hg, Pb, and Se in nestlings within GTNP and SRU during the two summers, 2006 and 2007. Table 2 summarizes levels of these environmental contaminants by year.

Nest Site	Hg		Pb		Se	
	2006	2007	2006	2007	2006	2007
4LazyF Ranch	0.150	0.204	0.003	0.019	0.755	1.415
	0.261	0.210	0.003	0.028	0.823	1.758
		0.563		0.089		1.285
Elbow Nest	0.614	0.697	0.004	0.011	1.477	1.316
		0.742		0.011		1.599
Hoback Junction		0.358		0.014		1.044
Lower Slide Lake	0.975	0.539	0.006	0.011	1.191	0.980
		0.575		0.012		1.270
Moose Nest	0.096	0.230	0.008	0.012	0.505	1.896
	0.291		0.003		0.619	
Oxbow Bend		0.797		0.193		1.783
Refuge Nest	0.115	0.146	0.006	0.012	3.498	2.722
	0.142		0.007		3.648	
Spaulding Bay		0.360		0.021		0.549
		0.367		0.166		0.574
Triangle X Ranch	0.212	0.342	0.014	0.142	0.542	1.019
	0.242	0.407	0.005	0.120	0.654	1.318
Arithmetic Mean	**0.310**	**0.436**	**0.0059**	**0.0574**	**1.371**	**1.369**
Geometric Mean	**0.237**	**0.388**	**0.0052**	**0.0304**	**1.045**	**1.256**

Table 2. A comparison of Hg, Pb, and Se concentrations (ppm wet wt.) in nestling bald eagles by year and nest site.

On average (using the arithmetic mean), levels of Hg in nestlings increased 41% from summer 2006 to summer 2007, levels of Pb increased nine-fold (873%) from summer 2006 to summer 2007, and levels of Se essentially remained unchanged over the course of the two summers. Using the geometric mean, levels of Hg in nestlings increased 64% from summer 2006 to summer 2007, levels of Pb increased five-fold (481%) from summer 2006 to summer 2007, and levels of Se increased 21% over the course of the two summers.

Results of the independent-samples t-tests for investigating if contaminant loads had increased from summer 2006 to summer 2007 are listed in Tables 3 through 5 below.

	Raw Data		Log-transformed Data	
	F	p-Value	F	p-Value
Hg	0.13	0.7220	0.728	0.402
Pb	31.61	0.0000	13.002	0.001
Se	6.56	0.0170	4.496	0.045

Table 3. Summary of Homogeneity of Variance tests for the three contaminants.

Because the homogeneity of variance assumption was violated (at a significance criterion of 0.05), degrees of freedom were appropriately adjusted in the 2-sample independent t-tests summarized below.

	Mean 2006	Standard Deviation 2006	Mean 2007	Standard Deviation 2007	t-Value	Degrees of Freedom	p-Value
Hg	0.310	0.2767	0.436	0.2063	-1.306	23	0.102
Pb	0.0059	0.0033	0.0574	0.0657	-3.030	14*	0.005
Se	1.371	1.4994	1.369	0.5472	0.007	12*	0.497
Molar Ratio Se:Hg	20.464	27.1023	11.346	11.6329	1.161	11*	0.337**

Table 4. Summary of 2-sample independent t-tests for raw data (H_1: Levels of contaminants have increased from 2006 to 2007).

* Degrees of freedom based on violation of homogeneity of variance test (see Table 4)

** H_1: Molar Ratio has changed from 2006 to 2007

	Mean 2006	Standard Deviation 2006	Mean 2007	Standard Deviation 2007	t-Value	Degrees of Freedom	p-Value
Hg	-1.442	0.7289	-0.947	0.5167	-1.992	23	0.058
Pb	-5.254	0.5025	-3.494	1.1456	-5.242	21*	0.000
Se	0.044	0.7284	0.235	0.4240	-0.751	13*	0.466

Table 5. Summary of 2-sample independent t-tests for log-transformed data (H_1: Levels of contaminants have increased from 2006 to 2007).
* Degrees of freedom based on violation of homogeneity of variance test (see Table 4)
** H_1 Molar Ratio has changed from 2006 to 2007.

Results of the analysis indicate that levels of Se essentially remained unchanged from summer 2006 to summer 2007 (p=0.466, log-transformed data). Levels of Pb in nestlings increased from summer 2006 to summer 2007 (p=0.000, log-transformed data). There was no difference in levels of Hg in nestlings from summer 2006 to summer 2007 (p=0.058, log-transformed data). The molar ratio (2.54 ppm Se: 1 ppm Hg) of Se to Hg did not change from 2006 to 2007 (p=0.337, raw data), although a 45% decrease in molar ratio was observed.

Results of the paired-sample t-tests conducted on the raw data to investigate if contaminant loads had significantly increased from summer 2006 to summer are given in Table 6 below.

	t-Value(d.f. = 5)	p-Value
Hg	-0.02	0.4933
Pb	-1.65	0.0794
Se	-0.90	0.2049

Table 6. Summary of 2-sample independent t-tests for log-transformed data (H_1: Levels of metals have increased from 2006 to 2007).

Levels of soluble trace elements tested in 2006 and 2007 are summarized in Table 7. Results of the paired-sample analysesindicate no difference in contaminant loads from summer 2006 to summer 2007. Even though a p-value of 0.0794 for Pb is nearly significant at the 0.05 level of significance, because data are sparse (only six nest sites), strong statistical conjecture is dubious at best.

For the most part, the six soluble trace elements listed in Table 2 were not detected or detected at low levels. Information about these trace elements is given at the end of this report (see *BIOLOGICAL RELEVANCE OF THE ANALYZED CONTAMINANTS).* Exceptions of concern include As in two nestlings (Refuge nest 2006 and Lower Slide Lake nest 2007); Cd in 4 nestlings (Lower Slide Lake nest 2007, Spaulding Bay nest 2007, and Triangle X Ranch nest 2007 at); Cr in 6 nestlings (4LazyF Ranch nest 2007, Oxbow Bend nest 2007, Spalding Bay nest 2007, and Triangle X Ranch nest 2007); and Ni in four nestlings (4LazyF Ranch 2007, Spaulding Bay nest 2007, and Triangle X Ranch nest 2007 at). Levels of all these metals in the nestlings, though elevated above detectable thresholds, are below toxic thresholds and will not be further discussed.

✦ DISCUSSION

Environmental contaminants in bald eagles are a persistent issue in Montana and Wyoming. Although blood from nestling eagles surveyed during the summers of 2006 and 2007 suggest the riparian ecosystem supporting these birds contains generally low levels of contaminants, several issues of concern emerged.

Analyses of contaminants (using geometric means) in the blood of nestlings (from summer 2006 to 2007) showed a 64% increase in Hg, a five-fold increase in Pb (481%), and a 21% increase in Se levels. In a study involving ospreys, Odsjo *et al*. (2004) noted that a 1:1 molar ratio (2.54ppm Se: 1ppm Hg) is considered efficacious for detoxifying Hg. From 2006 to 2007, the molar ratio in nestlings of our study area decreased from 20:1 to 11:1. Although it is well above the 1:1 threshold, a decrease of nearly 45% is a matter of importance. Two concerns are revealed: 1) Because Se mitigates the toxic effect of Hg, nestlings could succumb to Hg toxicity if Hg levels increased while Se levels remained unchanged (as demonstrated by a 44.5% decrease in molar ratio of Se:Hg from 2006 to 2007) Currently, Se appears available to nestling bald eagles in sufficient quantities to mitigate any effects of current Hg contamination, but if the trend continues, Hg toxicity could prove fatal to nestlings, and 2) All nests that we surveyed fall within a National Park or are within geographical jurisdictions that protect the environment from contaminants. An increase in the levels of these contaminants is therefore not expected. A monitoring program may be indicated to identify potential long-term changes within the GYE.

Nest Site	Soluble Trace Element											
	As		Sb		Cd		Cr		Ni		Tl	
	2006	2007	2006	2007	2006	2007	2006	2007	2006	2007	2006	2007
4LazyF Ranch	0.007	0.0050	nd*	nd*	0.004	0.0005		0.012		0.020	0.002	nd*
	0.007	0.0080	nd*	0.009	0.004	0.0180[1]		0.044		0.102[1]	0.002	nd*
		0.0005		nd*		0.0040		0.130[1]		0.039		nd*
Elbow Nest	0.004	0.0005	nd*	nd*	0.004	0.0005		0.009		0.006	0.002	nd*
		0.0005		nd*		0.0005		0.011		nd*		nd*
Hoback Junction		0.0005		nd*		0.0005		0.010		nd*		nd*
Lower Slide Lake	0.003	0.0060	nd*	nd*	0.009	0.0180[1]		0.010		0.005	0.002	nd*
		0.0310[1]		nd*		0.0005		0.010		nd*		nd*
Moose Nest	0.003	0.0005	nd*	nd*	0.005	0.0005		0.008		0.014	0.002	nd*
	0.003		nd*		0.003						0.002	nd*
Oxbow Bend		0.0005		nd*		0.0005		0.210[1]		0.026		nd*
Refuge Nest	0.006	0.0005	nd*	nd*	0.006	0.0005		0.008		0.006	0.002	nd*
	0.015[1]		nd*		0.007						0.002	nd*
Spaulding Bay		0.0005		0.007		0.0005		0.100[1]		0.016		nd*
		0.0005		nd*		0.0380[1]		0.300[1]		0.142[1]		nd*
Triangle X Ranch	0.005	0.0005	nd*	nd*	0.004	0.0310[1]		0.220[1]		0.095[1]	0.002	nd*
	0.004	0.0005	nd*	nd*	0.004	0.0350[1]		0.220[1]		0.106[1]	0.002	nd*

Table 7. Soluble trace elements (ppm wet wt.) detected in blood of nestling bald eagles by year and nest site.
[1]= atypically high value, relative to other values
nd*=metal tested for, but not detected.

Independent t-tests were performed on both the original data and log-transformed data (using the natural logarithm) as a comparative analysis for Hg, Pb, and Se (refer to Tables 5 and 6).

All tests show a drop in p-value for transformed data, but of noteworthy interest is Hg which dropped from 0.102 for raw data to 0.058 for transformed data, suggesting an increase in power (detecting significant differences when they exist). When data are expressed in ppm, the log-transformation is the correct approach, and a p-value of 0.058 suggests further investigation with larger samples before any firm conclusions are postulated.

In addition to our investigation of Pb, Hg, and Se, other contaminants of concern including As, Cd, Cr, and Ni were encountered in some nestlings at atypically high levels when compared to other nestlings in the same nest (see Table 7). This suggests that the affected nestling may have ingested the contaminant from a specific food source (for example, a contaminated prey item). Although below toxic thresholds (see *BIOLOGICAL RELEVANCE OF THE ANALYZED CONTAMINANTS*), we suggest continued monitoring of these contaminants in the future.

Independent samples t-tests assume independence of nestlings within and between groups over the two summers. As an alternative procedure, we treated *nest site* as the experimental unit and performed a repeated measures analysis to investigate if contamination was occurring within specific environments at a generalized level from summer 2006 to summer 2007. If more than one nestling inhabited a specific nest site, levels of contaminants were averaged over all nestlings at the site. This analysis was performed on the raw data (not log-transformed) because the calculations involved do not incorporate a geometric mean if the log-transform is applied to the data. Results of this analysis indicated no difference in contaminant concentration between summer 2006 and summer 2007 for the nest sites. However, with respect to Pb, a p-value of 0.0794 was nearly significant at the 0.05 level of significance.

	Hg		Pb		As		Cd	Cr	Ni
	2006	2007	2006	2007	2006	2007	2007	2007	2007
4LazyF Ranch		0.204		0.019		0.0050[1]	0.0005	0.012	0.020
		0.563[1]		0.089[1]		0.0080[1]	0.0180[1]	0.044	0.102[1]
		0.210		0.028		0.0005	0.0040	0.130[1]	0.039
Lower Slide Lake						0.0060	0.0180[1]		
						0.0310[1]	0.0005		
Moose Nest	0.096								
	0.291[1]								
Refuge Nest					0.006				
					0.015[1]				
Spaulding Bay				0.021			0.0005	0.10	0.016
				0.166[1]			0.0380[1]	0.30[1]	0.142[1]
Triangle X Ranch			0.005						
			0.014[1]						

Table 8. Noteworthy differences in contaminant loads in nests containing more than one nestling.
[1] = atypically high value (>2x), relative to other values in the same nest.

Because only six nest sites were included in the analysis, it is questionable whether the increase in Pb from summer 2006 to summer 2007 is due to pure chance, or perhaps from some environmental contamination effect. Therefore, we suggest that: 1) the repeated measures analysis approach be implement when larger sample sizes are available - it is a powerful analysis technique that minimizes the effects of extraneous variables; and, 2) potential localized sources of Pb contamination (for example, elk harvest where lead rifle bullets are allowed, or lead shot used in fishing) be identified and removed from the proximity of any nest site(s), with continued monitoring in the future (Craighead and Bedrosian 2008).

Several nests containing more than one nestling demonstrated substantially higher levels of contaminant loads in some nestlings when compared to other nestlings in the same nest. Table 7 below summarizes these atypically higher levels defined by *at least twice the level* (>2x) of other nestlings in the same nest.

Assuming that the higher levels were not a result of inaccurate laboratory analyses, the discrepancies may most likely result from contaminated prey consumed by the nestling. Contamination may be generated locally (herbicides, pesticides, poison-laced bait, lead shot, mining, etc.) or on a grander scale (environmental contamination).

Natural degassing of the earth's crust is the major source of environmental Hg worldwide (Heinz 1996) and coal-fired utilities are the largest single unregulated anthropogenic source of Hg emissions in the United States (USEPA 1997). However, recent data indicate wildfires are responsible for massive aerosols of Hg (Friedli *et al.* 2003) and could release 15 times more Hg into the air than every U.S. coal-fired power plant combined (Friedli *et al*. 2001).

Biswas *et al*. (2003) indicated combustion of litter and green vegetation resulted in virtually complete release of Hg stored in fuel and forests in the Rocky Mountain region. Montana and Wyoming forests may contain large reservoirs of Hg deposited during the industrial age that can be released during fires. Additionally, Hg concentrations in fish were related to ratio of the clear-cut (forest logging) size to lake area in Canadian boreal forests (Garcia and Carignan 2005), suggesting large scale logging operations contribute to Hg contamination of higher trophic-level piscivorous predators (Driscoll *et al.* 1994), which may bioaccumulate in higher trophic-level predators.

Geometric-mean Hg concentrations were higher in nestling bald eagles sampled in Wyoming than those in Montana but both were well below that considered toxic (Harmata 2006). Perhaps higher concentrations in Wyoming nestlings are a function of their proximity to Yellowstone National Park where large, extensive forest fires occur regularly and geothermal activity abounds. Less human and industrial activity occur in the Snake River watershed above nest sites of nestling eagles sampled in Wyoming, unlike areas in the Upper Missouri River watersheds above nest sites of nestling eagles sampled in Montana. High Hg concentrations in eagles may therefore be a result of recent, large, intense forest fires in the Canadian boreal forest. These fires release Hg into the atmosphere not only from trees consumed but especially peat that absorbed disproportionate amounts of atmospheric Hg emitted during the industrial age (Turetsky *et al.* 2006). Advancing global climate change and associated desiccation and emolation of temperate and boreal forests, exacerbated by extensive clear-cutting may increase poisoning of aquatic ecosystems with high levels of Hg in the future. Hence, we suggest continued monitoring to identify potential long-term trends within the GYE.

BIOLOGICAL RELEVANCE OF THE ANALYZED CONTAMINANTS

Hg

Hg, in the form of methylmercury (CH_3Hg^+), is bioaccumulated in organisms, has no biological benefit, and is responsible for deleterious effects in birds (USEPA 1997, Boening 2000, Nacci *et al*. 2005). Dietary Hg affects raptorial species neurologically (Fimreite and Karstad 1971), physiologically (Boening 2000), and reproductively (Fimreite and Karstad 1971, Wiemeyer *et al.* 1993). Neurological effects appear to be manifested in a threshold effect resulting in overall weakness and wasting. None of the nestling eagles sampled in this study displayed symptoms of Hg poisoning but 7 of 13 eagles submitted for rehabilitation in Montana did. Eagles submitted for rehabilitation exhibiting symptoms had Hg concentrations in blood (geometric mean = 0.9ppm) higher than those that did not (geometric mean = 0.31, N = 6). Hg in blood of bald eagles submitted for rehabilitation was above that considered toxic (≥0.4ppm wet weight; Burgess et al. 2005) and suggests these eagles fed on a highly contaminated food supply (Wiemeyer 1991). However, without feather analysis for perspective, determining if contamination was acute (recent, high level) or chronic (long-term, low level) is problematic.

Se

Se is a natural component of soils, is essential to all plants and animals, and is present at high concentrations in some arid areas of the western U.S. Se is an essential micronutrient with important biological and biochemical functions in organisms because of its unique antioxidant properties and its ability to regulate thyroid gland metabolism, but at high concentrations, it can be toxic (Lemly 1993). Dissolution of Se and other potentially toxic elements from soils and their accumulation in ecosystems are accelerated by irrigation (Eisler 1985). Burning of fossil fuels is another major source of Se contamination of aquatic ecosystems and elevated concentrations commonly occur in water and soils of semiarid regions of the western U.S., including Montana and Wyoming (Ohlendorf 1989).

Attributing Se toxicity to eagles is tenuous. Se induced mortality has been documented in waterfowl, but the effects are primarily teratogenic or manifested in reduced natality or productivity (Eisler 1985, Ohlendorf *et al.* 1986, Heinz *et al.* 1989, Hoffman *et al.* 1990). Although congenital mandibular deformities have been observed in bald eagles in the Great Lakes Region, Se was an unlikely causative agent (Bowerman *et al.* 1994) and similar effects have not been recorded for eagles elsewhere. No nestling eagles exhibited physical symptoms of Se poisoning despite some with very high concentrations in blood (>3ppm) in Wyoming. However, aberrant pied plumage has been noted in nestlings in the Greater Yellowstone Ecosystem (Harmata and Montopoli 1998) where Se concentrations have been historically elevated (arithmetic mean >1ppm in nestlings, >3ppm in adults; Harmata and Oakleaf 1992).

Hg – Se Relationship

Se toxicity in birds is manifested mostly in embryos (Poley and Moxon 1938, Ohlendorf *et al.* 1986). Se may mitigate effects of Hg, or vice versa in organisms (Rudd *et al.* 1980, Pelletier 1985, Eisler 1985, Chen *et al.* 2006). Toxicity of CH_3Hg^+ to birds may be highly dependent upon the availability of dietary Se

(Weech *et al.* 2003). A 1:1 molar ratio (2.54ppm Se: 1ppm Hg) is considered efficacious for detoxifying Hg (Odsjo *et al*. 2004) but ratios in some seabird species in the United Kingdom had ratios of 5 to 45 to one (Hutton 1981).

Pb

There are abundant studies in the literature describing the effects of Pb on raptors, especially eagles (*e.g.*, Pattee *et al.* 1981, Pattee and Hennes 1983, Kramer and Redig 1997). However, symptoms attributable exclusively to Pb toxicosis were not exhibited by any eagles in this study. Origin and implications of exposure in Wyoming nestlings will be explored in-depth by cooperators at Beringia South, Inc. (B. Bedrosian, pers. comm.).

Sb

Sb is found at very low levels throughout the environment. The concentration of Sb in ambient air ranges from less than 1 nanogram per cubic meter (ng/m^3) to about 170 ng/m^3. However, concentrations may be greater than 1,000 ng/m^3 near factories that convert Sb ores into metal or make Sb oxide. Soil usually contains very low concentrations of Sb (less than 1 part per million [ppm]). However, higher concentrations have been detected at hazardous waste sites and at Sb-processing sites. Food contains small amounts of Sb: the average concentration of Sb in meats, vegetables, and seafood is 0.2 to 1.1 parts per billion (ppb). People who work in industries that process Sb ore and metal, or make Sb oxide, may be exposed to Sb by breathing dust or by skin contact. (ATSDR 1992).

Animal studies have reported effects on the respiratory and cardiovascular systems and kidney from chronic inhalation exposure. Animal studies involving oral consumption of Sb have reported effects on the blood, liver, central nervous system, and gastrointestinal effects (ATSDR 1992). A National Toxicology Program (NTP 1992) 14-day drinking water study of potassium antimony tartrate reported an increase in relative liver and kidney weights in the high dose group (females only). A 13-week intraperitoneal injection study, also by the NTP, reported inflammation and/or fibrosis of the liver in mice dosed with potassium Sb tartrate. EPA has not established a Reference Concentration (RFC, or non-toxic threshold) for Sb. However, EPA has established an RFC of 0.0002 milligrams per cubic meter (mg/m^3) for Sb trioxide based on respiratory effects in rats.

As

As is a carcinogen, teratogen, and possible mutagen in mammals (ATSDR 1993). Chronic exposure can result in anemia, neuropathy, and skin lesions that can develop into skin cancer in mammals. Benthic feeders are more susceptible to As than other aquatic organisms. In birds, tolerance to As varies among species, but effects include destruction of gut blood vessels, blood cell damage, muscular incoordination, debility, slowness, jerkiness, falling, hyperactivity, fluffed feathers, drooped eyelids, immobility, seizures, and systemic, growth, behavioral, and reproductive problems (Stanley *et al*. 1994; Whitworth *et al*. 1991; Camardese *et al*. 1990).

Literature and electronic search revealed no instances of arsinecosis or mortality of bald eagles directly attributable to As. Levels in blood of eagles found here may be reflective of background levels, sensitivity of analysis, or both. One-hundred percent of Wyoming nestlings exhibited detectable levels of As, one 15 times the detection limit. As contamination may be inconsequential but continued monitoring is indicated.

Cd

Cd is highly toxic to wildlife; carcinogenic, teratogenic, and potentially mutagenic, with severe sublethal and lethal effects at low environmental concentrations (Eisler 1985a). Cd is associated with inhibited molt, depressed respiration, low enzyme levels, muscle contractions, decreased growth and reproduction. Cd bioaccumulates at all trophic levels, accumulating in the livers and kidneys of fish (Shindayigaya *et al*. 1994; Sadiq 1992). However, insects and birds may be especially resistant to biocidal effects of Cd (White and Finley 1978). In the absence of mortality, morbidity, or reduced productivity attributed to Cd in local populations, Cd residues may be inconsequential but should be monitored.

Cr

Cr occurs in the environment primarily in two valence states, trivalent Cr (Cr III) and hexavalent Cr (Cr VI). Exposure may occur from natural or industrial sources of Cr. Cr III is much less toxic than Cr (VI). The respiratory tract is also the major target organ for Cr (III)

toxicity, similar to Cr (VI). Cr (III) is an essential element in humans. The body can detoxify some amount of Cr (VI) to Cr (III).

The respiratory tract is the major target organ for Cr (VI) toxicity, for acute (short-term) and chronic (long-term) inhalation exposures. Shortness of breath, coughing, and wheezing were reported from a case of acute exposure to Cr (VI), while perforations and ulcerations of the septum, bronchitis, decreased pulmonary function, pneumonia, and other respiratory effects have been noted from chronic exposure. Human studies have clearly established that inhaled Cr (VI) is a human carcinogen, resulting in an increased risk of lung cancer (ATSDR 1998).

Animal studies have shown Cr (VI) to cause lung tumors via inhalation exposure. Animal studies have not reported reproductive or developmental effects from inhalation exposure to Cr (VI). Oral studies have reported severe developmental effects in mice such as gross abnormalities and reproductive effects including decreased litter size, reduced sperm count, and degeneration of the outer cellular layer of the seminiferous tubules. (ATSDR 1998, USEPA (1) 1998). A study of mice fed high levels of Cr (III) in their drinking water has suggested a potential for reproductive effects, although various study characteristics preclude a definitive finding. (USEPA (2) 1998).

Ni

Ni occurs naturally in the environment at low levels. Ni is an essential element in some animal species, and it has been suggested it may be essential for human nutrition. Ni dermatitis, consisting of itching of the fingers, hands, and forearms, is the most common effect in humans from chronic (long-term) skin contact with Ni. Respiratory effects have also been reported in humans from inhalation exposure to Ni. Human and animal studies have reported an increased risk of lung and nasal cancers from exposure to Ni refinery dusts and Ni subsulfide. Animal studies of soluble Ni compounds (i.e., Ni carbonyl) have reported lung tumors. Pulmonary fibrosis and renal edema were reported in humans and animals following acute (short-term) exposure to Ni carbonyl. EPA has classified Ni refinery dust and Ni subsulfide as Group A, human carcinogens, and Ni carbonyl as a Group B2, probable human carcinogen (USEPA 1986).

Ni is an essential nutrient for some mammalian species, and has been suggested to be essential for human nutrition. By extrapolation from animal data, it is estimated that a 70-kg person would have a daily requirement of 50 µg per kg diet of Ni. Animal studies have reported reproductive and developmental effects, such as a decreased number of live pups per litter, increased pup mortality, and reduction in fetal body weight, and effects to the dam from oral exposure to soluble salts of Ni. Sperm abnormalities and decreased sperm count have been reported in animals exposed to Ni nitrate orally and Ni oxide by inhalation, respectively (ATSDR 1997).

Th

Th is not a rare element, being 10 times more abundant than silver. It enters the environment primarily as a trace contaminant from coal combustion and smelting. Some Th compounds are removed from the atmosphere in precipitation and persist in water and soil for long periods. Th may be absorbed by plants and enters the food chain where it is bioaccumulated in fish and higher trophic level consumers (ATSDR 1995). A recent study with planktonic communities showed that Tl^{3+} ions, a common form of Th in aquatic environments, are about 34,000 times more toxic than Cd ions (Twining *et al.* 2003), suggesting toxicity to higher vertebrates at low concentrations. For example, waterfowl have died from ingesting Th-contaminated foods obtained from aquatic environments in Japan (Mochizuki *et al.* 2005).

Secondary poisoning from thallium-treated grain used for ground squirrel (*Spermophilus spp.*) control was identified early in the last century (Linsdale 1931). Carnivorous mammals and predatory and scavenger birds (especially eagles) have been killed by Th sulfate ($Tl_2 SO_4$) and Th poisoning was reported in bald eagles in Wyoming in 1971, presumably from ingestion of $Tl_2 SO_4$ laced baits (Cromartie *et al*. 1975). Implications of Th residues in nestling bald eagle blood found in this study are unknown. In the absence of mortality, morbidity, or reduced productivity attributed to Th in local populations residues may be inconsequential but should be monitored.

Organochlorines

DDE (a metabolite of DDT) was the primary contaminant reducing reproductive success of bald eagles in North America with the majority of exposure from the avian portion of the diet (Wiemeyer 1991). Although DDE is less toxic to birds than most organochlorines, it can elicit abnormal behavior, eggshell thinning, and adult and embryonic mortality (Risebrough 1986). Low concentrations found in our study reflect the 1973 ban on DDT and subsequent decline in use, but continued presence (*i.e*., detection frequency) indicates long-term persistence of the chemical. A sequence of increasing residues is evident progressing downstream in the Missouri River watershed. A continual decline in residues can be expected barring unforeseen legalization and increasing use.

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✦ LITERATURE CITED

ATSDR (Agency for Toxic Substances & Disease Registry). 1992. *Toxicological Profile for Antimony.* U.S. Public Health Service, U.S. Department of Health and Human Services, Atlanta, GA.

ATSDR 1993. *Toxicological Profile for Arsenic.* Public Health Service, U.S. Department of Health and Human Services, Atlanta, GA.

ATSDR 1995. ToxFAQs™ for Thallium. Case number 7440-28-0. http://www.atsdr.cdc.gov/tfacts54.html

ATSDR 1997. *Toxicological Profile for Nickel (Update)*. Public Health Service, U.S. Department of Health and Human Services, Atlanta, GA.

ATSDR 1998. *Toxicological Profile for Chromium*. U.S. Public Health Service, U.S. Department of Health and Human Services, Atlanta, GA. 1998.

Biswas, A., J. D.Blum and G. J. Keeler 2003. Forest fire effects on mercury and other trace metal concentrations in a Rocky Mountain forest ecosystem. EOS Transactions of American Geophysical Union 84 (46). Fall Meeting. Supplemental. Abstract #B32C-05.

Boening, D.W. 2000. Ecological effects, transport, and fate of mercury: A general review. Chemosphere 40:1335-1351.

Bowerman, W. W. IV, E. D. Evans, J. P. Giesy, and S. Postupalsky. 1994. Using feathers to assess risk of mercury and selenium to bald eagle reproduction in the Great Lakes region. Archives of Environmental Contamination and Toxicology 27: 294-298.

Burgess, N.M, D. C. Evers, and J.D. Kaplan. 2005. Mercury and other contaminants incommon loons breeding in Atlantic Canada. Ecotoxicology 14:241-252.

Camardese, M. B., D. J. Hoffman, L. J. LeCaptain, and G. W. Pendleton. 1990. Effects ofarsenate on growth and physiology in mallard ducks. Environmental Toxicology and Chemistry 9:785-95.

Chen, C., H. Yu, J. Zhao, B. Li, L. Qu, S. Liu, P. Zhang, and Z. Chai . 2006. The roles of serum selenium and selenoproteins on mercury toxicity in environmental and occupational exposure. Environmental Health Perspectives 114:297–301.

Craighead, D. and B. Bedrosian, 2008. Blood levels of common ravens with access to big game offal. Journal of Wildlife Management.

Cromartie, E., W.L. Reichel, L.N. Locke, A.A. Belisle, T.E. Kaiser, T.G. Lamont, B.M. Mulhern, R.M. Prouty, and D.M. Swineford. 1975. Residues of organochlorine pesticides and polychlorinated biphenyls and autopsy data for bald eagles, 1971-72. Pesticide Monitoring Journal 9:11-14.

Driscoll, C.T., C. Yan, C.L. Schofield, R. Munson, and J. Holsapple. 1994. The mercury cycle and fish in the Adirondack lakes. Environmental Science and Technology 28:136A-143A.

Eisler, R. 1985a. Cadmium hazards to fish, wildlife, and invertebrates: A Synoptic Review. U.S. Department of Interior, Fish and Wildlife Service Biological Report 85 (1.2).

Eisler, R. 1985b. Selenium hazards to fish, wildlife, and invertebrates: A Synoptic Review. U.S. Department of Interior, Fish and Wildlife Service Biological Report 85 (1.5).

Fimreite, N. and L. Karstad. 1971. Effects of dietary methyl mercury on Red-Tailed Hawks. The Journal of Wildlife Management, 35(2):293-300, doi:10.2307/ 3799603

Friedli, H.R., L. F. Radke, and J. Y. Lu. 2001. Mercury in smoke from biomass fires. Geophysical Research Letters 28:3223–3226.

Friedli, H.R., L.F. Radke, J.Y. Lu, C.M. Banic, W.R. Leaitch, J.I. Mac Pherson. 2003. Mercury emissions from burning of biomass from temperate North American forests: laboratory and airborne measurements. Atmospheric Environment 37:253-267

Garcia, E. and R. Carignan. 2005. Mercury concentrations in fish from forest harvesting and fire-impacted Canadian boreal lakes compared using stable isotopes of nitrogen. Environmental Toxicology and Chemistry 24:685-693.

Harmata, A. R. 1996. Bald eagle management plan for Greater Yellowstone: 1995 Update. Greater Yellowstone Bald Eagle Working Group. Wyoming Game & Fish Dept., Lander, Wyoming. 47 pp.

Harmata, A. R _ 2006. Monitoring mercury and other contaminants in bald eagles in southwestern Montana & northwestern Wyoming. Interim Report – 30 November 2006

Harmata, A. R and G.J. Montopoli. 1998. Pied plumage in bald eagles. Journal of Field Ornithology 69:326-335.

Harmata, A. R., and B. Oakleaf. 1992. Bald Eagles of the Greater Yellowstone Ecosystem: An ecological study with emphasis on the Snake River, Wyoming. Wyoming Game & Fish Dept., Lander. 368 pp.

Heinz, G.H. 1996. Mercury poisoning in wildlife. Pgs. 118–127 *In* Noninfectious diseases of wildlife. A. Fair-brother, L.N. Locke, and G.N. Hoff (eds.). Iowa State University Press, Ames, Iowa.

Heinz, G.H, D.J. Hoffman, and L.G. Gold. 1989. Impaired reproduction of mallards fed an organic form of selenium. The Journal of Wildlife Management 53: 418-428.

Henny, C.J., E.J. Kolbe, E.F. Hill, and L.J. Blus. 1987. Case histories of bald eagles and other raptors killed by organophosphorus insecticides topically applied to livestock. Journal Wildlife Diseases 23:292-295.

Hoffman, R.J., R.J. Hallock, T.G Rowe, M.S. Lico, H.L. Burge, and S.P. Thompson. 1990. Reconnaissance investigation of water quality, bottom sediment, and biota associated with irrigation drainage in and near Stillwater Wildlife Management Area, Churchill County, Nevada. Water Resource Invest. Rep. 89-4105. U.S. Geological Survey, Carson City, Nevada, 150 pp.

Hutton, M. 1981. Accumulation of heavy metals and selenium in three seabird species from the United Kingdom. Environmental Pollution. 26: 129-145.

Kramer, J.L. and P.T. Redig. 1997. Sixteen years of lead poisoning in eagles, 1980-95: An epizootiologic view. Journal of Raptor Research 31:327-332.

Lemly, A.D. 1993. Guidelines for evaluating selenium data from aquatic monitoring and assessment studies. Ecotoxicology and Environmental Safety 26:181-204.

Linsdale, J.M. 1931. Facts concerning the use of Th in California to poison rodents: Its destructiveness to game birds, song birds and other valuable wild life**.** Condor 33:92-106.

Mochizuki, M., M. Mori, M. Akinaga, K.Yugami, C. Oya, R. Hondo, and F. Ueda. 2005. Th Contamination in Wild Ducks in Japan. Journal of Wildlife Diseases 41:664-668.

Nacci, D., M. Pelletier, J. Lake, R. Bennett, J. Nichols, R. Haebler. 2005. An approach to predict risks to wildlife populations from mercury and other stressors**.** Ecotoxicology 14: 283 – 293.

NTP (National Toxicology Program). 1992. *Toxicity Studies of Antimony Potassium Tartrate* (CAS no.28300-74-5) in F344/N Rats and B6C3F1 Mice (Drinking Water and Intraperitoneal Injection Studies). Research Triangle Park, NC: U.S. Department of Health and Human Services, Public Health Service, National Institutes of Health.

Odsjo, T., A. Roos, and A.G. Johnels. 2004. The tail feathers of osprey nestlings (*Pandion haliaetus L.*) as indicators of change in mercury load in the environment of southern Sweden (1969-1998): a case study with a note on the simultaneous intake of selenium. Ambio 33:133-137.

Ohlendorf, H.M., R.L. Hothem, C.M. Bunck, T.W. Aldrich, and J.F. Moore. 1986. Relationships between selenium concentrations and avian reproduction. Transactions of the North American Wildlife and Natural Resources Conference 51:330-342.

Ohlendorf, H.M. 1989. Bioaccumulation and effects of selenium in wildlife. Pgs. 133-177 *in* Selenium in Agriculture and the Environment. Soil Science Society of America Special Publication no. 23.

Pattee, O.H., S.N. Wiemeyer, B.M. Mulhern, L. Sileo, and J.W. Carpenter. 1981. Experimental lead-shot poisoning in bald eagles. Journal of Wildlife Management 45:806-810.

Pattee, O.H. and S.K. Hennes. 1983. Bald eagles and waterfowl: The lead shot connection. Proceedings of the North American Wildlife Conference 48:230-237.

Pelletier, E. 1985. Mercury-selenium interaction in aquatic organisms: a review. Mar. Environ. Res. 18: 111-132.

Poley, W.E., A.L. Moxon, and K.W. Franke. 1937. Further studies of the effects of selenium poisoning on hatchability. Poultry Science 17:72-76.

Risebrough, R.W. 1986. Pesticides and bird populations. P *in* R.F. Johnston, *ed*. Current Ornithology, V3:397-427. Plenum Press, NY.

Rudd, J.W.M., M.A. Turner, B.E. Townsend, A. Swick, and A. Furitani. 1980. Dynamics of selenium in mercury-contaminated experimental ecosystems. Canadian Journal of Fishery & Aquatic Science 37:848.

Sadiq, M**.** 1992. Toxic metal chemistry in marine environments. Marcel Dekker. New York.

Sindayigaya, E., R.V. Cauwnbergh, H. Robberecht, and H. Deelstra. 1994. Copper, zinc, manganese, iron, lead, cadmium, mercury, and arsenic in fish from Lake Tanganyika, Burundi. The Science of the Total Environment. 144:103-115.

Stanley, T.R., Jr., J.W. Spann, G.J. Smith, and R. Rosscoe. 1994. Main and interactive effects of arsenic and selenium on mallard reproduction and duckling

growth and survival. Archives of Environmental Contamination and Toxicology. 26:444-451.

Turetsky, M.R., J.W. Harden, H. Friedli, M. Flannigan, N. Payne, J. Crock, L. Radke. 2006. Wildfires threaten mercury stocks in northern soils. Geophysical Research Letters 33:10.

Twining, B.S., M.R.Twiss, and N.S. Fisher. 2003. Oxidation of Th by Freshwater Plankton Communities. Environmental Science & Technology 37:2720 – 2726.

U.S. Environmental Protection Agency. 1986. *Health Assessment Document for Nickel*. EPA/600/8-83/012F. National Center for Environmental Assessment, Office of Research and Development, Washington, DC.

U.S. Environmental Protection Agency. 1997. Mercury Study Report to Congress. USEPA, Washington, D.C. 8. www.epa.gov/mercury/report.htm

U.S. Environmental Protection Agency (1) 1998. *Toxicological Review of Hexavalent Chromium*. National Center for Environmental Assessment, Office of Research and Development, Washington, DC.

U.S. Environmental Protection Agency (2) 1998. *Toxicological Review of Trivalent Chromium*. National Center for Environmental Assessment, Office of Research and Development, Washington, DC.

Weech, S.A., L. K. Wilson, K. M. Langelier, and J. E. Elliott. 2003. Mercury residues in livers of Bald Eagles (*Haliaeetus leucocephalus*) Found Dead or Dying in British Columbia, Canada (1987–1994). Archives of Environmental Contamination and Toxicology 45:562-569

Wiemeyer, S.N. 1991. Effects of environmental contaminants on raptors in the Midwest. Pages 168-181 *in* Proceedings of the Midwest raptor management symposium and workshop. National Wildlife Federation, Washington, D.C.

Wiemeyer, S.N., C.M. Bunck, and C.J. Stafford. 1993. Environmental contaminants in bald eagle eggs-1980-84--and further interpretations of relationships to productivity and shell thickness. Archives of Environmental Contamination and Toxicology 24:213-227.

White, D.H. and M.T. Finley. 1978. Uptake and retention of dietary cadmium in mallard ducks. Environmental Research 17:53-59.

Whitworth, M.R., G.W. Pendleton, D.J. Hoffman, and M.B. Camardese. 1991. Effects of dietary boron and arsenic on the behavior of mallard ducks. Environmental Toxicology and Chemistry 10:911-916.

MERCURY TOXICITY IN WILDLAND FIREFIGHTERS
A PROGRESS REPORT

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✦ ABSTRACT

After the sudden emergence of mercury (Hg) poisoning in bald eagles in the Greater Yellowstone Ecosystem in December 2005, we began a preliminary study to investigate if Hg accumulated at toxic levels in wildland firefighters who were exposed to smoke and other particulates while fighting fires in the western United States during summer 2007. Deviating from our original design, we were able to analyze blood from 12 subjects, and repeated blood draws occurred for only four of those subjects. Three of the subjects had measurable Hg levels that approached the limit of a non-toxic Hg concentration (<10 mcg/L). A fourth subject had a measurable level of 4 mcg/L. All other subjects had levels designated by <4 mcg/L. For the four subjects with repeated blood draws, two demonstrated an increase in mercury levels over time (<4 to 7 mcg/L, and 5 to 8 mcg/L), one showed no change over time (<4 to <4 mcg/L), and one demonstrated a decrease in mercury levels over time (4 to <4 mcg/L). Beside Hg, blood analyses were performed for the presence of four other metals: lead, cadmium, cobalt, and thallium. Levels of these metals were well-below toxic thresholds and within normal range for all subjects. Although we recorded times of exposure to smoke for all subjects, our sample was too small to investigate any statistical inference about the relationship between the duration of exposure to smoke and changes in blood Hg concentration. As forest fires continue to ignite in the western U.S. at unprecedented levels, burning areas such as dried bogs and marshes, we highly recommend continued research and a mercury-monitoring program to ensure the continued health and safety of our firefighting crews.

✦ INTRODUCTION

Since December 2005, approximately 15 bald eagles and one golden eagle (*Aquila chrysaetos*) were submitted for treatment to the Montana Raptor Conservation Center (MRCC). Analysis revealed that eagles contained toxic levels of Hg in their blood (≥0.4ppm wet weight,. Six died, one was released, and the rest

remain in treatment but most likely will not be releasable. Symptoms of Hg toxicity were expressed by at least three other eagles submitted prior to December 2005, but their blood was not analyzed specifically for this metal. We suspect that Hg poisoning may have emerged prior to December 2005, but was not diagnosed. The presence of Hg or other contaminants in bald eagles suggests environmental contamination that may eventually manifest itself in the human population.

Since summer 2006, blood samples from more than 100 nestling, migratory (fall and spring), and wintering eagles in Montana and Wyoming were collected in an attempt to monitor and locate the source of the mercury poisonings (Harmata 2006, Montopoli *et al*. 2008). They expected to locate origins of the contaminants, but none materialized. All eagles had detectable levels of contaminants in their blood, most notably Hg. For example, during fall 2007, Harmata et al. trapped 22 wintering bald eagles in southwestern Montana, and results indicated that Hg loads in the bald eagles were very high (geometric mean = 10.0 mcg/L; toxicity level > 4 mcg/L); and, during summers 2006 and 2007, nestlings in northwestern WY (10 and 15, respectively) were sampled for contaminants and results suggested elevated levels of Hg that increased by 64% over the two summers.

Natural degassing of the earth's crust is the major source of environmental Hg worldwide (Heinz 1996) and coal-fired utilities are the largest single unregulated anthropogenic source of Hg emissions in the United States (USEPA 1997). However, recent data indicate wildfires are responsible for massive aerosols of Hg (Friedli *et al.* 2003, Wiedinmyer and Friedli 2007) and could release 15 times more Hg into the air than every U.S. coal-fired power plant combined (Friedli *et al*. 2001). Biswas *et al*. (2003) indicated combustion of litter and green vegetation resulted in virtually complete release of Hg stored in forests in the Rocky Mountain region. Montana and Wyoming forests may contain large reservoirs of Hg deposited during the industrial age that can now be released into the atmosphere during fires. Also, Hg concentrations in fish are influenced by the extent (size) of clear-cut forests in relation to area of lakes in the Canadian boreal forests (Garcia and Carignan 2005). These data suggest large scale logging operations contribute to Hg contamination and bioaccumulate in higher trophic level piscivorous predators (Driscoll *et al.* 1994).

Harmata (2006) speculated that "... Perhaps higher concentrations in Wyoming nestlings are a function of their proximity to Yellowstone National Park where large, extensive forest fires occur regularly and geothermal activity abounds...These fires release Hg into the atmosphere not only from trees consumed but especially peat that absorbed disproportionate amounts of atmospheric Hg emitted during the industrial age (Turetsky et al. 2006). Advancing global climate change and associated desiccation and emolation of temperate and boreal forests, exacerbated by extensive clear-cutting, may increase poisoning of aquatic ecosystems with high levels of Hg in the future."

In late May 2007, while discussing the issue of Hg poisoning in bald eagles, we theorized that, if forest fires are the source of Hg contamination in the bald eagles, the contaminant could also manifest itself in other species, most notably wildland firefighters who occupy the immediate environment while combating forest fires. Exposure of firefighters to Hg may occur: 1) after its release into the atmosphere as a result of combustion of mercury-laden tree bark and other organic plants; and, 2) while firefighters inhale particulates resulting from activities such as digging fire line in unburned areas, especially peat bogs where microorganisms methylized the inorganic mercurial ion under riparian conditions.

During summer 2007, we therefore initiated a preliminary study to investigate if Hg accumulated at toxic levels in wildland firefighters who were exposed to smoke and other particulates while fighting fires in the western United States.

✦ ANALYSIS AND RESULTS

The null and alternative research hypotheses were defined by:

> H_0: There are no statistically discernible differences in Hg levels in blood of firefighters after exposure to smoke-related contaminants.
> H_1: There is a statistically discernible increase in Hg levels in blood of firefighters

after exposure to smoke-related contaminants.

The original, proposed design involved the collection and analysis of 10mL blood samples drawn from 26 subjects that were involved in fighting wildland fires during summer 2007. Full-time employees (seasonal or permanent) of Grand Teton National Park and Bridger Teton National Forest qualified as potential subjects in the study. We intended to take 2 draws per subject (pre- and post-contaminant exposure) and analyze the results using a related-samples t-test based on the repeated-measures design. A power analysis based on the difference score (post-Hg level minus pre-Hg level) allowed the detection of a medium effect due to Hg (Cohen's d = 0.5, alpha = 0.05 and power = 0.8; Cohen 1988). All tests were performed by a lab certified for the detection of Hg (St. John's Medical Center, P.O. Box 428 Jackson, WY 83001).

Participants were also asked to answer a brief questionnaire containing questions about demographics, prior mercury exposure, immediate exposure to smoke and particulates, and contact information.

Circumstances which we did not anticipate required us to substantially deviate from our original design. We were able to analyze blood from 12 subjects, and repeated blood draws occurred for only four of those subjects. Table 1 summarizes data obtained in our study.

Although our study specifically investigated Hg, analyses were performed for four other metals (lead, cadmium, cobalt, and thallium). Levels of these metals were well-below toxic thresholds and within normal ranges for all subjects.

Eleven of the 12 subjects were males, and the average age of all subjects was 32.5 years. Prior to the first blood draw, each subject was exposed to smoke for 20.1 days, at 11.6 hours per day on average. Prior to the second blood draw, each subject was exposed to smoke for 21.9 days, at 10.8 hours per day on average.

			Exposure to Smoke			
	Hg Level (mcg/L)		Draw 1		Draw 2	
Subject	Draw #1	Draw #2	Days	Hours/ day	Days	Hours/ day
1	<4	7	6	12	30	12
2	4	<4	?	?	21	14
3	<4	<4	14	6	14	6
4	<4	*	3	15	*	*
5	<4	*	40	14	*	*
6	<4	*	34	16	*	*
7	5	8	14	8	14	8
8	<4	*	30	10	*	*
9	*	7	*	*	14	16
10	*	<4	*	*	25	14
11	*	<4	*	*	12	8
12	*	<4	*	*	45	8

Table 1. Blood Hg Level (mcg/L) of Firefighters and Their Exposure to Smoke
? Indicates missing information
* Indicates no blood draw for the subject

✦ DISCUSSION

This study was motivated by the sudden emergence of Hg poisoning in bald eagles in the Greater Yellowstone Ecosystem, specifically southwestern Montana in December 2005. Subsequent research of nestling, migratory and wintering bald eagles of southern Montana and northwestern Wyoming starting summer 2006 and continuing through the present further indicated abnormally high, and sometimes toxic, levels of Hg and other contaminants in these populations. Investigation into possible sources of contamination led us to the hypothesis that the high levels of Hg encountered in bald eagles originated from the extensive forest fires that the western United States is currently experiencing. These fires are releasing smoke and other particulates containing Hg at unprecedented levels from trees contaminated with Hg during our industrialization, and from peat bogs containing biota that absorbed Hg and have recently dried out due to our current warming climate trend.

During May 2007, we speculated that wildland firefighters in the western United States were being exposed to Hg as a result of the combustion of mercury-laden tree bark and peat bogs. Realizing the significance of Hg contamination to our firefighters and

environment, we proposed to investigate if Hg accumulated at toxic levels in the blood of the firefighters.

Circumstances which we did not anticipate required us to substantially deviate from our original design. The Institutional Review Board (IRB) process, a required procedure when conducting human-oriented research, was substantially more involved than anticipated. After realizing the research topic in late May and assembling the research team in mid-June, we obtained substantial assistance from the University of Washington's Medical School in procuring IRB approval in late July. Consequently, we were not able to obtain blood samples for subjects prior to the start of the fire season, nor were we able to sample 26 subjects as originally proposed (the fire season had ended for many of the seasonal employees). We were, however, able to analyze blood from 12 subjects, and repeated blood draws occurred for four of those subjects.

Conclusions drawn from such a small sample are tenuous at best. However, the following results merit attention:

1) Beside Hg, blood analyses were performed for the presence of four other metals (lead, cadmium, cobalt, and thallium). Levels of these metals, though not precisely reported (<3.0 mcg/dL, <0.5 mcg/L, <1.0 mcg/L, and <1.0 mcg/L, respectively, for all subjects), were well-below toxic thresholds and within normal range for all subjects.
2) Three of the subjects had measurable Hg levels (7 mcg/L, 7 mcg/L, and 8 mcg/L) that approached the limit of a non-toxic Hg concentration (<10 mcg/L). A fourth subject had a measurable level of 4 mcg/L. All other subjects had levels designated by <4 mcg/L.
3) For the four subjects with repeated blood draws, two demonstrated an increase in mercury levels over time (<4 to 7 mcg/L, and 5 to 8 mcg/L), one showed no change over time (<4 to <4 mcg/L), and one demonstrated a decrease in mercury levels over time (4 to <4 mcg/L).
4) Although we recorded times of exposure to smoke for all subjects, our sample was too small to investigate any statistical inference about the relationship between the duration of exposure to smoke and changes in blood Hg concentration.

We initiated this preliminary study to investigate if Hg was accumulating at toxic levels in wildland firefighters who were exposed to smoke and other particulates while fighting fires in the western United States. We experienced limitations to our original design because we sampled only 12 subjects who had lower exposure to smoke than anticipated. However, we still encountered Hg at measureable levels in four subjects, while no other metals were even precisely measureable in any of the subjects. Consequently, we feel this research merits further investigation with the following modifications:

1) The study should be expanded to a significantly larger sample of wildland firefighters in the western United States (at least 150, contingent on funding). A majority of the firefighters should belong to hot-shot crews that are extensively exposed to fire contaminants (smoke and particulates) over the duration of the summer. Other firefighters with less exposure can be used as a comparative sample.
2) It is essential that Hg levels in each subject are analyzed a minimum of two times during the firefighting season, optimally: i) prior to commencement of the fire season; and ii) well into, or at the end of, the fire season after considerable exposure to fire particulates.
3) Time of exposure to smoke particulates by firefighters should be estimated more precisely.
4) Hg levels in subjects should be analyzed precisely, perhaps by an alternate method. Dr. Redeem Sumicab (pers. comm. 2007) has suggested a new procedure that analyzes urine from subjects drawn immediately upon awakening in the morning.
5) If the budget permits, hair samples from the back of the neck (which are fast growing) could be easily harvested to determine if mercury levels are due to chronic or acute exposure.

Analyses of data from ongoing bald eagle research indicate that elevated and toxic levels of Hg in nestling, migrating, and wintering eagles of southern Montana and northern Wyoming are persisting – even increasing – in the environment. Nestling bald eagles in Grand Teton National Park have experienced a 64% increase in mercury blood levels (Montopoli et al. 2008). As evidenced by the bald eagles in the

rehabilitation center, once Hg toxicity fully manifests itself, there is poor prognosis for recovery. The same is true for humans.

Symptoms of elemental Hg toxicity in humans include central nervous system (CNS), renal, and pulmonary dysfunction: tremors; irritability; insomnia; memory loss; neuromuscular changes; headaches; slowed sensory, motor and cognitive function; mild transient proteinuria; acute renal failure; chest pains; dypsnea; cough; pulmonary function impairment; and interstitial pneumonia (ATSDR 1999, U.S. EPA 1997). Acute inhalation of methyl mercury results in severe CNS effects including blindness, deafness, and impaired level of consciousness (WHO 1990).

If research supports our hypotheses, we can implement immediate actions to prevent Hg toxicity and neurological compromise in wildland firefighters, such as: 1) the use of specialized equipment such as a wildland firefighter's mask; 2) periodic urine exams to monitor Hg concentration in body tissues; and/or, 3) if Hg concentrations become elevated, the use of DMSA (meso-2,3-dimercaptosuccinic acid) to remove the Hg. As forest fires continue to ignite in the western U.S. at unprecedented levels, burning areas such as dried bogs and marshes, we highly recommend a mercury-monitoring program to ensure the continued health and safety of our firefighting crews.

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✦ LITERATURE CITED

Agency for Toxic Substances and Disease Registry (ATSDR) 1999. *Toxicological Profile for Mercury*. Public Health Service, U.S. Department of Health and Human Services, Atlanta GA.

Biswas, A., J. D.Blum and G. J. Keeler 2003. Forest fire effects on mercury and other trace metal concentrations in a Rocky Mountain forest ecosystem. EOS Transactions of American Geophysical Union 84 (46). Fall Meeting. Supplemental. Abstract #B32C-05.

Cohen, J. 1988. Statistical power analysis for the behavioral sciences (2nd ed.). New York: Academic Press.

Driscoll, C.T., C. Yan, C.L. Schofield, R. Munson, and J. Holsapple. 1994. The mercury cycle and fish in the Adirondack lakes. Environmental Science and Technology 28:136A-143A.

Garcia, E. and R. Carignan. 2005. Mercury concentrations in fish from forest harvesting and fire-impacted Canadian boreal lakes compared using stable isotopes of nitrogen. Environmental Toxicology and Chemistry 24:685-693.

Harmata, A., 2006. Monitoring Mercury And Other Contaminants In Bald Eagles In Southwestern Montana & Northwestern Wyoming, Interim Report – 30. November 2006.

Friedli, H.R., L. F. Radke, and J. Y. Lu. 2001. Mercury in Smoke from Biomass Fires. Geophysical Research Letters 28:3223–3226.

Heinz, G.H. 1996. Mercury poisoning in wildlife. Pgs. 118–127 *In* Noninfectious diseases of wildlife. A. Fair-brother, L.N. Locke, and G.N. Hoff (eds.). Iowa State University Press, Ames, Iowa,

Montopoli, G., H. Harlow, A. Byerly, S. Wolff, S. Patla. 2008. Monitoring of heavy metal contaminants in nestling bald eagles of Grand Teton National Park. Submitted to Grand Teton National Park, April, 2008.

Radke, L.F., J.Y. Lu, C.M. Banic, W.R. Leaitch, J.I. MacPherson. 2003. Mercury emissions from burning of biomass from temperate North American forests: laboratory and airborne measurements. Atmospheric Environment 37:253-267

Sumicad, R. 2007. Personal comments. St. John's Medical Center, P.O. Box 428 Jackson, WY 83001.

Turetsky, M.R., J.W. Harden, H. Friedli, M. Flannigan, N. Payne, J. Crock, L. Radke. 2006. Wildfires threaten mercury stocks in northern soils. Geophysical Research Letters 33:10.

U.S. Environmental Protection Agency. 1997. *Mercury Study Report to Congress, Volume V: Health Effects of Mercury and Mercury Compounds*. Office of Air Quality Planning and Standards, Office of Research and Development.

Wiedinmyer, C and H. Friedli. 2007. Mercury emissions from fires: an initial inventory for the United States. Environmental Science Technology. 41, 8092-8093.

World Health Organization (WHO) 1990. *Methyl Mercury. Volume 101*. Distribution and Sales Service, International Programme on Chemical Safety, Geneva, Switzerland.

CLIMATIC FACTORS, REPRODUCTION SUCCESS AND POPULATIONS DYNAMICS IN THE MONTANE VOLE *MICROTUS MONTANUS*

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✦ OBJECTIVES

A variety of hypotheses has been proposed to explain multiannual fluctuations in population density ("cycles") of small rodents (for reviews see Finerty 1980, Taitt and Krebs 1985). Doubtless, such cycles – known since antiquity (Elton 1942) - result from an interaction of a multitude of factors. However, the inability of extant hypotheses, alone or in combination, to explain the causality of cycles rests in no small measure with the fact that long-term studies of the phenomenon are notoriously uncommon.

The objectives of this project are to continue the long-term study of population dynamics of the montane vole, *Microtus montanus*, in Grand Teton National Park. Earlier observations (Negus et al. 1992,Pinter 1986, 1988) indicate that environmental variables might contribute to the population density cycles of these rodents, possibly by influencing their growth and various aspects of their reproduction.

✦ METHODS

In 2006 *Microtus montanus* were livetrapped at two times of the year: the second half of May (spring study period) and mid-July to mid-August (summer study period). Animals were killed with an overdose of Metofane as soon as possible after capture. They were aged using weight, total length and pelage characteristics. Reproductive organs, the spleen and the adrenal glands were collected from all animals and preserved in Lillie's neutral buffered formalin for further histological study. Flat skins were prepared from all animals.

Population density was estimated on the basis of trapping success in a permanent grid (established in 1970). The grid consists of 121 stations placed in a square, 5 m apart, 11 stations (50 m) on a side. Each station is marked with a stake. Trapping in this grid was performed only during the summer study period. One unbaited Sherman livetrap was set at each station. Additional trapping was carried out in nearby meadows away from the grid to obtain additional females for litter size determination.

During the spring study period trapping was carried out at a number of sites, all of them well removed from the permanent grid. The purpose of this was to leave the grid site as undisturbed as possible since the grid was the major source of information on population density. The main objective of the spring study period was to determine (on the basis of embryo size) the onset of reproduction on a population-wide basis. This information is very important for two major reasons: (1) onset of reproduction in M. montanus in Grand Teton National Park can vary by as much as 40 days among years, and (2) the time at which reproduction begins has significant repercussions on the productivity of the population for the year.

Weather data were obtained from records at the Jackson Lake Dam. Although Moran 5WNW is not a Class A weather station, it is located less than 2 km from the permanent grid. Data collected included temperature,

precipitation, and the date of complete spring melt-off.

✦ RESULTS AND DISCUSSION

In 2006, in Grand Teton National Park, populations of *Microtus montanus* exhibited a dramatic decline in numbers. Indeed, the population fell to the lowest level documented within the past decade. The decline appeared to have taken place during the winter of 2005-2006; this could be detected at the very beginning of the 2006 field season. During the spring study period there was virtually no vole sign (cuttings, droppings, runways). Furthermore, trap success during the spring study period was also noteworthy for two reasons: (1) the number of voles trapped was the lowest ever for any spring period within the 37 years of this long-term study, and (2) absolutely no females were trapped. A feature attesting to the unusually low population density was a virtual absence of fighting among the males. There were no bite marks either on their hip glands (the most common target of intraspecific strife among male montane voles) or on any other parts of the body. In years of higher density fighting among males is the rule, resulting in damage such as scarring of the hip glands and of the skin (especially on the rump), torn ears and missing digits.

Since no females were captured during the spring study period, the onset of reproduction within the vole population could not be ascertained from direct observations (e.g., number of females pregnant, stage of pregnancy, presence or absence of lactation). However, one of the many advantages of a long-term study is that gradually parameters become evident that can be used to make reliable correlations. One of these parameters in the spring study period is meltoff, since reproduction in the montane vole in Grand Teton National Park is closely linked to the disappearance of snow cover. The spring of 2006 in Jackson Hole was early; consequently, the onset of reproduction on a population-wide basis must also have been early. In other words, all of the females would have been pregnant; indeed, some of the females were probably already pregnant with their second litter. Since young born before the first week in July can become reproductively active in the year of their birth, the earlier the onset of reproduction in the spring, the larger the numbers of breeders in a given year.

In spite of the early onset of reproduction in the spring, the population densities attained in 2006 were 50% lower than those in 2005. This represents a second consecutive year of a decline in population density of *Microtus montanus*. This result is not surprising. First, and probably most importantly: the initial breeding population was exceedingly small – although reasons behind the winter crash of the population remain totally unknown. Second, litter sizes in 2006 were not significantly different from those observed in 2005, yet these litter sizes were being produced by a dramatically smaller breeding population. Third, the general area continued to experience a drought; the consequent early senescence and drying of the preferred food plants of *Microtus montanus* contributed to an early cessation of reproduction. A simultaneous coincidence of suboptimal parameters led to the dramatic decline in population densities of montane voles in 2006.

✦ CONCLUSIONS

The fluctuations in the population density of montane voles from year to year are doubtless caused by several poorly understood variables (e.g., diet, climate, disease –Watkins et al. 2006) and equally poorly understood interactions among such variables. The data collected during the 2006 field season clearly demonstrate the critical significance of one of these variables – the size of the breeding population at the onset of the breeding season. In the spring of 2006 this population was exceptionally small. The early onset of reproduction in 2006, although conducive to a rapid growth in population density, was unable to compensate for the near-record low in the population density of the initial breeding population.

✦ ACKNOWLEDGEMENTS

I gratefully acknowledge the availability of the facilities at the University of Wyoming-National Park Service Research Center and the enthusiastic support of the Research Center staff without which it would have been impossible to accomplish this work. I also thank Steven Cain and Megan Callahan for their unfailing cooperation and administrative

support. I am particularly grateful to the Steering Committee of the UW-NPS Research Center and to the National Park Service for their cognizance of the fact that an understanding of microtine cycles can be gained only from long-term studies in undisturbed habitats.

✦ LITERATURE CITED

Elton, C. S. 1942. Voles, mice and lemmings. Clarendon Press, Oxford. 496 pp.

Finerty, J. P. 1980. The Population Ecology of Cycles in Small Mammals. Mathematic Theory and Biological Fact. Yale Univ. Press, New Haven. 234 pp.

Negus, N. C., P. J. Berger and A. J. Pinter. 1992. Phenotypic plasticity of the montane vole (*Microtus montanus*) in unpredictable environments. Canadian Journal of Zoology. 70:2121-2124.

Pinter, A. J. 1986. Population dynamics and litter size of the montane vole, *Microtus montanus.* Canadian Journal of Zoology. 64:1487-1490.

Pinter, A. J. 1988. Multiannual fluctuations in precipitation and population dynamics of the montane vole*, Microtus montanus.* Canadian Journal of Zoology 66:2128-2132.

Taitt, M. J. and C. J. Krebs. 1985. Population dynamics and cycles. In: Biology of New *Microtus*. R. H. Tamarin, ed. Spec. Pub. American Society of Mammalologists. 8:567-620.

Watkins, R. A., S. E. Moshier and A. J. Pinter. 2006. The flea, *Megabothris abantis*: an invertebrate host of *Hepatozoon* sp. and a likely definitive host in *Hepatozoon* infections of the montane vole, *Microtus montanus*. Journal of Wildlife Diseases, 42:386-390.

EXPLORING THE ECOLOGY OF THE ENDEMIC JACKSON LAKE SPRING SNAIL: DISTRIBUTIONS AND INTERACTIONS WITH THE INVASIVE NEW ZEALAND MUD SNAIL

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✦ INTRODUCTION

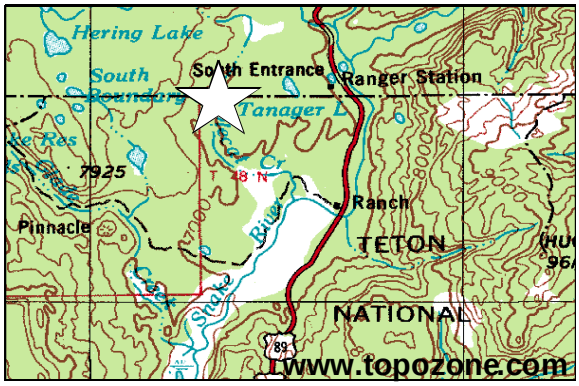
Endemic species make a unique contribution to global biodiversity by only existing in one or a few locations. Unfortunately, because of their limited range, endemic species are particularly susceptible to extinction from a range of disturbances, whether anthropogenic or natural. The introduction of non-native species can disrupt community interactions and accelerate extinctions for narrowly endemic species by competing with and/or preying upon native species. On a global scale, community interactions between invasive and native species have changed current patterns of biodiversity and will continue to influence the distribution of biodiversity well into the future.

Freshwater ecosystems are particularly vulnerable to the impacts of invasive species and could be the most detrimental stressor to species west of the continental divide. The New Zealand mud snail (NZMS: *Potamopyrgus antipodarum*), a worldwide freshwater invader, is now becoming a nuisance species in many areas of conservation significance. The NZMS was first recorded in streams in the western U. S. in 1987 and now has a widespread distribution, including streams within Grand Teton, Grand Canyon and Yellowstone National Parks. The NZMS is also sympatric with many endemic spring snails that are listed as threatened or endangered in the intermountain west.

Within the Greater Yellowstone Ecosystem (GYE), the distribution of the NZMS completely overlaps with that of a closely related federal candidate-threatened species, the Jackson Lake spring snail (JLSS: *Pyrgulopsis robusta*). The current known range of the JLSS is limited to one spring stream (Polecat Creek) and an unnamed tributary (referred to here as Marmot Spring) (Map 1). Since the introduction of the NZMS, JLSS densities have declined and NZMS densities have increased to 500,000 snails/m^2 in some areas of Polecat Creek. While both species remain abundant in Marmot Spring, some of our previous work indicates that the NZMS competes with and slows the growth of the endemic JLSS in this tributary (Fig. 1).

Because the NZMS could eventually exclude the JLSS from the current range in Marmot Spring and Polecat Creek, we have undertaken a series of studies of the competitive interactions and long-term population trends. The goal of our 2005 field sampling was two-fold. First, we continued to monitor yearly variation in the two snail populations in Marmot Spring to predict whether the NZMS is displacing the JLSS from this tributary. The presence of the NZMS is the most likely stressor for reducing or extirpating this population.

Second, we explored the historic range of the JLSS to search for refuge populations that might still exist near springs in Jackson Lake, Wyoming (Grand Teton National Park). Historically, the main pressure on the survival of the spring snail populations in Jackson Lake included habitat modification (i.e. impoundment by the dam). However, the NZMS has not been introduced to Jackson Lake, so any JLSS populations that survived habitat changes in this lake over the past 30 years would be free from competition with the invasive species.



Map. 1 Polecat Creek and Marmont Spring (star) are located in the John. D. Rockefeller Parkway between Yellowstone and Grand Teton National Parks. The northern tip of Marmot Spring crosses the south boundary of Yellowstone.

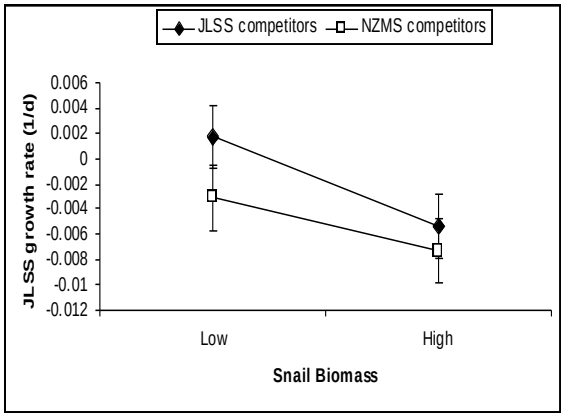


Fig.1. JLSS grows slower when competing with NXMS than when competing with conspecifics at both low and high levels of total snail biomass. Competition experiments were conducted in 2002.

In 2001, samples from aquatic vegetation in the current range of JLSS suggested that the NZMS was displacing the JLSS from Polecat Creek, but that the two species were coexisting in Marmot Spring (Fig. 2). Densities of the two species were positively correlated in Marmot Spring, but negatively correlated in the main stem of Polecat Creek. Continued sampling (sites 1 – 5, Fig. 2) through the summer of 2005 reveals that – so far – the two species are still coexisting in Marmot Spring. JLSS and NZMS abundance vary widely between years in both cobble (Fig. 3) and vegetative habitats (Fig. 4), but no consistent trends have emerged. Increases in NZMS abundance are not directly related to decreases in JLSS abundance in either habitat over this short time scale. Interestingly, though, the dynamics of the two species in vegetative habitat suggest that JLSS abundance might be increasing in 2005 in response to a decline in the NZMS in 2003 and 2005, but with a time lag (Fig. 4). Samples collected in the upcoming summer (2007) will help determine whether these two populations are indeed cycling in a predictable manner.

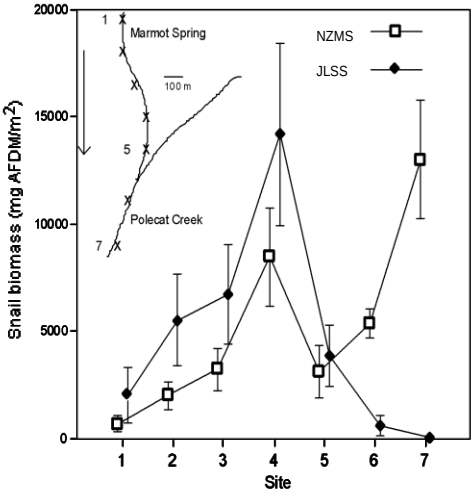


Fig. 2 JLSS and NZMS biomass are positively correlated at all sites in Marmot Spring (1-5) but negatively correlated at two sites in Polecat Creek (6-7). Samples were collected in vegetation in 2001.

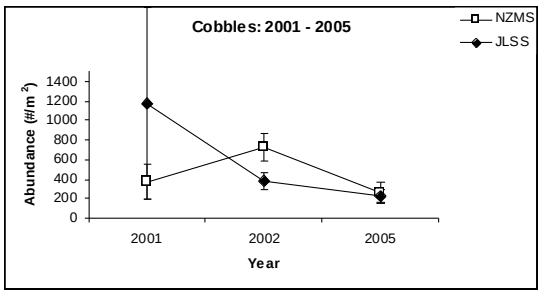


Fig. 3 NZMS and JLSS abundance are lower on cobbles than vegetation and have fluctuated each year. Note that 2003 samples are not included in this graph. Samples were collected at sites 1-5 each year and will also be collected in 2007.

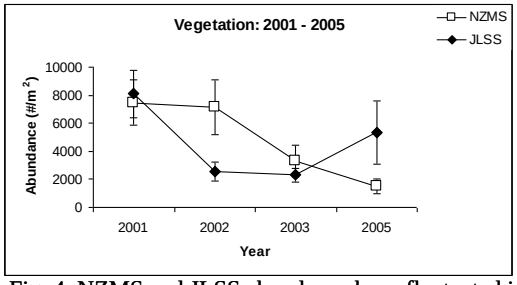
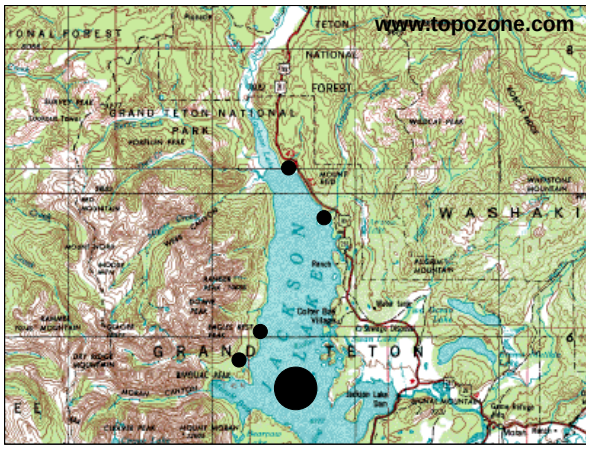


Fig. 4. NZMS and JLSS abundance have fluctuated in Marmot Spring from 2001 – 2005. Samples were collected at sites 1 – 5 each year and will also be collected in 2007.

In 2001, samples from aquatic vegetation in the current range of JLSS suggested that the NZMS was displacing the JLSS from Polecat Creek, but that the two species were coexisting in Marmot Spring (Fig. 2). Densities of the two species were positively correlated in Marmot Spring, but negatively correlated in the main stem of Polecat Creek. Continued sampling (sites 1 – 5, Fig. 2) through the summer of 2005 reveals that – so far – the two species are still coexisting in Marmot Spring. JLSS and NZMS abundance vary widely between years in both cobble (Fig. 3) and vegetative habitats (Fig. 4), but no consistent trends have emerged. Increases in NZMS abundance are not directly related to decreases in JLSS abundance in either habitat over this short time scale. Interestingly, though, the dynamics of the two species in vegetative habitat suggest that JLSS abundance might be increasing in 2005 in response to a decline in the NZMS in 2003 and 2005, but with a time lag (Fig. 4). Samples collected in the upcoming summer (2007) will help determine whether these two populations are indeed cycling in a predictable manner.

The current documented range of the JLSS is restricted to Polecat Creek and Marmot Spring, but the historic range of the JLSS was much larger, encompassing shoreline areas of Jackson Lake and Elk Island (located in the middle of Jackson Lake) (Map 2). No documented collections of the JLSS have occurred from any area of Jackson Lake since at least 1975. We focused efforts around Elk Island by systematically sampling six locations in July of 2005 (Map 2). We chose sites where habitat characteristics indicated a higher likelihood of finding springs (i.e. different vegetation from surrounding area, etc.). At each site, we waded with kicknets and sieves to collect invertebrates from shallow habitat. We also snorkeled in deep water, farther from the shoreline, and collected samples from the substrate with kicknets. In addition, we systematically sampled four other likely sites around Jackson Lake, where springs or streams were entering the lake (Map 2).



Map 2. Collecting sites for JLSS in the historic range represented by black dots. The large black dot represents the six sites sampled around Elk Island.

We failed to locate the JLSS at any sites in Jackson Lake, including the six locations around Elk Island and the four other sites on the shores of Jackson Lake. The North Moran Bay site on the western side of Jackson Lake was the most similar to habitat characteristics found in the current range of the JLSS (Map 2). This site consisted of three spring streams with similar riparian vegetation to Marmot Spring (i.e. *Mimulus* (monkeyflower) and *Heracleum* (cow

parsnip)). In addition, one spring had high densities of another snail, *Stagnicola* spp., suggesting that this site is capable of supporting a dense population of a similar species.

In conclusion, the current range of the JLSS is restricted to a small portion of the historic range where it competes with the NZMS. We found no evidence of the JLSS at ten sites within Jackson Lake. We cannot exclude the possibility that the JLSS might still exist in some unexplored pockets of Jackson Lake and tributaries, but it is unlikely given that many of the sites chosen were historic sampling locations. Within the current range, competition from the NZMS threatens to reduce the JLSS population. In the short term, the NZMS slows the growth of the endemic JLSS, but strong evidence for competitive displacement of the JLSS is not yet apparent and could take years to manifest. The introduction of the NZMS has disrupted stream community members in many ways, including the JLSS, but only continued sampling will reveal how this JLSS population will respond to a competitive invasive species.

✦ ACKNOWLEDGEMENTS

The NPS official linked to this project is Susan E. O'Ney, hydrologist, in Grand Teton National Park .

HOW ARE BREWER'S SPARROWS AFFECTED BY THE ENCROACHMENT OF THE EXOTIC GRASS SPECIES, SMOOTH BROME *(BROMUS INERMIS LEYSS.)*?

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✦ INTRODUCTION

Sagebrush habitats *(Artemisia spp.)* across the western United States have been continuously altered since the arrival of early European settlers. Habitat loss and fragmentation in sagebrush-dominated habitats has been attributed to domestic livestock, introduction of non-native vegetation, agricultural expansion, urbanization, and changes in ecological processes that regulate ecosystems (Knick et al. 2003). These alterations have resulted in landscape level changes; for example, it is estimated that between 50-60% of the nearly 63 million hectares once covered by sagebrush in the west have been either completely converted to non-native grasslands or now contain non-native grasses in the understory (Miller and Eddleman 2001, West 2000 and1996). The encroachment of non-native plants that compete with native vegetation has been identified as one of the most serious threats to the health and integrity of sagebrush ecosystems throughout the west (Paige and Ritter 1999).

Grand Teton National Park is not immune to the decline of historic sagebrush habitat. For example, early settlers to Jackson Hole cultivated approximately 4,400 hectares of formerly sagebrush habitat known as the Kelly hayfields for hay with various perennial grasses (Daugherty 1999). One of these grasses, smooth brome *(Bromus inermis* Leyss.*)*, is a native of Europe that reproduces by seed, rhizome, and tillers. This hardy perennial, introduced to North America from Europe and Asia, was highly successful in out-competing native vegetation and became the dominant grass species across the Kelly hayfields. Smooth brome has remained the dominant species at the Kelly hayfields despite the termination of farming in the early 1970's, and a mixture of sagebrush and smooth brome comprise the surrounding areas. In addition, over the last decade noxious weeds have spread into the Kelly hayfields and vicinity, competing with the native flora and further degrading the quality of sagebrush communities.

Grand Teton National Park is currently developing a plan to restore the Kelly hayfields to native vegetation. This project will have widespread effects on the native flora and fauna in the park. For example, several wildlife species will likely benefit from the restoration of this area including ungulates (e.g., bison, elk, pronghorn antelope and moose), breeding birds (e.g., greater sage-grouse, neotropical migratory birds), and numerous small mammals (e.g., jumping mice). In fact, the restoration of the Kelly hayfields is recommended in several alternatives for the management of the park except the no action alternative in the Bison and Elk Environmental Impact Statement (Morgenweck and Snyder 2005), a plan that aims to create and maintain natural foraging areas for elk and bison in the Jackson Hole area. Prior to the initiation of restoration efforts, park managers must determine benchmark goals for

native habitat restoration.

This project used the avian community as a means of better understanding what comprises "suitable" habitat in the sagebrush ecosystem. We compared avian communities and Brewer's Sparrow reproductive success within the targeted restoration area with nearby undisturbed patches of sagebrush-dominated habitats. We determined threshold levels of smooth brome tolerated by sagebrush obligate bird species. We hope that this information will assist park biologists and managers in determining the extent of restoration needed for wildlife associated with sagebrush ecosystems. Furthermore, by using birds as indicators to measure the health of these park lands, we plan on using our findings when evaluating restoration plans.

Purpose: The purpose of this study was to determine the effects of non-native grass encroachment on sagebrush bird communities, as well as to compare bird use in sagebrush habitats experiencing varying levels of smooth brome invasion. Specific objectives include:

- To determine if sagebrush obligate bird species currently utilize sagebrush patches with a smooth brome understory.
- To compare nest success of Brewer's Sparrows in altered sagebrush habitat with nearby patches dominated by native species.
- To identify threshold levels of smooth brome encroachment beyond which Brewer's Sparrows will not occupy a site.
- To compare bird communities over varying degrees of habitat alteration.

✦ METHODS

The study area was in the Kelly hayfields and surrounding sagebrush communities located at the southeast corner of Grand Teton National Park (GRTE), Wyoming. In unaltered habitats, the dominant shrub species was mountain big sagebrush (*Artemisia tridentata* spp. *Vaseyana)*, occasionally intermixed with antelope bitterbrush (*Purshia tridentata)* or low sagebrush (*Artemisia arbuscula)*. Common native grass species included Idaho fescue (*Festuca idahoensis)*, junegrass (*Koeleria macrantha)*, and bluegrass (*Poa* spp), while common forbs include sulphur buckwheat (*Eriogonum umbellatum)*, yarrow (*Achillea millefolium)*, arrowleaf balsamroot (*Balsamorhiza sagittata)*, and lupine (*Lupinus spp)*. The remnant hayfields consist primarily of smooth brome (*Bromus inermis)*, but also contain other non-natives such as musk thistle (*Carduus nutans)* and Kentucky bluegrass (*Poa pratensis).*

Study sites included 1) altered patches within the Kelly hayfields that contain smooth brome with little to no sagebrush, 2) sagebrush habitats adjacent to the Kelly hayfields with smooth brome encroachment and 3) intact, native sagebrush vegetation communities. Transects were randomly located and selected using GIS. Each transect was approximately 2km long and consisted of at least 15 points separated by 125m. A minimum of 5 transects were surveyed for each vegetation type.

Several components were measured to assess the effects of smooth brome encroachment on avian communities: species diversity and occupancy, Brewer's Sparrow density, vegetation structure and species composition at and around nest sites, and Brewer's Sparrow reproductive success. To determine bird occupancy and diversity, we followed protocols already described in the GRTE Landbird Monitoring Protocol (2005). In summary, birds were surveyed using point count techniques. Fifteen points were located 125 meters apart on each transect. Surveyors visited each transect 3 times per season**.** Every point along each transect was surveyed for birds, beginning 15 minutes after sunrise and ending no later than 10AM. All birds seen and/or heard were recorded and their distance from each point was measured using a rangefinder. Bird surveys began in mid-May and were completed by the end of June, the time when breeding birds were most actively singing and establishing territories. Vegetation components measured along each transect included structure, cover, species composition, as well as ground litter type and depth.

Nest success of Brewer's Sparrows was measured using standard sampling protocols for nest searching and monitoring (Martin and Geupel, 1993). Using parental cues and systematic searching, surveys for nests were conducted during the nesting period to locate all birds nesting within 100 meters of each transect. All nests located were re-visited every 3-5 days

to determine nest occupancy, number of eggs, and if young fledged. Nest failure was documented and determined if it was due to predation or abandonment, when possible. For example, egg fragments were inspected to identify if the egg was scavenged upon or if chick hatched. If eggs remained intact but without parental presence for an extended period of time (>1 hour), the nest was considered abandoned. Vegetation components surrounding each nest were also measured. These included cover, location of nests within shrub, vegetation species utilized for nesting, as well as distance to nearest differing vegetation patch. Nest success rates were calculated using the Mayfield method (Mayfield 1961, 1975).

✦ RESULTS AND DISCUSSION

A total of 84 Brewer's Sparrow nests were located and monitored. Of these, 30 were found in sage/smooth brome habitat and 54 were found in native sage habitat. Although nests seemed to be more densely packed in the native sagebrush habitat, this area had a higher rate of failure when compared to the sage/smooth brome habitat (see table 1). Simple proportional figures of failure/success have been calculated.

	% Fail	% Success	% Unknown
Native Sage	55	43	2
Sage/smooth brome	41	58	0

Table 1: Nest Fate by Habitat

Nests that failed were examined to determine cause of failure. This information is broken down in order to show potential differences by habitat type (see figure 1). The most common cause of failure in both native sage and sage/smooth brome habitats was predation. The only predator observed in nests was the Wandering Garter Snake, although it is suspected that chipmunks and ground squirrels are also common predators. No Brown-headed Cowbird parasitism was observed.

A significant weather event occurred on June 14, 2006 and contributed to 34% of failures within the sage/smooth brome habitat type. This strong hailstorm impacted one study site, causing many of the incubating adults to abandon nests. However, it was noted that adults in this area began renesting attempts as early as 2 days after the weather event. Also of interest was the presence of dud eggs (eggs that never hatched) in the sage/smooth brome habitat type. This was never observed in the native sage habitat. Although dud eggs comprise a small portion of failure, this causes one to question if this could be attributed to difference in diet and/or overall health of adult Brewer's Sparrows between the two habitat types.

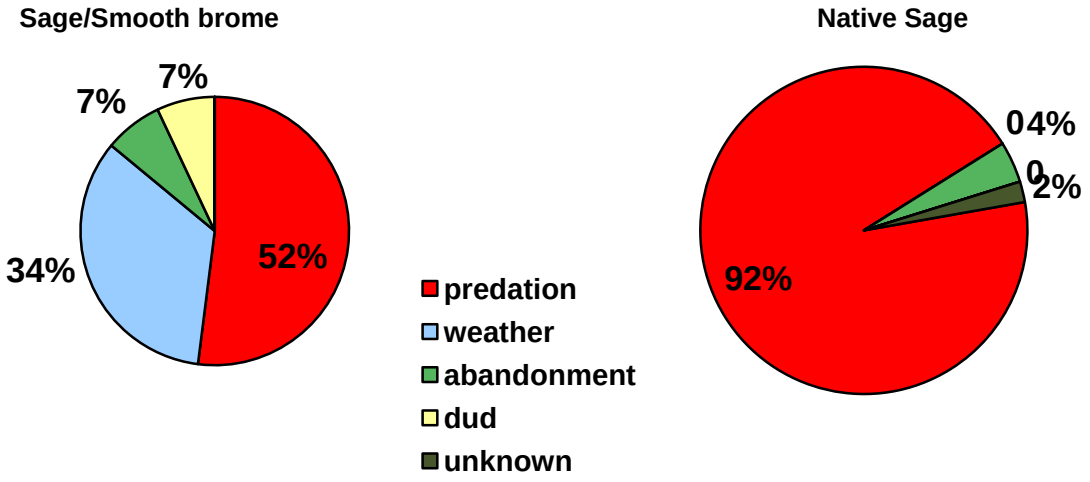

Figure 1: Cause of Failure by Habitat

Although more rigorous analyses are required for this study, it is apparent that there

are interesting trends between these two habitat types. The question of what exactly caused the difference in failure rates between habitat types opens many avenues for discussion and additional research. For example, this difference in failure rate could be attributed to predator abundance. Predators may simply be more abundant in the native sagebrush areas and not as well suited to the conditions that an understory of smooth brome creates. Additionally, nest concealment also likely plays a large role in nest fate. It often appears that nests in the sage/smooth brome habitat are well concealed due to the height and growing characteristics of smooth brome.

✦ LITERATURE CITED

Daugherty, J. 1999. A place called Jackson Hole: the historic resource study of Grand Teton National Park. Grand Teton National Park Service. Moose, WY.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. Van Riper III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. The Condor 105:611-634.

Martin, T. E., and G. R. Geupel. 1993. Nest monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology 64:507-19.

Mayfield, H. F. 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255-261.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456-466.

Miller, R. F., and L. Eddleman. 2001. Spatial and temporal changes of Sage Grouse habitat in the sagebrush biome. Oregon State University Agricultural Experiment Station Technical Bulletin 151, Corvallis, Oregon.

Morgenweck, R., and M. Snyder. 2005. Draft Bison and Elk Management Plan and Environmental Impact Statement for the National Elk Refuge, Grand Teton National Park, and John D. Rockefeller, Jr., Memorial Parkway. July 21, 2005. www.fws.gov/bisonandelkplan/

Paige, C., and S. A. Ritter. 1999. Birds in sagebrush sea: Managing sagebrush habitats for bird communities. Partners in Flight Western Working Group, Boise, ID.

West, N. E. 1996. Strategies for maintenance and repair of biotic community Diversity on rangelands, p. 342-346. *In* R. C. Szaro and D. W. Johnston (EDS.), Biodiversity in managed landscapes: theory and practice. Oxford University Press, New York.

West, N. E. 2000. Synecology and disturbance regimes of sagebrush steppe ecosystems, p. 15-26. *In* P. G. Entwistle, A. M. DeBolt, J. H. Kaltenecker, and K. Steenhof (compilers), Proceedings: sagebrush steppe ecosystems symposium. USDI Bureau of Land Management Publication BLM/ID/PT-001001+1150, Boise, ID.

RECIPROCAL INTERACTIONS BETWEEN BARK BEETLES AND WILDFIRE IN SUBALPINE FORESTS OF THE GREATER YELLOWSTONE ECOSYSTEM

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✦ INTRODUCTION

Wildfire and bark beetle epidemics are two ecologically important natural disturbances in the Intermountain West, yet we know very little about how these two phenomena interact. It is widely believed that beetle-killed trees increase the risk of severe fires; and trees that are weakened, but not killed by fire, are thought to be more susceptible to beetle invasion. However, few studies have rigorously tested these hypotheses. The GYE is currently experiencing an outbreak of unprecedented intensity and complexity, involving several species of bark beetles, including the mountain pine beetle. The outbreak is affecting multiple species of coniferous trees in and near recently burned areas, providing a timely opportunity to investigate these interactions at multiple scales.

In addition to the basic ecological questions posed above, forest managers throughout the western US are grappling with how to deal with the most extensive bark beetle outbreaks ever recorded for the region. Following various kinds of natural disturbance, salvage harvest may be conducted to extract economically valuable timber and/or to reduce perceived risk of subsequent disturbance. However, the consequences of such post-disturbance management on stand structure and function in the context of the current bark beetle outbreaks are largely unknown. There has been some recent attention to salvage harvest in the literature, but empirical studies are relatively scarce. Therefore, as part of this study, we are quantifying the effects of post-beetle salvage logging on fuels, regeneration, and nitrogen cycling in lodgepole pine forests on the Bridger-Teton National Forest.

By means of seven closely related projects (described below), we conducted field work in 2007 in Yellowstone and Grand Teton National Parks, as well as on the Bridger-Teton and Shoshone National Forests, to answer four fundamental questions:

1. What are the current patterns of beetle outbreaks in the Greater Yellowstone Ecosystem, and what factors explain these patterns? [Projects #1 and #2]

2. What are the consequences of bark beetle outbreaks and post-beetle salvage harvest on nitrogen dynamics? [Project #3]

3. How do mountain pine beetle outbreaks influence the risk and severity of wildfire? [Projects #4 and #5]

4. Does fire injury in lodgepole pine affect colonization rates, reproductive success, and potential for population increase of mountain pine beetle? [Projects #6 and #7]

Project #1: Remote Detection of Bark Beetle Damage

The objective of this research is to map the magnitude, spatial patterns and temporal trend of several concurrent beetle outbreaks including mountain pine beetle, spruce beetle and Douglas-fir beetle. A visit to the area was made in 2007 for the purpose of gaining on-the-ground familiarity with the topography and vegetation patterns, but most of the analysis was conducted in the remote sensing laboratory at the University of Wisconsin – Madison. A 9-year (1999-2007) time series of Landsat imagery was employed to estimate the probability that each pixel was disturbed on yearly basis. The probability map for each year was developed from the difference image of Moisture Stress Index (MSI: Landsat band 5/band 4) between a disturbance year and the base date (1999) using the normalized distribution of spectral data for the larger study area.

We have detected the initial year of attack as the time at which MSI showed increases that were sustained in subsequent years (Figure 1).

The MSI difference values (disturbance year minus base year) were then related to field measurements of beetle damage collected during the summers on 2006 and 2007. These values were related to the MSI index difference for 2007 (expressed as a P-value of the statistical distribution from subtracting 19999 MSI from 2007 MSI). This analysis showed a very strong linear relationship between the MSI difference and percent mortality (Figure 2). This suggests that we can also map a continuous measure of beetle damage.

The relationship between MSI and field measures then facilitated mapping total percent damage for the entire study area (Figure 3).

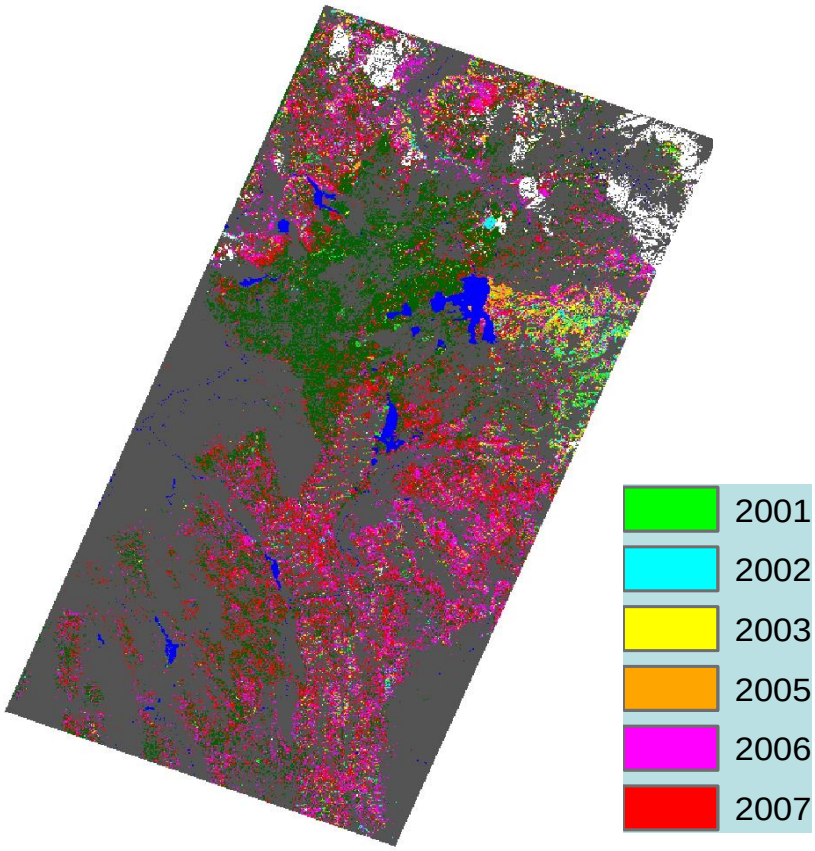

Figure 1. Temporal pattern of initial attack date. Dark green areas are unattacked forests (show no increases in Moisture Stress Index, MSI). Note that some areas marked as attacked in 2006 and 2007 (magenta and red) are mapped as such because they exhibited increases in MSI. If those increases are not sustained in images from subsequent years, then those areas may switch to being mapped as not attacked -- see also Figure 3 (preliminary results – please do not distribute).

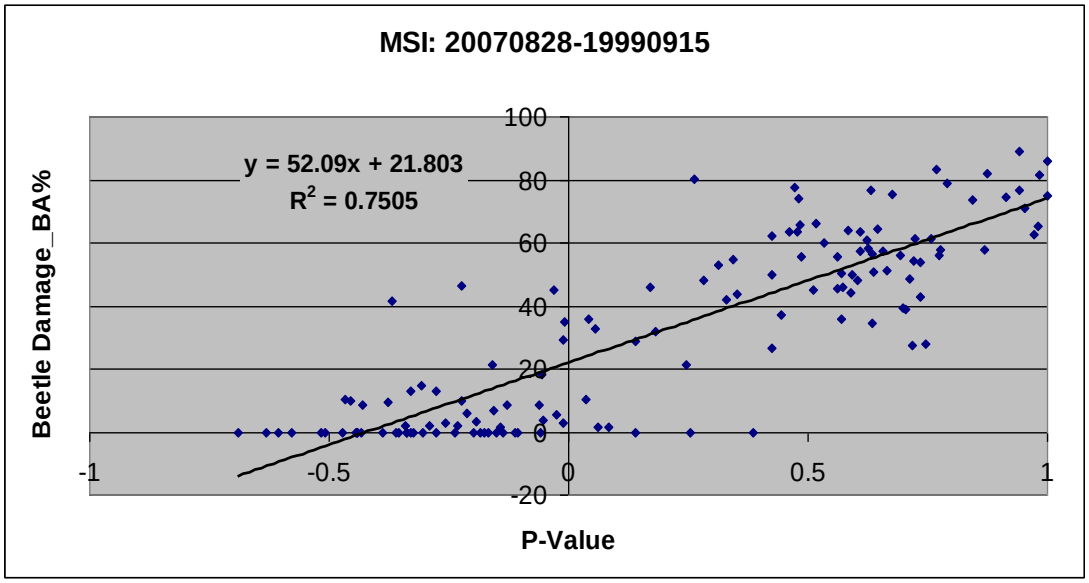

Figure 2. Mapped probability of disturbance showed a linear regression relationship with field data (%mortality), R^2 is 0.75 *(preliminary results – please do not distribute)*.

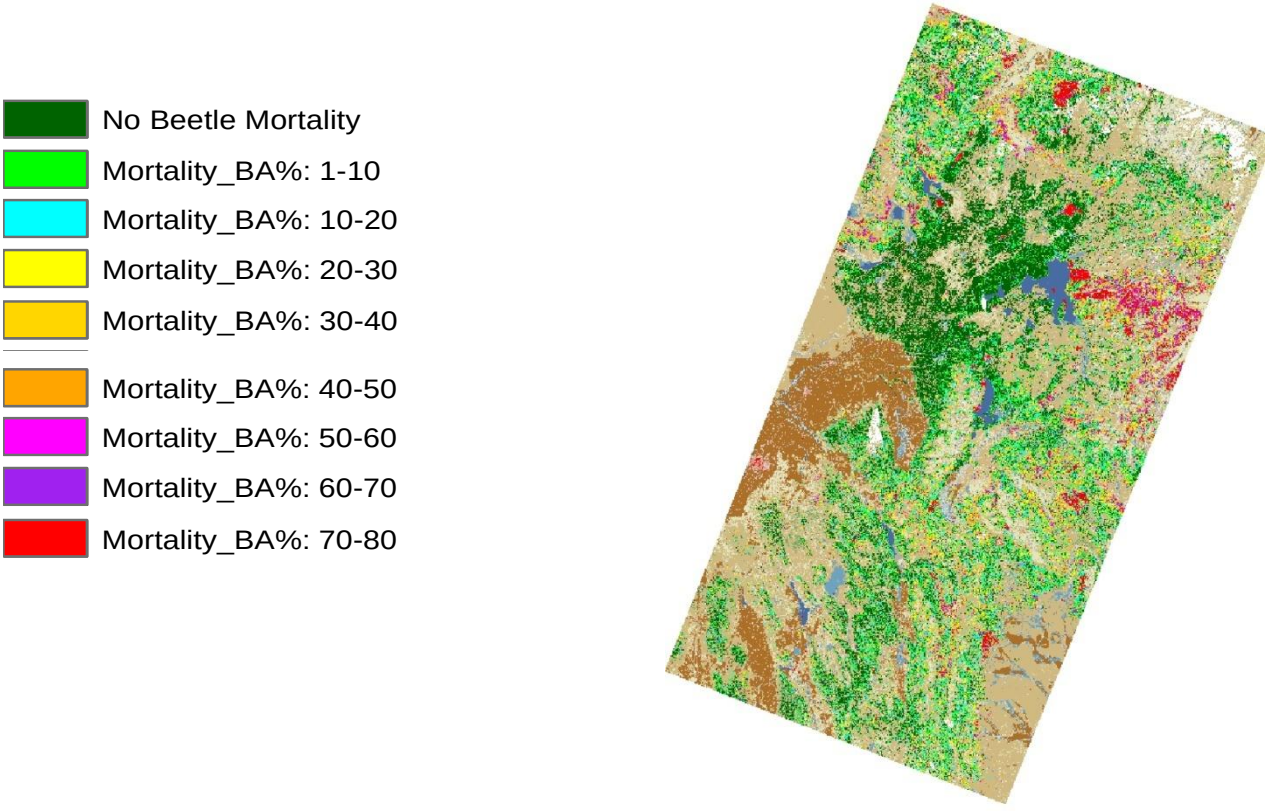

Figure 3. Spatial pattern of forest mortality for 2007. Note the extensive area of forests with low mortality that were mapped as first attacked in 2006 or 2007 in the Figure 1. True attack and mortality will be assessed with future images *(preliminary results – please do not distribute)*.

Several aspects of the research are ongoing as we work to write up our results. First, the maps simply identify forest disturbance, regardless of cause. We will use YNP fire perimeter data and the USGS dNBR (normalized burn ratio, equivalent to a burn severity index) data to mask out damage from fire and other sources. Second, the maps do not distinguish between pest species. We will employ the best existing forest type map to identify host species and label the likely pest species. Lastly, we will use the disturbance index of Healey et al (2005) (to identify logged areas. We expect that the percent mortality maps will remain accurate, although there may be some confusion between partially logged areas and beetle killed forests.

Project #2: Explaining broad-scale infestation patterns of three bark beetle species

The objective of this project is to determine what factors explain bark beetle infestation patterns being mapped at broad scales (project #1). Field data were collected in 2006 (working out of the AMK Ranch) on spatial patterns of four insect-host tree pairings: mountain pine beetle in whitebark pine, mountain pine beetle in lodgepole pine, Douglas-fir beetle in Douglas-fir, and spruce beetle in Engelmann spruce. One week of additional sampling was conducted in 2007 to supplement the previous year's effort. Data analysis is still underway, and results are not yet available.

In summer 2006 we sampled 64 stands (16 of each lodgepole pine, whitebark pine, Douglas-fir, and Engelmann spruce) that were either severely damaged or undamaged by the beetles. During summer 2007, we sampled 56 additional stands (14 stands of each species) to complement the previous year's effort. In each stand, we determined 1) forest attributes (composition, % mortality, serotiny for lodgepole pine); 2) stand structure (density, diameter, and age); 3) presence and damage by bark beetles; 4) soil characteristics; and 5) site conditions (elevation, slope, aspect, site index, surficial deposits, etc.). Sampling was done in two National Parks and two National Forests.

Project #3: Effects of bark beetle outbreaks and of post-beetle salvage logging on fuel dynamics and nutrient cycling

In 2007 we sampled 20 lodgepole stands that were heavily attacked by mountain pine beetle 2-4 years ago and measured stand structure, tree regeneration, and the quantity and distribution of surface and canopy fuels. We took soil samples to determine available N and installed buried resin cores to determine annual fluxes of N. Half (n = 10) of these plots are scheduled to be salvage logged in summer 2008, after which we will return to re-sample all of the stands. Data analysis is still underway, and results are not yet available.

Project # 4: Time-Since-Beetle chronosequence

The objective of this project is to characterize long-term (0 to 30 years after outbreak) effects of mountain pine beetle outbreaks on forest structure and regeneration; surface and canopy fuels; and nitrogen dynamics. Field sampling was initiated in 2006 (working out of the AMK Ranch), and six weeks of additional sampling were conducted in 2007. Data analysis is still underway, and results are not yet available.

Project #5: landscape patterns and the risk of high-severity fire

We sampled lodgepole pine stands that were attacked by mountain pine beetle at different times in the past (2, 4, 25, and 35 years ago), as well as undamaged stands (5 replicates per class; n = 25). In each stand we measured stand structure, regeneration, and the quantity and distribution of surface and canopy fuels. We will apply these field data to a suite of fire behavior models (e.g., Behave and Nexus) to evaluate how changes in the fuel complex will likely influence fire behavior under a range of weather conditions. Data analysis is still underway, and results are not yet available.

Project #6: Host preference of MPB

The objective of this project is to compare mountain pine beetle "performance" (success of attack, growth of larvae, and overall reproductive success) on its two major tree hosts in the Greater Yellowstone Ecosystem: lodgepole pine and whitebark pine. This project was initiated in 2006 (working out of the AMK

Ranch), and addition sampling was conducted during two weeks in 2007. Data analysis is still underway, and results are not yet available.

Project #7: Fire-injured lodgepole pine as a potential reservoir for mountain pine beetle

The objective of this project is to determine if fire injury in lodgepole pine affects colonization rates, reproductive success, and potential for population increase of mountain beetle. Field sampling was initiated in 2006 (working out of the AMK Ranch), and ten weeks of additional sampling were conducted in 2007. We deployed pheromone traps near 4 areas that burned in 2006 (two on the Bridger-Teton NF, one in Yellowstone NP, and one in Grand Teton NP) to document beetle population densities. At each site, we installed transects perpendicular to the fire edge, from the burned area to the unburned forest, and quantified fire injury and presence of bark beetles on individual trees. Data analysis is still underway, and results are not yet available.

✦ LITERATURE CITED

Healey, S.P., Cohen, W.B., Yang, Z.Q., & Krankina, O.N. 2005. Comparison of Tasseled Cap-based Landsat data structures for use in forest disturbance detection. Remote Sensing of Environment, 97, 301-310.

RELIEF HISTORY AND COUPLING OF EROSIONAL PROCESSES IN THE TETON RANGE, WYOMING

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✦ INTRODUCTION

Erosional processes influence topographic relief in mountain landscapes, but the spatial variation between differential processes and influence on tectonic uplift is poorly understood. Deep canyons and adjacent high peaks distinguish the Teton Mountains from nearby ranges, making it an ideal location to study how glacial, fluvial, and hillslope erosion interact to maintain high topographic relief. The purpose of this study is to quantify erosion rates of individual geomorphic processes in this complex system using a variety of techniques to see how each process contributes to landscape evolution in this mountain range.

To identify differential erosion throughout deep incised canyons we are using stream and moraine detrital apatite (U-Th)/He thermochronometry, terrestrial cosmogenic radionuclides produced in surficial bedrock, and talus fan volumes and distribution to quantify the effects of glaciers, streams and mass wasting. Previous studies revealed that erosion is more effective in basins than summits, causing topographic relief to increase (Small et al., 1997). Yet, in purely fluvial systems, Stock et al. (2006) concluded that streams erode uniformly in small mountain catchments. We are interested in measuring how the efficiency of erosional processes evolves with changing climatic conditions. We hypothesize that substantial erosion occurred in the basins during the last glaciation, and continued erosion through fluvial and hillslope processes has maintained the high relief preserved in the Teton Range after glaciation. If these processes are not effectively eroding the bedrock, then the topographic characteristic of the Teton Range has been preserved since the last glacial event in the region.

The summits of the Teton Range vary from other Laramide and Basin and Range mountains. In ranges such as the Beartooth, Wind River, Front Range, and Sierra Nevada mountains, the peaks are more gently sloping (Small and Anderson, 1998). In the Teton Range, peaks are very rugged with steep slopes dipping into deep canyons. Laramide ranges formed as a result of compressional tectonics folding large layers of sedimentary rocks. The Teton Range shows evidence of this deformation in nearby sedimentary rocks. Fission track ages calculated from apatite fission tracks also indicated that the rocks were compressed and folded (Roberts and Burbank, 1993). The front of the Teton Range is now defined by a large normal fault, which originated at approximately the same time as Basin and Range extension began in the nearby region of the Western U.S. Since activation, ~7 km of slip has caused the peaks to rise and the floor of Jackson Hole to subside. Earthquakes related to the Yellowstone Hotspot enhance the movement along the normal fault, which has been active in the last 10, 000 years (Byrd, 1995; Love et al., 2003; Roberts and Burbank, 1993). While the tectonic evolution of the Teton Range has been slightly different from other Laramide Ranges, it is unclear if these differences are the cause of topographic variations.

Foster et al. (2007) modeled topographic characteristics of canyons within mountain ranges of the Northeastern Basin and Range, including the Teton Range. They compared hypsometry and along-canyon profiles and found that the landscape in the Teton Range is different from other ranges in the region. They suggested that this difference may reflect a response to climatic conditions. Hampel et al. (2007) modeled uplift on the Teton Fault and found that uplift likely increased as a result of deglaciation of the Yellowstone ice cap.

Three glacial advances incised deep canyons into the Teton Mountains. The first event is less well dated and occurred at approximately the same time as the Illinoisan advance in the Midwestern U.S. During the Buffalo event, glaciers advanced to their southernmost extent in Jackson Hole and left deposits which still remain on high divides which were not affected by later advances or alpine glaciers (de la Montagne, 1956; Elias, 1996; Fryxell, 1929). This event would have been the first glacial event to begin carving U-shaped canyons into the Teton Mountains. Previous to that glacial event, only fluvial canyons controlled the landscape within the range. The Munger, or Bull Lake, event occurred ~140 ka. Ice sheets flowed south from the Yellowstone Plateau and filled Jackson Hole a second time. Glaciers continued to carve deep canyons and erode the front of the range (de la Montagne, 1956; Edmund, 1956; Elias, 1996). The Pinedale advance was the smallest advance within the basin. Ice from the north filled Jackson Hole and alpine glaciers spilled into Jackson Hole from the Teton canyons beginning ~44 ka. The moraines trapped ice and meltwater forming lakes on the west side of Jackson Hole which are still preserved (de la Montagne, 1956; Edmund, 1956; Elias, 1996; Love et al., 2003).

The timing of glacial events in the Teton and Yellowstone region has been well recorded based on moraine and outwash deposits in Jackson Hole, but the glacial deposits only record the age of the maximum glacial extent. Although the glaciers began receding by those times, erosion at high elevations would have continued until the glaciers melted completely. Cosmogenic ages from moraines on the Yellowstone Plateau indicate that the Pinedale glacial maximum was reached by ~14 ka (Licciardi et al., 2001).

✦ METHODS

To begin quantifying denudational processes we surveyed talus fans and collected bedrock and sediment in Garnet Canyon. We chose this canyon because the bedrock is mostly uniform within the catchment and it is adjacent to the highest peaks in the range. It also contains one of the remaining glaciers in the range.

We are evaluating mass wasting of canyon walls and ridges by observing characteristics and extent of talus fans. Last summer we started an inventory of talus fans in Garnet Canyon. We surveyed fan extent using a laser range finder to measure width and length of fans and place them on a geomorphic map. We also measured the slope of the bedrock walls directly above the apex of the talus fan to project the shape of the bedrock beneath talus deposits. We calculated volume based on the bedrock projection and fan height and width. With our geomorphic map, we calculated the area contributing material to the talus fans. The rate of erosion by mass wasting was calculated by dividing the total volume of talus fan debris by the contributing area and the time when glacial retreat began, ~14 ka (Licciardi et al., 2001).

To verify the erosion rates on ridges, we will compare our mass wasting rates to weathering on bedrock surfaces. We started collecting rock samples around Garnet Canyon for this purpose. The rates will be determined with in situ cosmogenic radionuclides (CRN) ^{10}Be and ^{26}Al. Rocks exposed at the surface experience a bombardment of cosmic rays from the sun producing ^{10}Be and ^{26}Al in quartz grains. The concentration of these isotopes increases with time if the rock is continuously exposed, therefore a measurement of isotopes present in quartz grains can approximate the exposure age of the rock (Nishiizumi et al., 1993). We have started extracting quartz grains from rock samples by crushing and separating the minerals. The samples will be sent to the University of Edinburgh in Scotland to complete the mineral extraction and measure the concentration of ^{10}Be with accelerator mass spectrometry (AMS). In a previous study in the region, Nishiizumi et al. (1993) collected one rock from the peak of the Grand Teton. They calculated an erosion rate of 0.048 mm/yr in the Teton Range based on a single CRN exposure age. With our samples, we
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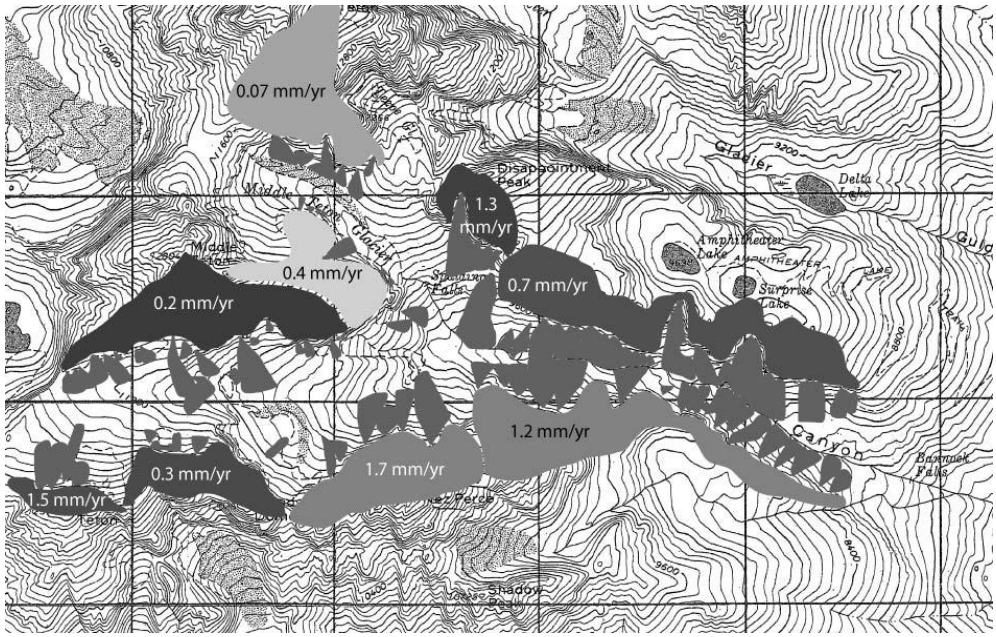

Figure 1. Talus fans and contributing bedrock areas are marked in this preliminary geomorphic map. Numbers represent mass wasting erosion rates for the surrounding bedrock area. Areas below the bedrock without numbers show the extent of the talus deposits.

hope to test if this rate is consistent around the rest of the canyon and in other locations in the range

In order to determine the spatial distribution of erosion we are using detrital apatite (U-Th)/He thermochronometry (AHe). This technique determines the age of individual apatite grains and compares the distribution of ages to a hypsometric analysis of topography. This method was developed by Brewer et al. (2003) and Ruhl and Hodges (2005) and applied by Stock et al. (2006) with AHe thermochronometry in the Sierra Nevada Mountains. AHe thermochronometry measures the concentration of uranium, thorium, and helium in apatite grains. Before tectonic uplift, rocks located deep in the crust experienced temperatures greater than 70 ^{o} C. At these temperatures, uranium and thorium decay and helium is completely diffused outside of the apatite grain. As rocks exhume and cool, helium is trapped within the apatite grain, providing a record of time since cooling began (Ehlers and Farley, 2003). We collected rocks along a 1200m vertical transect to determine the range of ages in these mountains and to verify that ages increase linearly with elevation. We determined hypsometry of the catchment in Garnet Canyon using GIS (Geographical Information Systems). The next step is to combine the hypsometry with age-elevation gradient to predict sediment age distribution. The product is a probability distribution function or PDF (Brewer et al., 2003; Ruhl and Hodges, 2005; Stock et al., 2006), which predicts what erosion should be if erosion is uniform throughout the entire catchment. We are using this method to analyze stream and glacial sediment to see how age distributions vary during glacial and interglacial periods.

We are also testing fluvial erosion rates with a catchment-wide measurement using the CRN method mentioned above applied to stream sediments collected at the mouth of canyons. Quartz grain ages collected from streams are integrated to get an average of canyon-wide erosion rates (Binnie et al., 2006; Nishiizumi et al., 1993). We collected sediments from Garnet Canyon and Cascade Canyon streams to test variability of rates between these two canyons.

✦ RESULTS

We calculated the volume of talus fan debris and used this information to calculate canyon-wide erosion rates due to mass wasting processes. The total volume is 1.6×10^{7} m^{3}. The canyon-wide accumulation rate is 1.42 mm/yr

and the erosion rate is 0.76 mm/yr. These results indicate that post-glacial hillslope erosion is keeping pace with estimated uplift of these mountains, which is ~2 mm/yr (Byrd and Smith, 1991; Hampel et al., 2007; Machette et al., 2001). We also notice spatial variability in the rates of mass wasting within the canyon (Figure 1). Rates are higher at lower elevations in the canyon than at the higher elevations. This could result from gradual deglaciation over time. The glaciers at the higher elevations were distributing the mass wasting debris away from where it was deposited more recently since the glacial extent has gradually decreased. Since this method only measures one process over a relatively short time scale we can see that the system is not in equilibrium and mass wasting is contributing to the Teton landscape. This is expected since the rock is highly jointed with many precariously positioned rocks hanging over steep walls. We cannot determine the long-term relief history with this method, so results from CRN analyses will provide important additional data.

We dated 5 bedrock samples from Garnet Canyon and 50 individual apatite grains from one Garnet Canyon stream deposit. The bedrock does show a linear increase in age with elevation (Figure 2). The distribution of grain ages shows erosion is concentrated at lower and higher elevations (Figure 3) than predicted.

There are two possible explanations for higher erosion at lower elevations. One reason could be explained by sediment transport. There are places in the canyon where sediment may be trapped. If this is the case, then the only sediments making it to the base of the canyon came from elevations lower than that of the trap. We did observe some areas where flow was slowed by talus debris and glacial deposits to form small, natural dams. The second explanation could be that fluvial erosion is more effective at these lower elevations.

Higher than predicted ages could indicate that the higher elevations are unstable, so erosion is high; or we have anomalous grains resulting from poor apatite quality. We did date some grains that must be anomalous because the ages were older than our oldest bedrock sample. These anomalous ages may result from inclusions of zircon or zoning within the apatite grains. These factors may increase the concentrations of uranium, thorium, and helium to give artificially older ages.

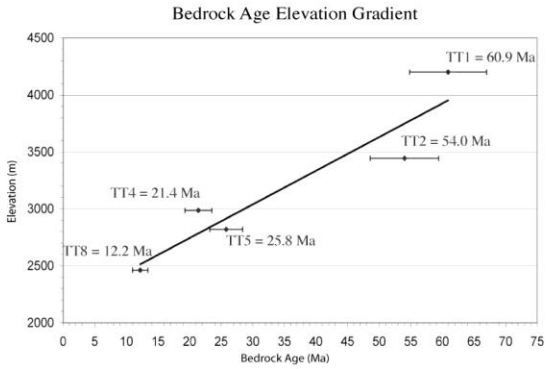

Figure 2. Age-elevation gradient for bedrock collected in Garnet Canyon. More rocks will be analyzed to fill in gaps in this line.

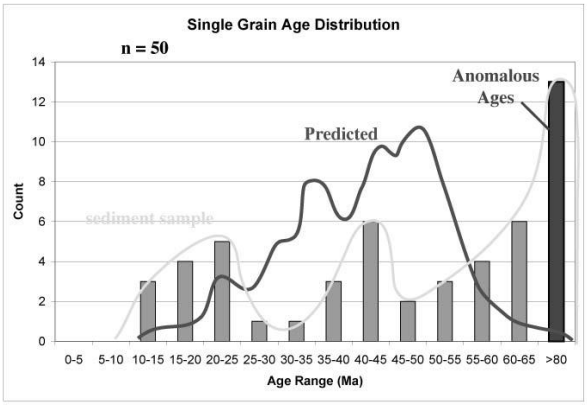

Figure 3. Single ages show concentration of erosion at higher and lower elevations. Since we have observed some inclusions and zoning in apatite grains, some ages may be anomalously old, indicating that they may be distributed among the younger ages beneath the predicted curve.

Since ~20% of the grains have anomalously old ages, we looked at grains a little more closely. If apatite crystals have inclusions or zones, the amounts of uranium and thorium are not uniform within a single grain. To test how the quality may affect the results of our study, we have analyzed individual grains with scanning electron microscopy (SEM) and cathodoluminescence (CL) at Virginia Tech. So far, ~12% of the apatite grains in the sediment had inclusions containing zircon and 26% of the grains had zoning. Zircon inclusions add helium, which would interfere with the apatite age. Zoning may affect our measurements since we assume that concentrations of uranium and thorium are uniform in the mineral, and age calculations are dependent on the grain size. Our next step is to analyze our bedrock samples with the same techniques to see if all bedrock contains poor quality grains, or if these grains are only

coming from a few rocks within the catchment. We will continue to date additional grains to get a statistically significant number of individual valid ages. We will also date moraine sediments to compare the erosion patterns in the glacial and fluvial systems.

✦ SUMMARY

So far, we see that recent mass wasting has been caused by jointing and low rock mass strength, which has enabled rapid hillslope denudation. The rate of hillslope erosion is comparable to long-term uplift rates. We will continue to study the effect of these processes by directly measuring ridge denudation with cosmogenic radionuclides in quartz minerals.

Detrital thermochronometry is indicating that post-glacial erosion is not uniform and excess sediments are sourced from low elevations. The apatite quality may affect the distribution of ages, so more apatite grains will be dated as well as studied with various techniques to see how significant these anomalous grains are throughout the canyon.

Overall, we see that erosional processes are fluctuating spatially and temporally, leading to non-uniform denudation at a given time. Yet when integrated over the long term, interacting denudational processes may balance tectonic rock uplift and maintain high topographic relief between glacial and interglacial periods.

✦ LITERATURE CITED

Binnie, S. A., W.M. Philips, M.A. Summerfield and L.K. Fifield. 2006. Sediment mixing and basin-wide cosmogenic nuclide analysis in rapidly eroding mountainous environments Quaternary Geochronology. 1:1-14.

Brewer, I. D., D.W. Burbank and K.V. Hodges. 2003. Modeling detrital cooling-age populations: insights from two Himalayan catchments: Basin Research. 15(3): 305-320.

Byrd, J. O. D., 1995. Neotectonics of the Teton Fault, Wyoming [Doctor of Philosophy thesis]: The University of Utah.

Byrd, J. O. D., and R.B. Smith. 1991. Geodetic evidence for aseismic reverse creep across the Teton fault, Teton Range, Wyoming: Geophysical Research Letters. 18(6): 1083-1086.

de la Montagne, J., 1956. Review of glacial studies in Jackson Hole, *in* Wyoming Geological Association 11th Annual Field Conference, Jackson Hole. p. 29-32.

Edmund, R. W., 1956. Resume of structures and physiography in the Northern Teton Mountains, Wyoming, Wyoming Geological Association Guidebook 11th Annual Field Conference: Casper, WY, Wyoming Geological Association. p. 151-157.

Ehlers, T. A. and K.A. Farley. 2003. Apatite (U-Th)/He thermochronometry: methods and applications to problems in tectonic and surface processes: Earth and Planetary Science Letters. 206: 1-14.

Elias, S. A., 1996. The ice-age history of National Parks in the Rocky Mountains: Washington, Smithsonian Institution Press. 170 p.

Foster, D., S.H. Brocklehurst and R.L. Gawthorpe. 2007. The Glacial Buzzsaw in the Northern Basin and Range: the Importance of Glacier Size and Uplift Rates: Eos, Transactions, American Geophysical Union, 88 Fall Meeting Suppl. Abstract H53C-1378.

Fryxell, F. 1929. Glacial Features of Jackson Hole, Wyoming: University of Chicago. 128 p.

Hampel, A., R. Hetzel and A.L. Densmore. 2007. Postglacial slip-rate increase on the Teton normal fault, northern Basin and Range Province, caused by melting of the Yellowstone ice cap and deglaciation of the Teton Range?: Geology. 35(12): 1107-1110.

Licciardi, J. M., P.U. Clark, E.J. Brook, K.L. Pierce, M.D. Kurz, D. Elmore, P. and Sharma. 2001. Cosmogenic 3He and 10Be chronologies of the late Pinedale northern Yellowstone ice cap, Montana, USA. Geology. 29(12): 1095-1098.

Love, J. D., J.C. Reed Jr. and K.L. Pierce. 2003. Creation of the Teton Landscape, A Geologic Chronicle of Jackson Hole and the Teton Range: Moose. WY. Grand Teton Natural History Association.

Machette, M. N., K.L. Pierce, J.P McCalpin, K.M. Haller and R.L. Dart. 2001, Map and data for Quaternary Faults and Folds in Wyoming.

Nishiizumi, K., C.P. Kohl, J.R.. Arnold, R. Dorn, J. Klein, D. Fink, R. Middleton and D. Lal. 1993. Role of *in situ* cosmogenic nuclides ^{10}Be and ^{26}Al in the study of diverse geomorphic processes: Earth Surface Processes and Landforms. 18: 407-425.

Roberts, S. V. and D.W. Burbank. 1993. Uplift and thermal history of the Teton Range (northwestern Wyoming) defined by apatite fission-track dating: Earth and Planetary Science Letters. 118: 295-309.

Ruhl, K. W., and K.V. Hodges. 2005. The use of detrital mineral cooling ages to evaluate steady state assumptions in active orogens: An example from the central Nepalese Himalaya: Tectonics. 24: TC4015-.

Small, E. E. and R.S. Anderson. 1998. Pleistocene relief production in Laramide mountain ranges, western United States: Geology. 26(2): 123-126.

Small, E. E., R.S. Anderson, J.L. Repka and R.C. Finkel. 1997. Erosion rates of alpine bedrock summit surfaces deduced from in situ 10Be and 26Al: Earth and Planetary Science Letters. 150: 413-425.

Stock, G. M., T.A. Ehlers and K.A. Farley. 2006. Where does sediment come from? Quantifying catchment erosion with detrital apatite (U-Th)/ Hethermochronometry. Geological Society of America. 34(9): 725-728.