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29th ANNUAL REPORT 2005

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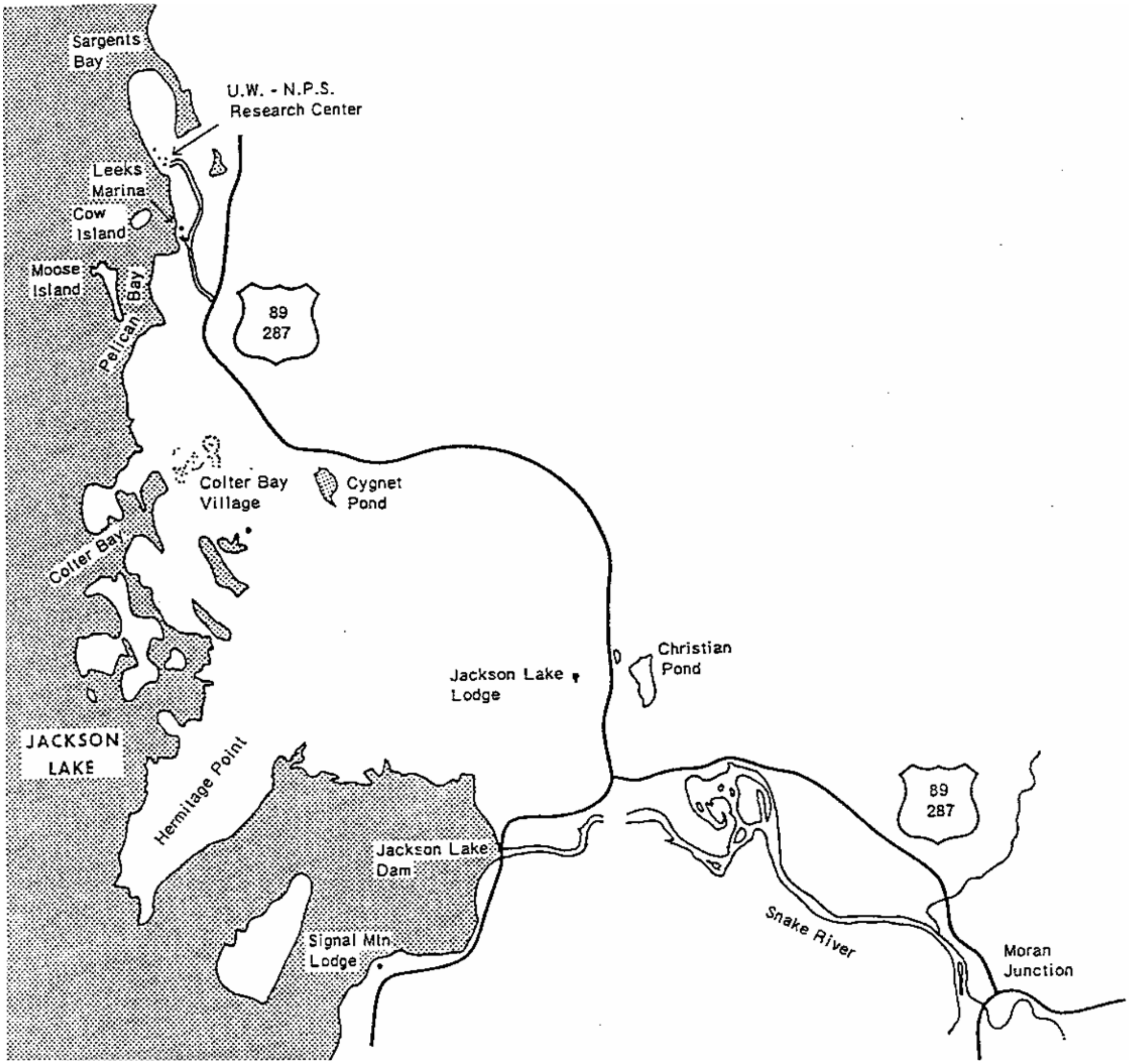

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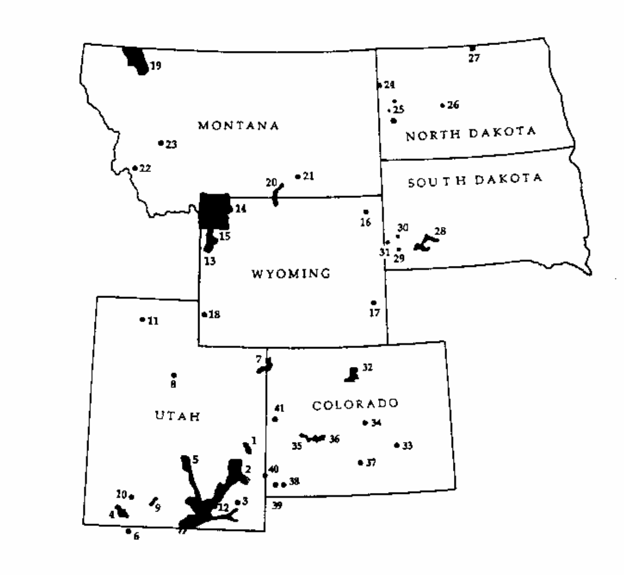

✦ SOUTH DAKOTA

28. Badlands National Park
29. Wind Cave National Park
30. Mount Rushmore National Memorial
31. Jewel Cave National Monument

✦ UTAH

1. Arches National Park
2. Canyonlands National Park
3. Natural Bridges National Monument
4. Zion National Park
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
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INTRODUCTION

2005 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 50 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 permissionfrom the author(s).

FEATURE ARTICLE

INVESTIGATION OF *BATRACHOCHYTRIUM DENDROBATIDIS* IN FOUR BOREAL TOAD (*BUFO BOREAS BOREAS)* POPULATIONS IN WYOMING

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IDAHO STATE UNIVERSITY ✦ POCATELLO

✦ INTRODUCTION

Batrachochytrium dendrobatidis (Figure 1) is a newly described chytridiomycete fungus that infects amphibian keratin (Berger et al. 1998). It is reported to cause disease and mortality in metamorphosed amphibians around the world (Lips 1998; Young et al. 2001; Bradley et al. 2002; Muths et al. 2003). In several cases, this pathogen is believed to be the primary cause of extinction for amphibian species (Daszak et al. 1999).

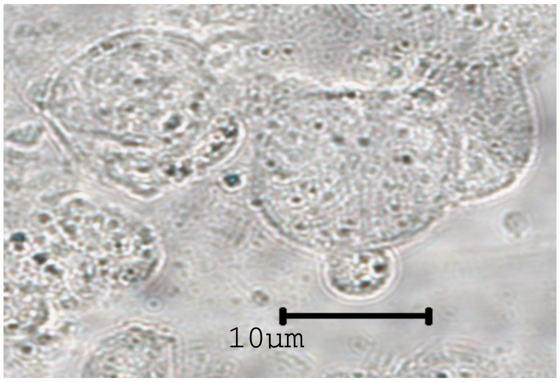

Figure 1. *Batrachochytrium dendrobatidis* sporangia containing zoospores (400x).

Within the last few years, the United States Geological Survey (USGS), in conjunction with Idaho State University (ISU) and the National Park Service, has been screening amphibian populations for *B. dendrobatidis* in the Rocky Mountain area. Boreal toads (*Bufo boreas boreas)* (Figure 2), once common in Colorado, have likely been decimated by chytridiomycosis (disease associated with *B. dendrobatidis*) (Muths et al. 2003). In a recent study by Carey et al. (2006) the boreal toad from Colorado was found to be susceptible to the *B. dendrobatidis* under laboratory conditions.

Figure 2. Boreal toad, *Bufo boreas boreas*

On the other hand, *B. dendrobatidis* has been identified in at least 4 populations of boreal toads in Grand Teton National Park (Figure 3) and the adjacent Bridger-Teton National Forest (Erin Muths and Susan Wolff, personal communication) and 2 populations in the adjacent National Elk

Refuge (D. Patla, personal communication), yet significant mortality has not been reported. Repeated sampling of tagged boreal toads by USGS suggests animals can survive from one year to the next with the fungus (E.Muths, personal communication). Similar variation in the mortality rates associated with this fungus has been reported in other parts of the world (Berger et al 1998; Retallick et al 2004). These findings have given rise to a number of questions regarding the host, pathogen and environmental factors involved in the manifestation of chytridiomycosis.

Figure 3. Grand Teton National Park

More information on the spatial and temporal distribution of this potential pathogen within the Greater Yellowstone Ecosystem, and the factors necessary to induce chytridiomycosis is required. The breeding sites in the greater Grand Teton area provide a unique opportunity to study this fungal pathogen in a region where it does not appear to cause significant acute disease in amphibians.

✦ METHODS

We sampled different life stages of boreal toads at four sites where *B. dendrobatidis* has been detected in recent years on the skin of adult amphibians. These data provide additional information on the infection status of populations sampled in previous years. In addition, the data provide information on the life stage(s) when toads become infected with the pathogen. Data were collected in collaboration with members of the USGS amphibian monitoring program (Erin Muths and Steve Corn), and the Grand Teton National Park biologist (Susan Wolff). The sampling scheme used also provided us with the opportunity to culture of *B. dendrobatidis* isolates for our laboratory-based pathogenicity studies.

Four boreal toad breeding sites (Blackrock area oxbow pond on the Bridger-Teton National Forest, Snake River Quarry near Flagg Ranch in the J.D. Rockeller Memorial Parkway of GTNP, Nowlin Creek on the National Elk Refuge, and Lower Schwabacker in GTNP) within a 60 mile radius of the UW-NPS Research Station were visited (Figure 4). Different life stages of amphibians were collected and tested for *B. dendrobatidis* using PCR techniques and culture as described in Annis et al (2004) and Rachowicz and Vredenburg (2004), respectively.

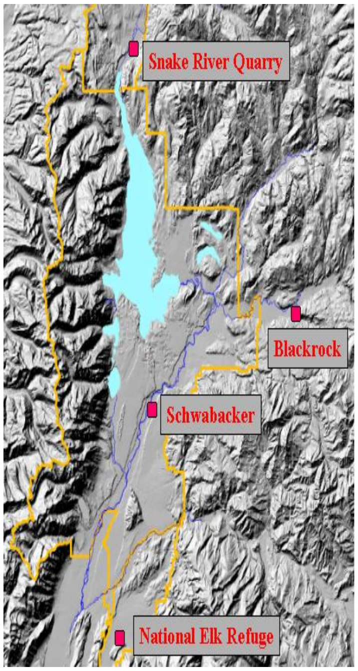

Figure 4. Study sites in relation to Grand Teton National Park

Approximately twenty metamorphs (toadlets) from each of the sites (except Schwabacker where no metamorphs were found) were also swabbed in a similar manner as the adult toads with the exception that cotton swabs were used for both the fungal culture sample and the PCR sample.

Approximately twenty adults were non-lethally sampled during the breeding season at each of the locations. Adults were also tested whenever they were found on subsequent visits. Animals were swabbed twice, once with a sterile plastic bioloop (Fisher cat # 13-075-3) and a second time with a cotton tipped wooden applicator stick (Fisher cat # 14-959-91) (Figure 5). The plastic loop was stored in ethanol and the cotton swab was stored in TGhL culture broth (Johnson, Amphibian Diseases Ecology Group, School of Public Health and tropical Medicine, Townsville, Australia).

Up to 6 strands of eggs (5 cm in length) at each of the four study sites, with the exception of the Snake River Quarry where no eggs were found, were collected in ethanol for PCR testing. Between 20 and 40 tadpoles were euthanized in Tricaine methane sulfonate (MS-222), examined for mouthpart abnormalities at 10X magnification, and stored in ethanol for subsequent testing by PCR.

Figure 5. *Bufo boreas boreas* being swabbed ventrally for chytrid

Adult[1] and metamorph PCR samples were tested at Idaho State University. Tadpoles and eggs were sent to Pisces Molecular laboratory (Boulder, Colorado) for evaluation. For tadpoles, only the mouthparts were submitted for testing as only these parts contain keratinized tissue necessary for chytrid growth (Longcore et al. 1999). Mouthparts were pooled into groups of three to five animals from similar locations. An attempt was also made to only submit the outer layer of the egg membrane for PCR testing to avoid dilution of the samples.

Chytrid PCR Protocol (ISU)

Swabs in ethanol were vortexed and all liquid was decanted into a centrifuge tube. Samples with plastic loops were centrifuged directly. Tubes were spun at 13000 RPM for 10 minutes in a micro-centrifuge. The ethanol was then decanted and discarded, while the sample tubes with pellet were dried at 37° C for approximately 30 minutes, or until all ethanol had evaporated. Pellets were then re-suspended in 25 µl of sterile-filtered TRIS. This was used directly in the PCR reaction.

Each PCR reaction consisted of 50-µl total volume in a 0.2 mL thin-walled PCR tube. Each reaction consisted of 5 µl of 10x buffer, 29.5 µl of nuclease-free water, 8 µl of dNTPs (di-nucleotriphosphates), 1 µl of forward primer Bd1a, 1 µl of reverse primer Bd2a, 0.5 µl of Polymerase and 5 µl of sample template. The PCR primers used in this study are described in Annis et al. (2004). Primer Bd1a was
5'-CAGTGTGCCATATGTCACG-3'
and Bd2a was
5'-CATGGTTCATATCTGTCCAG-3' ; both were made by Integrated DNA Technologies.

PCR reaction tubes were placed in a thermocycler and were run on the following program: 10 minutes at 95 ˚C to lyse cells, 40 cycles of 1 minute at 95˚C, 1 minute at 60 ˚C (annealing) and 1 minute at 72 ˚C (elongation), followed by a final elongation of 4 minutes at 72˚C. Samples were then stored at 4 ˚C.

For each PCR product, 5 µl was added to 1 µl of 6x bromophenyl blue loading dye and loaded into a 1 % agarose gel stained with Ethidium Bromide. The gel was run in an electrophoresis block at 98 V constant for approximately 25 minutes, then removed. Gels were viewed using a photo imager using the program "Flour-S". A fluorescent band at 300 base-pairs indicated a positive PCR reaction for the primers used in this study. Bands from a select number of positive samples were sequenced to confirm the product.

Culture

Broth and agar media containing Tryptone, hydrolysed gelatine, lactose, and the antibiotics streptomycin, tetracycline and Penicillin G were made as described by Johnson (http://www.jcu.au/school/phtm/PHTM/frogs/protocol/bd-media-protocol.pdf). Subsequent media for the toadlet swab samples was made using Fluconozole (an anti-yeast agent).

Swabs were inoculated in the TGhL broth at least overnight and up to 3 days at approximately 18^0 C. These were subsequently plated on TGhL agar plates and placed at 18 ^{0}C for 7 days. The plates were examined for growth every other day. Colonies were examined under 1000X light microscopy. Plates with excessive growth were sub-sampled, and later examined for identification of organism(s). Gram stains were done on approximately 30 smears.

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[1] The 4 adult toads sampled from the National Elk Refuge were sent to Pisces Molecular Laboratory for PCR testing.

✦ RESULTS

PCR

Batrachochytrium dendrobatidis was detected by PCR and confirmed by sequencing on adults during the breeding season at all four study sites sampled in 2005 (Table 1). With the exception of the National Elk Refuge, the prevalence of *B. dendrobatidis* was relatively low (range between 2.8% and 25%). Only 4 adults were sampled from the National Elk Refuge during the breeding season, but 2 of these were PCR positive for *B. dendrobatidis.* The only metamorph that tested positive by PCR was also from the National Elk Refuge (Table 1).

	Number tested	Number positive
Blackrock		
Adults during breeding season	36	1 (2.8%)
Adults during summer	5	2 (40%)[2]
Eggs	5 strands	0
Tadpoles	9 samples (36 tadpoles[1])	0
Metamorphs	21	0
Schwabacker		
Adults during breeding season	19	1 (5.3%)
Adults during summer	10	0
Eggs	1 strand	0
Tadpoles	7 samples (20 tadpoles)	0
Metamorphs	1	0
National Elk Refuge (Nowlin)		
Adults during breeding season	4	2* (50%)
Adults during summer	11	0
Eggs	5 strands	0
Tadpoles	4 samples (8 tadpoles)	0
Metamorphs	32	1
Snake River Quarry		
Adults during breeding season	20	5 (25%)
Adults during summer	0	NA
Eggs	0	NA
Tadpoles	6 samples (28 tadpoles)	0
Metamorphs	20	0

Table 1. Summary of test results for animal sampled for *Batrachochytrium dendrobatidis*. Included are the location where the animal was sampled and its life stage.

*Pisces lab

[1] Two tadpoles had missing pigment on their mouth parts.

[2] One of these samples was abnormally shedding skin.

None of the tadpoles sampled or any of the egg samples were positive for *B. dendrobatidis* by PCR (Table 1).

Culture

No samples cultured positive for *B. dendrobatidis*. Many of the cultures were overgrown by yeast within 3 days. Samples cultured on TGhL agar plates containing fluconozole were negative for *B. dendrobatidis* by PCR and culture. These had limited yeast growth.

✦ DISCUSSION

Batrachochytrium dendrobatidis was identified by PCR in breeding adult boreal toads from each of the four locations sampled, which is consistent with previous studies conducted in these areas. However, with the exception of the adult toads sampled from the National Elk Refuge, which were tested at a different laboratory, the prevalence of the fungus in populations sampled in this study was generally lower than in previous years. The discrepancy in prevalence between sites and between years may be attributed to the different laboratories (and technique) used for PCR testing.

No mortalities were noted at any of the sites visited and all toads sampled, with the exception of one which was abnormally shedding its skin, appeared normal. The individual with clinical signs of chytridiomycosis (abnormally shedding its skin) tested positive for *B. dendrobatidis* by PCR (Table 1).

Based on these results it would appear that *B. dendrobatidis* is still present in the Grand Teton National Park area, and toads with the fungus generally do not have clinical signs of chytridiomycosis.

We did not detect the fungus on any eggs or tadpoles, and these findings were consistent with other reports that these life stages of the boreal toad are not susceptible to the fungus. However, a recent report by Blaustein et al. (2005) suggests tadpoles may be susceptible to disease when exposed to *B. dendrobatidis* experimentally. Based on the data in our study it would appear that toads are likely becoming infected with the pathogen as adults, and perhaps occasionally as metamorphs (toadlets).

Batrachochytrium dendrobatidis was not confirmed by culture in any of the samples collected (n≅150). In many cases, yeast was apparent on the cultures within 3 days. Whether or not this prohibited *B. dendrobatidis* from growing is unknown. Fluconozole was added to the culture media for the samples collected from the toadlets and the adults sampled late in the summer to suppress yeast; however, these individuals (with the exception of 1) were negative for the fungus by PCR so the media could not be properly assessed on field samples. Using an established laboratory culture Fluconozole appears to suppress *B. dendrobatidis* slightly.

FUTURE RESEARCH

More research is required on the role water quality parameters play in the manifestation of chytridiomycosis. The pH of water at the sites sampled last year was above 8.0 and the conductivity was greater than 140 µs (Table 2). These water quality parameters may not be conducive for *B. dendrobatidis* growth and may explain why it is not causing acute disease in toads found at the four sites sampled.

Location	UTM (Nad 27 z12)	pH	Conductivity (µs)	Temperature (C)
Blackrock	552480, 4853370	9.8	176.4	18
Schwabacker	526473, 4839952	8.4	161.7	16
National Elk Refuge	522372, 4818872	9.0	300	30
Snake River Quarry	525406, 4881761	9.58	139.5	24

Table 2. Location of sites where toads were sampled and water quality parameters at the sites. Water quality was taken the first week of August 2005.

In a study by Hawk (2000) it was found that the boreal toad populations with the best breeding success in the Greater Yellowstone area were those using ponds with high conductivity water. It was hypothesized that this water parameter reduced osmoregulatory stress (Hawk, 2000).

In the summer of 2006, we will investigate the role of water quality parameters on the development of chytridiomycosis by sampling more sites for *B. dendrobatidis* and collecting detailed water quality information, including temperature, conductivity and pH, over time at each location, and by conducting laboratory challenges using different water conductivity and pH. Our laboratory study will also permit us to evaluate the susceptibility of the boreal toad found in Wyoming to *B. dendrobatidis*. Furthermore, we will modify our culture media and attempt to culture the fungus again in 2006 on animals that are likely to be infected (i.e. breeding adults).

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GRAND TETON NATIONAL PARK

PARASITE INFECTION STATUS OF *POTAMOPYRGUS ANTIPODARUM*

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✦ ABSTRACT

Outside its native range, the invasive species *Potamopyrgus antipodarum* (New Zealand Mud snail; NZMS) has seldom been reported to harbor parasites. To test this intriguing observation, 7 sites along the Snake River and Polecat Creek in the Grand Teton National Park/John D Rockefeller Memorial Parkway area (Wyoming, USA) were surveyed for NZMS, native aquatic snails and parasites: digenean trematodes (specialist parasites of snails) and nematomorphs (horse hair worms, generalist parasites of aquatic invertebrates), in July 2005. Non-destructive examination of 96 native snails at each site revealed abundant presence of digeneans (parasites that specialize in snails) at 6 sites. Within 2 hours, up to 12.4% of lymnaeid snails shed furcocercous cercaria or xiphidiocercaria, and up to 50% of physid snails released furcocercous cercaria or echinostome cercaria. A total of ~900 NZMS (collected from 5 of the sites) were investigated for infection with digeneans by overnight shedding. One NZMS yielded amphistome-like metacercariae that had encysted in the observation tray. The dissection of 150 ethanol-fixed NZMS (30/site) revealed several types of internal metacercarial stages of digeneans in 5 snails (all from Polecat Creek). PCR-based assays targeting parasite rDNA sequences in DNA extracted from pools of ~150 snails each also indicated associations between digenean parasites and NZMS. All parasites were detected in NZMS from Polecat Creek. NZMS were not observed to harbor nematomorph parasites with any of the techniques used. In conclusion, the sites tested contained multiple native snail-digenean parasite associations, and the capacity of invasive NZMS outside the native range to serve as first and second intermediate host for digenean parasites may have been underestimated previously.

✦ INTRODUCTION

Potamopyrgus antipodarum, the New Zealand Mud snail (NZMS) is an invasive species that has spread far beyond its native range of New Zealand. The success of this invader, also present in the Greater Yellowstone Ecosystem (e.g. Kerans et al., 2005) has been considered in light of the capacity for parthenogenic (asexual) reproduction, tolerance for a wide range of abiotic conditions, and the (virtual) absence of parasitism in introduced ranges (Gerard et al., 2003). Generally, invasive organisms incur fewer (types of) parasites in introduced ranges as compared to the native range. This reduction likely benefits the fitness of invasive species (Torchin et al., 2003).

Invasive *P. antipodarum* may not have carried parasites, or their native parasites did not establish in the introduced range. However, newly colonized habitats contain a variety of parasitic organisms. Likely, these include digenean trematode parasites that specialize in using snails as intermediate host. Many digeneans exhibit specificity to particular snail species in which they can reproduce, but penetration of non-host snails also occurs. Both incompatible and compatible digeneans are a burden to snails. In the first case, snails mount a defense response to kill and destroy an incompatible invader. Over time, with repeated encounters, some parasites may adapt to previously incompatible snail species. In fact, digeneans have acquired new hosts across large phylogenetic distances (Brant and Loker, 2005), and a novel host-parasite association involving *P. antipodarum* and a sanguinicolid trematode was described from Europe (Gerard and Le Lannic, 2003). In the second case, compatible digeneans avoid or evade the host defenses and modify the physiology of the snail to benefit the asexual multiplication of intramolluscan parasite larvae. Some digeneans exert parasitic castration, severely impact host fitness by causing a snail to cease reproduction (Sorenson and Minchella, 2001).

Certain groups of digeneans provide additional risk of infection to snails. The cercaria from echinostome and plagiochid parasites emerge from the first intermediate host snail to penetrate to encapsulate as metacercaria within a second intermediate host, awaiting predation to reach the next host (e.g. Galaktionov and Dobrovolskij). Metacercaria evoke little host response and can persist in a variety of organisms, including invertebrates and vertebrates. Both native and invasive snails may be infected indiscriminately, at the expense of providing space, and possibly other resources to digenean metacercaria. Other generalist parasites may similarly infect any snail that they encounter. For instance, larval stages of nematomorphs (horse hair worms; parasites of arthropods) use aquatic invertebrates as transport hosts. One field study showed that close to 40% of physid snails harbored one or more nematomorph cysts (Hanelt et al., 2001). Although there was no clear pathology associated with the cysts, infected snails cause parasites to persist such that they may ultimately infect and impact their true host.

Thus, it is remarkable that invasive *P. antipodarum* are rarely reported to harbor parasites. However, detection of intramolluscan digenean and nematomorph parasites with traditional methods (shedding and dissection) is labor intensive and may yield false negative results. Detection rates may increase when using PCR-based methods to detect parasite-specific sequences in DNA extracted from (pools of) snails (Rognlie et al., 1994; Hanelt et al., 1997; Hamburger et al., 2004). Previous phylogenetic studies provide (nuclear ribosomal gene) sequences that can be targeted for detection by PCR of digeneans (Olsen et al., 2003), nematomorphs (Bleidorn et al., 2002), and NZMS (*Cytochrome B*, Neiman et al., 2005).

This study applied traditional and PCR-based methods to evaluate the presence of parasites of native snails, and the infection status of invasive *P. antipodarum* at several sites in the Grand Teton National Park/ John D Rockefeller Memorial Parkway area (Wyoming, USA).

✦ METHODS AND MATERIALS

Collection Sites

Several sites were located north of Jackson Lake along the Snake River and Polecat Creek. Also sampled were Oxbow Bend and Jackson Lake Dam, downstream of Jackson Lake. See table 1 for GPS coordinates of the seven locations.

Native Snails

Ninety-six native snails (independent of species) were collected from each field site and placed individually in wells of 24 well tissue culture plates containing 3 ml of water, and identified to genus level. The snails were kept in a shaded spot along the bank of the collection site for two hours to allow shedding of digenean parasites, and then returned to the field. In the laboratory, the water in each well was inspected using a dissection scope for digenean parasites. The parasites observed were collected, fixed in 100% ethanol, examined microscopically and destructively processed for DNA extraction.

NZMS

New Zealand mud snails were collected during a 2 hour time interval from each of the sites. Two NZMS were placed in each of 96 wells (3 ml of water) and examined the next day for shedding of parasites. Any parasites and the snails from which these originated were fixed in 100% EtOH. Other

New Zealand mud snails were fixed in 100% EtOH and stored at -30C. For dissection, snails were rehydrated to 25% ethanol. Individual snails (n=30 from each site) were crushed between glass slides and the tissues were examined microscopically for both digenean and nematomorph parasites.

DNA Extractions and PCR.

DNA was extracted directly from pools of live snails, or of ethanol-fixed snails (rinsed twice with water to remove ethanol), using a CTAB-based method (Winnepenninckx et al., 1993). After microscopical confirmation of species, 150 NZMS from each site were crushed in a DNA extraction buffer containing Hexadecyltrimethylammonium bromide (CTAB), SDS, EDTA and proteinase K. Following incubation at 60C (1 h), the sample was chloroform-extracted, DNA was precipitated from the aqueous phase with isopropanol, rinsed (76% methanol, 10 mM ammonium acetate) and dissolved in 200 □l milliQ water. The black color of the resulting samples precluded spectrophotometric measurement of DNA concentration, and 0.5 □l volumes were used as template for PCR reaction.

PCR experiments

PCR reactions were performed to amplify DNA sequences specific for NZMS snails (*Cytochrome C*, positive control for the quality of the sample), digenean parasites (18S and 28S) and *Nematomorpha* (18S). Primers (all shown 5'-3') for a 400 basepair fragment of *Cytochrome C* of *P. antipodarum* were designed from an alignment of 45 haplotypes (Neiman et al., 2005); PaCBF (AAR GTA AAG AAT CGG GTT AAA G) and PaCBR (CAG GAC TAT TTT TAG CAA TGC). PCR primers for detection of digenea were adopted from Olsen et al. (2003). Digenean 28S rDNA (also designated as large subunit; LSU): LSU-5 (TAG GTC GAC CCG CTG AAY TTA AGC A) and 1500R (GCT ATC CTG AGG GAA ACT TCG). Anticipated amplicons will be about 1400 bps; Also 12S rDNA (small subunit:SSU; about 1800 nt): Worm-A (A/GCG AAT GGC TCA TTA AAT CAG') and Worm-B (ACG GAA ACC TTG TTA CGA CT) with alternative Worm-B (C TTG TTA CGA CTT TAC TTC C). An alignment of 18S sequences of from nematomorpha (Bleidorm et al., 2002) and hydrobiid snails (the gastropod family that includes *P. antipodarum*, Wilke et al., 2001) yielded primers to amplify the 18S gene from the parasite with minimal chance of cross-reactivity with snail sequences. N18F (5'-CCAT GCA TGT VTM AGT ATR AAC-3') and N18R (5'-CAT TCC AAT TAC AGG GTC TC -3').

PCR reactions consisted of 2.5U of DNA polymerase AmpliTaq Gold (Applied Biosystems), 200mM of each dNTP, 0.5 µmolar of both forward and reverse primers, 1 µliter of DNA template and 4 mM of $MgCl_2$. The cycling profile was 10' 95C, 40 cycles of 1'95C, 30" at annealing temperature (between 50 and 65C, depending on primers), 1' 72C, final extension 7' 72C (T-gradient thermocycler, Biometra). Ethidiumbromide-stained PCR amplicons were visualized by UV transillumination following electrophoresis on 1.0% agarose gels (45', 85V).

✦

RESULTS

Native snails and Parasites

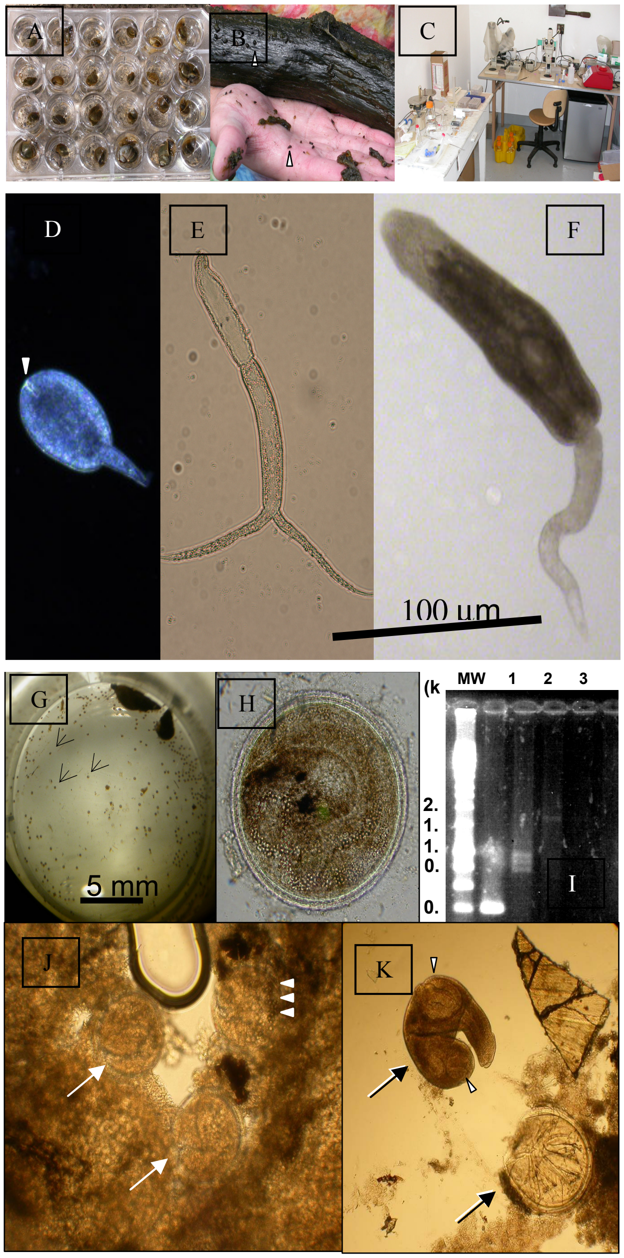

FIGURE LEGEND. **A)** Native snails collected from the field were kept in 3 ml wells of a tissue culture plate to shed parasites. After two hours, these snails were returned to the collection site. **B)** New Zealand Mud Snails were abundantly present in Polecat Creek. Many snails were on this log and easily transferred to hands of snail collectors (arrowheads). **C)** The lab space in the boat house of the UW/NPS research station, set up for examination of parasites, DNA extraction, PCR and DNA gel-electrophoresis. **D-F)** Examples of the main types of digenean trematode cercariae recovered from native aquatic snails, scale bar applies to all 3 figures; **D)** Xiphidiocercaria (phase contrast) collected from a lymnaeid snail (site 1). Note the characteristic short tail and the lancet (arrow head). **E)** Furcocercous cercaria with forked tail and showing two eye spots, recovered from a physid snail, site 5. **F)** Echinostomatid cercaria (note bifurcated intestine) from a physid snail, site 6. **G)** Overnight shedding of two NZMS (site 5), yielded multiple digenean parasite metacercaria (some indicated by arrows) that had encysted in the well. **H)** Close up of a (likely amphistome) metacercaria from the previous photo. Eye spots and a smooth double cyst wall are visible. **I)** Results from PCR with DNA extracted from pooled NZMS collected from site 6. Lane 1: 400 bp PCR amplicon from *cytochrome B* of NZMS (positive control); lane 2: 28S rDNA digeneans, multiple amplicons smaller than the expected product of ~1400nt may be diagnostic for parassites, but this will be confirmed by sequencing.; lane 3; digenean18S rDNA amplicon is of expected size at ~1800nt; lane 4; 18S rDNA digeneans (alternative primer combo). A weak amplicon of the expected size (~1800nt) is visible on the actual gel, lane 5: 18S rDNA from nematomorps, expected size ~420nt, no amplicon visible on gel. MW is molecular weight marker, size indicated in kilobases (kb). **J)** The tissue squash of one NZMS (site 6) revealed 3 round echinostome-type metacercariae (white arrows), displaying typical calcarious corpuscules (arrowheads). **K)** Non-identified metacercarial larva expressed from its cyst (black arrows) likely during the squashing of the tissues of one NZMS from site 6. This intramolluscan parasite displays two suckers, typical for digenean trematodes (arrowheads). The triangular shape is a small fragment NZMS shell.

Native aquatic snails were present in such numbers that it required little effort to sample 96 specimens at any of the collection sites. Several (non-determined) snail species of the bassomatophoran gastropod families Lymnaeidae and Physidae were present at all 7 sites. Planorbidae were represented by *Gyraulus* sp. (especially numerous at site 2 downstream of Jackson Lake Dam, but also observed at sites 4 and 6) and *Planorbella* sp. (only site 6, north of Jackson Lake). An amphibious stylomatophoran (*Succinea* sp.) was encountered at site 4 (Oxbow bend). Although not specifically documented, diverse animal life arthropods, annelids, fish, amphibians, reptiles, birds and mammals, potentially contributing to parasite life cycles, was observed during site visits. As summarized in table 1, the on-site shedding experiments (figure 1A), yielded a variety of digenean cercariae released from lymnaid and physid snails. No parasites were recovered from planorbid snails or from *Succinea*. The snails collected at site 2 did not shed any parasites. The parasites collected encompassed three main morphological types: xiphidiocercaria with or without eye spots (only from lymnaids); furcocercous cercaria with or without eye spots (lymnaeids and physids); and echinostomatid cercaria (physids only), see figures 1 D, E, F. No double infections were evident, individual snails shed only one morphological type of cercaria.

NZMS and Parasites

Potamopyrgus antipodarum was not observed downstream of Jackson Lake Dam or at Oxbow Bend. NZMS were present however, at the 5 collection sites along the north bank of the Snake River and at high numbers in Polecat Creek (Figure 1B). Snails collected during a 2 hour interval were transported to the lab for analysis (Figure 1 C). Overnight shedding of 192 live NZMS from each site (1344 snails total) resulted in one observation of parasites: encysted metacercariae in a well that contained NZMS from site 5. These cysts can only result from cercariae, shed from the NZMS. The morphology of the cysts is consistent with an amphistome digenean (Fig 1 G,H). PCR experiments indicated that DNA isolated from pooled NZMS from site 6 also contained digenean parasites (Figure I). Finally, dissection and microscopical examination revealed intramolluscan metacercarial cysts (one likely echinostome, one unknown) in 5 NZMS from site 6 (Figure 1 J, K), and one snail contained metacercarial cysts of both types. In summary, 6 individual NZMS from sites 5 and 6 (both along Polecat Creek) harbored parasites. This represents 6/(1344 + 150) or 4.01% of all NZMS that were examined individually either by shedding or dissection. The PCR results suggest that additional snails from site 6 carried digenean parasites, but numbers of infected snails can not be derived from this pooled sample.

✦ DISCUSSION

The cataloguing of native snails and their digenean parasites in the study area ascertained that the environment in the study area was supportive for maintaining (digenean) parasites-snail host associations in general. Nematomorph parasites were not observed and are not included further in this discussion. The unique failure to detect parasites from site 2 (Jackson Lake Dam) may reflect conditions that are less supportive of parasites, such as fast flowing and cold water. Also detection of parasites by shedding snails, especially for short time intervals, is error prone due to timing issues. Intramolluscan parasites may not yet have developed to the cercarial stage, especially if juvenile snails were collected. Snails may have already shed all available cercariae; parasite emergence can by ruled by circadian rhythms (for discussion see Hanelt et al., 1997; Hamburger et al., 2004). Whatever the cause for the failure to detect parasites, digeneans were again present at Oxbow Bend, downstream of this area.

Regardless, NZMS was not observed at these sites (2 and 4), south of Jackson Lake. The NZMS were present in the Snake River and Polecat Creek, north of Jackson Lake. These sites harbor multiple native snail-parasite associations and the NZMS are likely to repeatedly encounter potential parasites. Under these conditions, the incidence of digenean parasite infection in NZMS was about 4% of individually examined NZMS. This falls in the range of infection frequency of native snails (Table 1). However, the data for the native snails is based on a 2 h shedding assay that likely underestimates parasite incidence. Far greater scrutiny was applied to determine infection in NZMS, using an overnight shedding assay, greater numbers of snails, and multiple detection methods. The PCR-based detection of parasites proved feasible at the station, facilitated by setting up a lab with minimal equipment brought from off-site for DNA extraction, PCR and horizontal agarose gel-electrophoresis.

The combination of different techniques proved valuable. PCR analysis of pooled samples may show presence of parasites (plus/minus result) and although it does not allow distinction of the type of snail-parasite association, or the number of infected snails, PCR takes less effort to study large numbers of snails compared to shedding or dissection methods. Shedding of cercaria (resulting in metacercariae) shows that NZMS serves as a first host for a digenean parasite and helps propagate the life cycle of the parasite by releasing infective parasite larvae. Clearly, if this particular parasite can (adapt to) routinely develop in NZMS, the sheer numbers of potential snail hosts may have considerable impact. Either elevated transmission of the parasite will adversely affect the next host species in the life cycle, the parasite infection may prove deleterious to NZMS (consider Sorenson and Minchella, 2001) affording some level of control of the invasive nature of NZMS, or both. The intramolluscan metacercaria evidenced by dissection of NZMS (the third and final technique used) may also have different biological significance. These metacercariae resulted from random infection by cercariae that developed in another snail, and NZMS function as a transport host only. If predators or scavengers ingest infected snails, NZMS may again contribute to propagation of a parasite. However, if infected NZMS are not eaten these internal parasites ultimately die with the dead-end snail host. In the latter case, high numbers of NZMS may actually reduce the transmission of some digeneans by sequestering the infective stages of certain digenean parasites away from the environment. Further study will have to be done to clarify how these interactions between NZMS and digenean parasites play out. Finally, the parasite samples from native snails and from NZMS have been destructively sampled for DNA, and if successful, the obtained sequence will be used to identify parasites by comparison with published sequences for known parasites and the results of these efforts will be published elsewhere.

In conclusion, using several complementary methods, digenean parasite infection was documented from invasive *Potamopyrus antipodarum* in an introduced range. This is one of only few such reports in the literature. Parasite incidence was low and limited to NZMS collected from Polecat Creek. It remains to be determined whether rare parasite infection reflects either highly efficient internal defenses of NZMS, or the recent acquisition of NZMS as a novel snail first intermediate host by an endemic digenean parasite. The monitoring of NZMS as first and as second intermediate host for digenean trematodes may clarify the implications of such interactions for the Grand Teton National Park/John D Rockefeller Memorial Parkway area.

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DISTRIBUTION AND BODY SIZE DIVERSITY OF EMBERIZINE SPARROWS IN GRAND TETON NATIONAL PARK

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✦ INTRODUCTION

Over the last decade or so, we have monitored breeding bird densities over the entire range of habitats within GTNP, from grasslands and sagebrush to scrub, woodland, and forest. Many field workers, including park scientists, have contributed to the monitoring efforts. In all, there are 30 established monitoring sites, and each has been visited on average in two out of three years since 1995. Some sites, however, have been censused yearly, and on some of these the census record extends back for several decades. The monitoring work provides a rather complete assessment of the park's breeding bird communities, i.e. species over habitats among years, and to date some 160 species have been recorded in the monitoring effort, all but a handful of which are breeding birds. This report addresses specifically one prominent group of breeding birds, the emberizine sparrows and buntings.

The Emberizine Data

To date, 16 species of emberizines have been recorded at our monitoring sites. Three of these species are marginal contributors to the GTNP avifauna, and will not be considered further here: Spotted Towhee (*Pipilo maculatus*) occurred only in one site, Site 26/Upper Granite Canyon Spruce-fir, and in just 1/5 census years; Lark Bunting (*Calamospiza melanocorys*) was recorded in only two sites, once each in two different years at Site 4/JLJ Grass-sage and Site7/2OL Meadow; Lark Sparrow (*Chondestes grammacus*) also was a single-site and single year recording, in Site 7/2OL Meadow. Note that, while these less common species have low incidence within monitoring sites, we have encountered them more widely within the park. Of the remaining 13 species, listed in Table 1, some are widely distributed and some are more narrowly confined to specific habitat types. As a further constraint, several sites are not included here because they are undergoing successional changes in the vegetation, and thus the contingent of breeding emberizines is expected to (and does) change over time. Excluded from the site rankings are the sagebrush burn Site 5B, the Taggart Lake lodgepole burn Site 20, and the willows outgroup Site 10S (in Rocky Mountain National Park) where there has been a considerable degree of willows dieback. Also excluded from this summary are the high elevation monitoring sites in subalpine fir and alpine tundra, waterfowl counts on ponds, and the aerial-feeding swallows (Sites 27-30). However, a second willows outgroup site, Site 10N in Glacier National Park, is included for its contributions to the overall patterns.

The emberizine species are listed in the left-most column of Table 1; their body masses (in g), appropriate to the subspecies in GTNP, are listed in the adjacent column. The monitoring sites represented by the columns in Table 1 are ranked from those of the lowest vegetation height and mean breeding densities of the various bird species at the

Species Sites	Mass	Bl.h.grosbeak	Fox Sparrow	Gr.-t. Towhee	Wh.-cr. Sparrow	Vesper Sparrow	Dk.-eyed Junco	Song Sparrow	Savann. Sparrow	Lincoln's Sparrow	Lazuli bunting	Chipping Sparrow	Clay-col. Sparrow	Brewer's Sparrow		# Spp	∑(density: pr/ha)
		45.0	30.4	29.0	28.3	24.0	20.0	20.0	18.1	18.2	15.0	12.3	12.0	10.9	(g)		
Wolf Ranch Grass	1								1.27							1	1.27
JLJ Sedge Mdw	2								1.27							1	1.27
Elk Refuge Grass	3								1.70							1	1.78
JLJ Grass-sage	4				0.44	1.25			0.54					1.34		4	3.58
Antelope Flats Sage	5			0.21		0.52								0.89		3	1.62
Airport sage	6			1.16		0.54								175.00		3	3.45
Two Ocean Lk Mdw	7	0.44			0.95		0.54	0.14	0.34	0.54	1.24	0.10	0.09	0.25		9	4.26
Triangle X aspen scrub	8	0.08		0.60	0.83					1.38	0.17	0.29	0.17	0.36		9	4.42
RKO Dry willows	9	0.48	0.21		0.38			0.83		0.35						5	2.47
JLJ wet willows	10	0.13	0.57		0.35			1.21		0.80						5	3.12
GNP wet willows	11	1.17	0.27		0.16			0.42	0.13	0.23			0.38			7	2.75
Oxbow willo-aspen	12		0.46		0.26			0.85		0.34						4	1.91
Elk Ranch low aspen	13	0.26			0.54		0.38									3	1.24
Elk Ranch med aspen	14				0.52		23.00				0.14					3	0.88
Cow Lake tall aspen	15						0.65					0.61				2	1.40
Spread Ck cottonwoods	16	0.21	0.13		0.38		0.30			0.33		0.12				6	1.48
Schwabacher cottonwds	17	0.23			0.15		0.44	0.19				0.36				5	1.37
L. Granite Cyn pine-aspen	18	0.10		0.10			1.16					1.16				4	2.52
Timbered Island ldgpole	19						1.11					0.91				2	2.01
AMK lodgepole	20				0.09		1.16					0.54				3	1.79
Signal Mt. lodgepole	21						0.60					0.41				2	1.01
Spaulding Bay pine-fir	22			0.25	0.11		0.69			0.09		0.66				5	1.80
Lizard Ck spriuce-pine	23						0.80			0.42		0.20				3	1.42
Bradley Lk pine-spruce	24			0.12	0.17		0.51					0.32				4	1.31
Jenney Lake spruce-fir	25						0.69					0.52				2	1.36
U Granite Cyn spruce	26						0.78					0.23				2	1.01
# of Sites		9	5	6	14	3	15	6	6	9	3	14	3	5		98	

Table 1. Species identities, body masses, and distribution over GTNP monitoring sites of 13 commoner species of emberizine sparrows and buntings.

sites, in units of pr/ha, averaged over all census years. Some of the listed species make only marginal contributions to the breeding birds of certain sites; if a species has averaged <0.09 pr/ha at a given site over the census period, that record is removed from the data set presented here (Table 1). Row and column summaries are provided along the margins of this table: sites per species, species per site, and overall densities per species and site.

Body Size and Habitat Segregation amongst the Emberizines

The body masses of the 13 species of emberizines vary by nearly five-fold and the species segregate into four reasonably discrete body size categories. There is a single very large species (Black-headed Grosbeak *Pheuticus ludovicianus*, at 45 g, denoted here by size "X"), and three large species (Fox Sparrow *Passerella iliaca*, Green-tailed Towhee *Pipilo chlorura*, White-crowned Sparrow *Zonotrichia leucophrys*) between 28.3 and 30.4 g—size "L"). The largest size class, in terms of the number of occupant species, is that of the five medium-sized species ("M"); all are between 18.2 and 20 g except Vesper Sparrow (*Pooecetes grammineus*) which at 24 g is somewhat larger than the other class members. Finally, four small species ("S" -three *Spizella* sparrows and the Lazuli Bunting *Passerina amoena*) round out the list, spanning the range 10.9 g to 15 g. Note that, within a size group, the emberizines are broadly segregated over habitat, such that the group as a whole spans a broader range of vegetations types than does any one member species within it. This implies that species of similar sizes coexist within sites less frequently than do species of dissimilar sizes; similarly sized species tend to segregate over habitats.

In order to investigate in a more systematic fashion the tendency of emberizines of similar size to breed in different sites, and concomitantly that of dissimilarly sized species to co-occur in the same sites, a probability analysis is conducted in Table 2, and summarized in Table 3. The upper part of Table 2 is a condensed version of Table 1, where the number of species in the four different size classes is shown over census sites left to right across the habitat gradient. Note that sites at the grassland end of the gradient support a single species (Savannah Sparrow *Passerculus sandwichenis*), after which the number of coexisting species build rapidly to as many as nine in the sites (Site #s 7, 8) of forb/grassland with low, open scrub, and thereafter mostly varies between 2-5 species through the woodland and forested sites.

The number of representative species in each of the four size groups is given to the left in the lower portion of Table 2. Note that, as there is no significant tendency to size groups to differ in the extent to which they are represented over monitoring sites, these species numbers may be used as predictors for a null model of sparrow community composition by body size. We can ask questions such as: given a three species (3SPP) community, what are the probabilities that one, two or three body sizes are represented in it? The lower part of the table itemizes the various body size combinations for community sizes of one to five species (1SP-5SPP), and gives the probabilities of deriving each of the as a random sample of the available species. All one-species (1SP) sites have the medium-sized Savannah Sparrow (Table 2, lower section, left hand columns). Moving right in the table, the next columns investigate two-species (2SPP) sites. Two species pulled at random from the suite of candidates may be any one of the 9 size combinations ("Combo") listed, from SS (two small species) to LX (one large and one extra large species). Each size combination has the probability of occurrence, by chance, listed in the adjacent column (headed "Pr"). All five observations of 2SPP sites are of species from different size groups (all are "SM" communities). Moving right to the next columns, 3SPP sites are simulated by selecting triplets of species with the foregoing probabilities. There are 16 possible combinations (listed from SSS to LLX), each with their associated probabilities of occurrence, and these probabilities again can be associated with different size diversities, from one to three sizes represented. In fact, four of six observations of 3SPP sites all three size groups are represented.

Two additional sets of columns, further right in the lower part of Table 2, assess the probabilities of various body size mixes in 4SPP and 5SPP sites respectively. There are 22 possible combinations in 4SPP quartets, and 28 in 5SPP quintets (listed from SSSSM to MLLLX); in the latter case, there are 1349 ways of generating the different combinations, and these combine to yield the probabilities listed. In fact, three of the four 4SPP sites in the data set support species combinations with three or four body sizes, and in the four observations of 5SPP species sets, all have the characteristics of the ≥3 sizes , with ≤2 representatives per size category. These figures might happen by chance, and to examine this possibility we move to Table 3 in which the data are summarized. Here the expected and observed numbers of sites with different numbers of species, and with various ranges in body size representation, are compared. Included here also is the single 6SPP

	SITE:																									
SIZE	1	2	3	4	5	6	7	8	9	10	10N	11	12	13	14	15	16	17	18	19	21	22	23	24	25	26
SM				1	1	1	4	4			1			1	1	1	1	1	1	1	1	1	1	1	1	1
MED	1	1	1	2	1	1	3	2	2	2	3	2	1	1	1	2	2	1	1	1	1	2	2	1	1	1
LG				1	1	1	1	2	2	2	2	2	1	1		2	1	1		1		2		2		
XLG							1	1	1	1	1		1			1	1	1								
∑	1	1	1	4	3	3	9	9	5	5	7	4	3	3	2	6	5	4	2	3	2	5	3	4	2	2

1SPP	#SPP	OBS	2SPP	comb	Pr	OBS	3SPP	Comb	Pr	OBS	4SPP	Comb	Pr	OBS	5SPP	Comb	Pr	OBS
S	4	0	SS	6	0.08	0	SSS	4	0.014	0	SSSS	1	0.002		SSSSM	5	0.004	
M	5	3	SM	20	0.26	5	SSM	30	0.105	0	SSSM	20	0.031		SSSSL	3	0.002	
L	3	0	SL	12	0.15	0	SSL	18	0.063	0	SSSL	12	0.018		SSSSX	1	7E-04	
X	1	0	SX	4	0.05	0	SSX	6	0.021	0	SSSX	4	0.006		SSSMM	40	0.03	
			MM	10	0.13	0	SMM	40	0.140	0	SSMM	10	0.015		SSSML	60	0.044	
Sum	1	3	ML	15	0.19	0	SML	60	0.210	3	SSML	90	0.139		SSSMX	20	0.015	
			MX	5	0.06	0	SMX	20	0.070	0	SSMX	30	0.046		SSSLL	12	0.009	
			LL	3	0.04	0	SLL	12	0.042	1	SSLL	18	0.028		SSSLX	12	0.009	
			LX	3	0.04	0	SLX	12	0.042	0	SSLX	18	0.028		SSMMM	60	0.044	
							MMM	10	0.035	0	SMMM	40	0.062		SSMML	180	0.133	
			Sum	78	1	5	MML	30	0.105	1	SMML	120	0.185	1	SSMMX	60	0.044	
							MMX	10	0.035	0	SMMX	40	0.062		SSMLL	180	0.133	
							MLL	15	0.052	0	SMLL	60	0.092	1	SSMLX	90	0.067	
							MLX	15	0.052	1	SMLX	60	0.092	1	SMMMM	20	0.015	
							LLL	1	0.003	0	MMMM	5	0.008		SMMML	120	0.089	
							LLX	3	0.010	0	MMML	30	0.046		SMMMX	40	0.03	
											MMMX	10	0.015		SMMLL	120	0.089	1
							Sum	286	1	6	MMLL	30	0.046	1	SMMLX	120	0.089	1
											MMLX	30	0.046		SMLLL	20	0.015	
											MLLL	5	0.008		SMLLX	60	0.044	
											MLLX	15	0.023		MMMMM	1	7E-04	
											LLLX	1	0.002		MMMML	15	0.011	
															MMMMX	5	0.004	
											Sum	649	1	4	MMMLL	30	0.022	
															MMMLX	30	0.022	
															MMLLL	10	0.007	
															MMLLX	30	0.022	2
															MLLLX	5	0.004	
															Sum	##	1	4

Table 2. Above, site occupancy by emberizines of 4 body sizes (small to extra large; S, M, L, X; and below the likelihood of drawing different body size combinations in emberizine communities of 1-5 species (2SPP, 4SPP" etc.). The probability of drawing each size combination at random is given in the column headed "Pr". The number of observed combination in each category is included under "OBS."

community, which has species representative of all four size classes. Note that the three sites with >6 emberizines (Site 7: Two Ocean Lake Meadow, 9SPP; Site 8: Triangle X aspen scrub, 9SPP; and Site 10N: Coonsa Ck Willows, GNP, 7SPP) have species representative of all four body size classes. The simplest test (to which we are limited by dint of low sample sizes) is to ask to what extent to communities of different species numbers support the maximum body size range possible? That is, to what degree do 2SPP communities contain two different body sizes, 3SPP communities three body sizes, and so on up to four body sizes (the maximum range). A simple Chi-squared test is included at the bottom of the table, and this shows that there is a statistically significant tendency for the different sparrow communities, with different species composition and different species numbers, to cover the widest possible range of body sizes.

Emerizines in a Seasonal Context

Virtually all of the breeding emberizines of GTNP leave the park for the winter, and many winter thousands of kilometers to the south. In fact, rather more research has been conducted on the wintering ecology of emberizines than on there breeding ecology, especially in a community context. Fretwell (1972) initially suggested that populations in many sparrow species might be limited by winter resources rather than by those at the breeding site, and he supported his contention with data on Field Sparrows (*Spizella pusilla*) and a broad review. Pulliam (1975, 1983) and his associates (Pulliam & Brand 1975, Pulliam & Mills 1977) conducted intensive research on wintering emberizines 30 years ago, much of it based in the arid desert grasslands of the southwest USA where it is likely that at least some of the GTNP breeding species spend the winter. Notably, the *Spizella* species, Savannah Sparrow, Vesper Sparrow, Lark Sparrow and other GTNP breeding emberizines were found at his Research Ranch study site in southeastern Arizona. Pulliam's research associated body size with culmen size, and in turn culmen size with the ability to harvest and ingest seeds of different sizes. There were also correlations of body size with the use of space, distribution over vegetation types, and the extent of co-occurrence of different and differently-sized wintering species. It appears that, even though there is support for the argument that emberizine populations are sometimes, perhaps often, limited by winter site resources, there is also substantial evidence that emberizines segregate in the breeding season by habitat and feeding ecology, and by phenotypic characters associated with body size that affect foraging ecology and predator avoidance (e.g. Cody 1968). Thus the size patterns described here are interesting but not unexpected.

		BODY SIZE RANGE							
COMM		1 SIZE		2 SIZE		3SIZE		4SIZE	
SIZE	n	E	O	E	O	E	O	E	O
1SPP	3	3	3	-	-	-	-	-	-
2SPP	5	1.22	0	3.78	5	-	-	-	-
3SPP	6	0.31	0	3.44	2	2.24	4	-	-
4SPP	4	0.04	0	1.11	1	2.48	2	0.37	1-
5SPP	4	0	0	0.58	0	2.61	3	0.80	1
6SPP	1	-	-	0.05	0	0.71	0	0.24	1

Maximum size diversity in 2SPP-6SPP communities (Boxed is found in 12/20 cases (expected number = 7.43). Chi-square with 1 df + 4.47; p<0.05 that this occurs by chance

Table 3. Sparrow community sizes (left-hand column) may support a range of different body sized (see column heads across the table). The second column gives the number of examples of the different community sizes in the GTNP monitoring data. Entries in the table are the expected (E) and observed (O) numbers of the different body size ranges. There is a statistically significant tendency for the communities to support the maximum size range (e.g. 3 sizes in a 3SPP community).

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A BOTANICAL SURVEY IN GRAND TETON NATIONAL PARK: PLANTS USED BY NATIVE AMERICANS

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INTRODUCTION

For the first time, in Grand Teton National Park (GTNP) an ethnobotanical plant collection, archaeological and historic site reports, and the literature of early plant usage have been integrated into one document.

RESULTS

Twenty-two plant families from two periods in GTNP: Prehistoric and 2004-2005
Adoxaceae
Alismataceae
Apiaceae
Asteraceae
Betulaceae
Brassicaceae
Caprifoliaceae
Cornaceae
Cupressaceae
Cyperaceae
Ericaceae
Fabaceae
Lamiaceae
Liliaceae
Pinaceae
Poaceae
Polygonaceae
Ranunculaceae
Rosaceae
Salicaceae
Typhaceae
Urticaceae

Table 1. 22 plant families from two periods in GTNP, found in both 2004-2005 collections (Appendix C*), and in excavations from 23 hearths (Appendix A*).

The total botanical collections yielded 49 families, with 119 species (Appendix A*). The literature search produced a count of 328 ethnobotanically important taxa for GTNP. This count of 328 was reduced to 281 taxa, and of these 149 collections were made. Twenty-three species were collected more than once, one of these in the Scrophulariaceae, *Castelleja miniata*, is a hybrid cross with *C. sulphurea*, a first time collection, per B. Ernie Nelson of the Rocky Mountain Herbarium. One hundred seventy-nine taxa on the list were not encountered or, have no collection history in GTNP.

34 Archaeological Plant Families from 23 Excavated sites in GTNP
Family
Adoxaceae
Alismataceae
Apiaceae
Asteraceae
Betulaceae
Boraginaceae
Brassicaceae
Caprifoliaceae
Chenopodiaceae
Cornaceae
Cupressaceae
Cyperaceae
Ephedraceae
Ericaceae
Fabiaceae
Fagaceae
Juncaceae
Lamiaceae
Liliaceae
Malvaceae

* Appendix is available upon request. Contact UW-NPS through our website www.uwyo.edu/uwnps

Papaveraceae
Pinaceae
Poaceae
Polygonaceae
Potomogetonaceae
Ranunculaceae
Rosaceae
Ruppiaceae
Salicaceae
Solanaceae
Typhaceae
Urticaceae
Violaceae
Zannichelliaceae

Table 2. Thirty-four plant families from 23 excavated archaeological sites in GTNP. These 34 families have 22 families identical with the 2004-2005 collections, and thus have a commonality of 65%. Archaeological data is in Appendix A*.

The archaeological data generated a synthesis of 319 genera in 34 families. These are included in Appendix A*. Cultural continuity is exhibited by the comparisons of the archaeological and 2004-2005 collections in Table 2. The listing of so many of these taxa in the ethnobotanical literature, as traditionally useful plants, agrees with the evidence of plant use between 10,000 years BP and up until 100 years ago. The archaeological reports were also mostly unusable as a collection resource, having only three genera with species identified. These archaeological sources have been included as evidence of Native American plant use in this region.

Twenty-two families are common to both the archaeological sites and in the 2004-2005 GTNP collection (Table 3). This represents 45% (22/49 = .448) in common with the archaeological plant analysis and 65% (22/34 = .647) in common with the 2004-2005 plant collection (Table 2).

The plant uses by tribe, and if available, the part of the plant used with its preparation, are listed in Appendix C*. The information on usage is incomplete for many plants, the Native American tribal elders with this knowledge may not have passed it to younger individuals, and it became lost before it could be written down. Included in Appendix C *are plants searched for but not located or collected. Appendix D* contains a vocabulary from Appendix C*; some of it is antiquated terminology by nature of the time and resource, but it is included for those employing plants for the indicated use per the literature.

GTNP Plant Collection 2004-2005 48 Families: 118 Species 1 Fungal Order: 1 species	
Family	Species
Aceraceae	1
Adoxaceae	1
Alismataceae	1
Alliaceae	1
Apiaceae	8
Asteraceae	14
Berberidaceae	1
Betulaceae	2
Brassicaceae	1
Calochortaceae	1
Campanulaceae	1
Caprifoliaceae	2
Caryophyllaceae	1
Celastraceae	1
Convallariaceae	1
Cornaceae	1
Crassulaceae	1
Cupressaceae	1
Cyperaceae	1
Elaeagnaceae	1
Equisetaceae	2
Ericaceae	5
Fabaceae	3
Gentianaceae	2
Geraniaceae	1
Grossulariaceae	4
Hyacinthaceae	1
Hydrophyllaceae	1
Lamiaceae	2
Linaceae	1
Melanthiaceae	4
Nymphaeaceae	1
Onagraceae	1
Pinaceae	4
Poaceae	2
Polemoniaceae	2
Polygonaceae	3
Portulacaceae	1
Primulaceae	1
Ranunculaceae	8
Rhammaceae	1
Rosaceae	12
Salicaceae	3
Saxifragaceae	1
Scrophulariaceae	6
Typhaceae	2
Urticaceae	1
Valerianaceae	1
Lycoperdales, *Calvatia* sp.	1

Table 3. Plant collection from the 2004-2005 field seasons in GTNP. 48 Families: 118 Species, and 1 Fungal Order: 1 Species (Appendix B*). Twenty-two of these 49 families are identical with the **22** families (Table 6) from the 2004-205 collections, and thus have a commonality of 45%.

✦ DISCUSSION

The total possible taxa of ethnobotanically identifiable plants from literature searches and hearth

* Appendix is available upon request. Contact UW-NPS through our website www.uwyo.edu/uwnps

reports for this study began with 328 taxa. Fifteen percent of this original plant collection list was excluded from my collecting efforts, reducing species sought to 281. The following four classifications address these exclusions.

1. Genus with no species specified. When more than one species occurs in a genus these were excluded.
2. Misidentification of genus and/or species by untrained individuals.
3. Incomplete synonymic trail of antiquated names to modern binomials.
4. Two taxa have no record of modern collection in GTNP (Dorn 2001). These are archaeological pollen, *Quercus*, and *Ephedra* (Larson 1995).

The assumption is that these species were well within the annual migration and trade range of Shoshone hunter-gatherers (Shimkin 1947). Edibles, medicinals, ceremonials, or utilitarian plants could have been transported into GTNP, prepared in a roasting pit, and consumed at that time, leaving only pollen as evidence (Adams 2006).

A compiled list of plants and their uses came from earlier travelers, ethnographers, explorers and the photographer Edward Curtis in the 1800s. Early botanists or those with some formal botanical training provided out-dated binomials or colloquial common plant names. These archaic names have changed through the years; most of them have a lineage to follow into currently usable Linnaean nomenclature.

Archaeological data from twenty-three sites, involving testing by shovel, auger, or major excavation, were unusable as a collection resource, because only three genera had specific species identified. These archeological sources have been included as evidence of early Native American use of plants in GTNP. These are included in Appendix B*.

Considerations of why there are not more than twenty-two taxa in common between the prehistoric and the 2004-2005 collections may include reasons of seasonal gathering practices, the availability of plants to collect when people were present, seed bearing species dependency on annually fluctuating moisture levels, and the possibility of taxa becoming locally extinct through global change. Prehistoric hearths may not have been discovered due to the water levels of Jackson Lake being too high, or fire and regrowth of vegetation covering the sites, or hearths simply not being inventoried. The age of archaeological sites 48TE509 and 48TE1039 indicate occupation during the Altithermal period in ethnobotanical history

Ethnobotanical plants in and around GTNP are listed in Appendix C*. All of these plants were recorded as being used by, or present with the tribes, as referenced by their authors. Some plants may have been transported into GTNP (Shimkin 1947, Adams 2006, Reher 2004, Waldman 2000), as *Quercus* and *Ephedra* do not have a recorded history of growing in GTNP. *Quercus* is located in Carbon, Crook, and Campbell Counties in the State of Wyoming, Gallatin County in Montana and Uintah, Duchesne, Wasatch, Salt Lake, Davis, Weber and Cache Counties in Utah (USDA Plants Database). *Ephedra* has never been collected in the State of Wyoming Dorn (2001), but is reported to grow in Sweetwater County, Wyoming (USDA, Plants Database). These two plant taxa are from the Henn Site, (Larson 1995). Including those plants not found in GTNP, but reported in the literature as hearth contents, is important to illustrate the migration of peoples, the possibility of trade patterns, their understanding of plants, and their ways of living.

Botanical and ethnographic literature was compiled first, then, the addition of macrofloral and microfloral data gleaned from archaeological site reports and finally a plant collection from GTNP was included. By recognizing the traditional ways of plant use from the archaeological and literary records and using these same grounds for collecting, an old connection between culture and conservation is honored. Tribes of people returned yearly for plants and did not cause their extinction. Modern man needs to learn this lesson in so many areas of his life.

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DIGITIZATION OF THE GRAND TETON NATIONAL PARK HERBARIUM

✦

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✦ INTRODUCTION

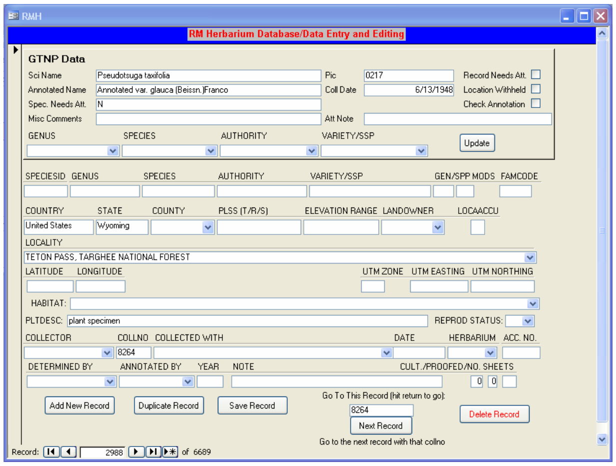
Examples of digitization projects in the history of science are understood to have lasting consequences for the intellectual history of their fields (Petersen, 2005; Roes 2001). Following this trend, herbarium collections around the world are beginning to be digitized with positive results for their institutions (Begnoche, 2002; Ong, 2002). Librarians, with their long history of making collections accessible, are participating in this trend (Foster, 2005). The University of Wyoming Libraries encourage Librarians to develop and maintain collections in a variety of subjects, and the Libraries are pursuing opportunities in digital collections. 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 an 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. Currently, it is housed in a converted walk-in freezer unit in an old wooden building near the Park Headquarters. It shares this limited space with storage collections of archaeological and cultural museum materials. It is available only by appointment, requires a park employee as an escort, and has no handicap access. The environment, while temperature controlled, is not ideal; there is very limited space with poor lighting. The specimens must be transported from the building to be used; there is no space to examine them in the building. The collection is not available for loan. Given this difficult access, a digital collection would be a valuable tool for Grand Teton and Yellowstone National Park employees; University of Wyoming/National Park Service Research Center investigators; University of Wyoming students, faculty and staff; Wyoming extension agents; Teton Science School faculty and students and amateur botanists everywhere. The GTNP research staff has listed herbarium management and access as a priority on their list of research projects.

A digital collection also reduces the necessity for handling the fragile specimens, helps maintain their current condition and contributes to management decisions. A digital collection expands herbarium use to local communities and extends its influence nationally.

✦ METHODS

The initial work was done at the University of Wyoming/National Park Center Research Station (UW/NPS) in Grand Teton National Park. The photographs were taken with a Canon model EOS-1DS Mark II Camera, the shutter speed was 1/25 second, aperture 16, ISO speed 100. 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 Campus.



RM Herbarium Database/Data Entry and Editing

Sci Name: Pseudotsuga taxifolia
Pic: 0217
Record Needs Att. ☐
Annotated Name: Annotated var. glauca (Beissn.)Franco
Coll Date: 6/13/1948
Location Withheld ☐
Spec. Needs Att.: N
Check Annotation ☐
Misc Comments:
Att Note:
COUNTRY: United States
STATE: Wyoming
LOCALITY: TETON PASS, TARGHEE NATIONAL FOREST
PLTDESC: plant specimen
COLLNO: 8264
CULT./PROOFED/NO. SHEETS: 0 0
Go To This Record (hit return to go): 8264
Record: 2988 of 6689

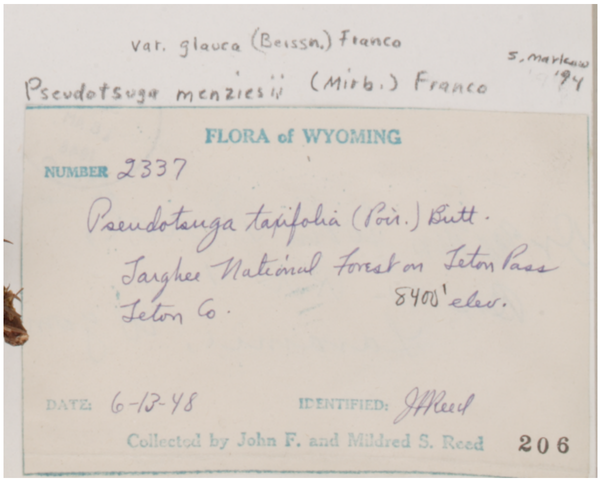
Fig. 1. Example of a page from the database.

✦ PRELIMINARY RESULTS

To date, 3,200 specimens have been photographed. The database has been transferred from the Excel file format given to us by National Park employees to relational tables in an Access database which will work with LUNA software for storing, retrieving and displaying images and their related metadata on the web. Work is continuing this winter on the database. Figure 1 is an example of a database page for a specimen. See Figure 2 for an example of a specimen photograph from the database.

Fig. 2a. Example of a photograph of a typical mounted specimen from the GTNP herbarium.

Fig. 2b Example of close up of the pine cone on the page in Fig 2a, illustrating detail.



var. glauca (Beissn.) Franco

Pseudotsuga menziesii (Mirb.) Franco

S. Markow
'94

FLORA of WYOMING

NUMBER 2337

Pseudotsuga taxifolia (Poir.) Britt.
Targhee National Forest on Teton Pass
Teton Co. 8400' elev.

DATE: 6-13-48 IDENTIFIED: JFReed

Collected by John F. and Mildred S. Reed 206

Fig. 2c Example of original label information on Fig. 2a specimen page.

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 photography, including shutter speed, aperture opening, type of equipment and imaging software used. We followed the Colorado Digitization Project (2005) best practices throughout the project.

It is the intention of the Libraries to support the database at the Laramie campus on a Library server. The project uses architecture designed to allow technology upgrades. Access 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.

✦ DISCUSSION

We anticipate that the GTNP herbarium database will be available on the websites at the University of Wyoming, the Rocky Mountain Herbarium and Grand Teton National Park. In addition, the database will be marketed to extension agents, natural history associations and public schools in Wyoming. We anticipate that future editions of field guides will include a link to the collections, and we will submit our site to lists of herbaria in the United States and worldwide. We also plan to share our expertise with smaller herbaria in Wyoming, such as the UW Research Stations, the five community colleges and community nature centers.

The project will continue during the summer of 2006. The photography will be finished in the summer and the metadata completed in the fall. The final project will be brought online in 2007.

✦ ACKNOWLEDGMENTS

UW/NPS provided housing, financial and material support for the project. Grand Teton National Park provided access to the collection and funds for a botany student intern, Erin Foley, in the summer. 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, the database expertise contributed by Matt Kelly and the support received from UW Libraries.

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AMK RANCH CULTURAL LANDSCAPE STUDY
GRAND TETON NATIONAL PARK

MARY M. HUMSTONE ✦ SARAH SCHILL ✦ AMERICAN STUDIES PROGRAM
UNIVERSITY OF WYOMING ✦ LARAMIE

During summer, 2005, the University of Wyoming American Studies Program conducted an intensive cultural landscape survey and analysis at the AMK Ranch. Research Scientist Mary Humstone, working with graduate assistant Sarah Schill, documented the historic buildings and landscape features that tell the history of the Sargents Bay peninsula. The team updated the existing National Register of Historic Places nomination to include detailed building and landscape descriptions and a comprehensive history. The following report is excerpted from the National Register nomination.

Cultural Significance of the AMK Ranch

The Jackson Hole valley, with its stunning topography and abundant wildlife, has long drawn people for seasonal use, settlement, recreation, and vacation. The history of the AMK Ranch encompasses the various stories that have drawn people to this area, from basic subsistence to vacation. The AMK Ranch is significant as a cultural landscape comprising human settlement on Jackson Lake from 1890 to the modern era, with significant buildings and cultural landscape features that tell the story of the development and use of the peninsula, and represent the larger story of the development of the Jackson Hole valley.

With its history of sustained human habitation extending back to 1890, the AMK Ranch represents two important phases of settlement in the Jackson Hole valley: homesteading and vacation homes. The property demonstrates a cultural shift from using the land to satisfy basic daily needs, as well as economic sufficiency, to a more dominant appreciation of land as scenery and a place for recreation.

The property is also significant for its well preserved buildings constructed in the Rocky Mountain Rustic style. The buildings retain integrity of materials, workmanship and design, and along with the landscape that surrounds them they convey the feeling and association of an early 20th century vacation property in Grand Teton National Park and contribute to the understanding of the history of this significant property.

John Sargent's Homestead (1890 – 1913)

The highpoint of the AMK Ranch peninsula marks the site of John Dudley Sargent's original homestead, built in 1890. Forest fires burned extensively in this area in 1856 and 1879 (UW-NPS Site Plan, 11), leaving the peninsula largely uninterrupted by trees when Sargent arrived with his partner, Robert Ray Hamilton. Originally from Machias, Maine, Sargent had traveled back and forth between the East Coast and the West for five years before he settled on Jackson Lake. Hamilton, an independently wealthy New York lawyer, ventured to Wyoming on a hunting trip in May, 1890. Although it is unclear how the two men met, they decided to combine Sargent's experience in the West and Hamilton's connections, both economic and social, to form a partnership and start a dude ranch on the peninsula during the summer of that same year. Sargent seems to have been closer to a land speculator than a farmer, although he did engage in subsistence farming. His partnership with Hamilton is a familiar one. "Many who came on hunting trips, bought their own ranches and remained, sometimes in partnership with an accompanying guide from the trip" (Caywood 1997).

By 1891, Sargent had completed a ten-room log house with a sod roof, which he called Marymere, to house his family and the future guests. He also built a barn and corrals, woodshed, chicken house, and boathouse, none of which are extant. Disaster befell Hamilton in August of 1890, before the ten-room house could be completed. Returning alone from an antelope hunt, Hamilton drowned fording the Snake River. Though no evidence supports it, many suspected Sargent of having a hand in the death of his partner. A search party looking for Hamilton finally discovered his body on September 2nd and lit a fire on Signal Mountain, memorializing the event in the name of the mountain.

Sargent's arrival in the Jackson Hole valley coincided with the federal government setting aside land in the greater Yellowstone area to protect the resources. In March of 1891, President Benjamin Harrison created the Yellowstone Park Timber Reserve, consisting of more than one million acres including the northern end of the Jackson Hole valley. This act closed the area to settlement, but Sargent's preemption papers, filed in July 1890, before the creation of the Reserve, enabled him to secure a land patent (Daugherty 120). The Sargent family spent the next six years moving back and forth between Idaho, Wyoming, and Maine, often wintering away from Marymere and spending summers along the shores of Jackson Lake.

Typical of early settlers, Sargent depended upon the immediate environment for his survival, drawing water from the lake, hunting area wildlife, and offering services to passersby to supplement his income. Although Sargent did house travelers and offer boating trips, Marymere never flourished as the intended dude ranch. Instead, Sargent made money where he could, renting out his boat and land for camping, as well as operating a small store. The store, located not far from the homestead on the Army road that ran north to Yellowstone, was likely a "self-serve establishment with a limited inventory" (Diem, 1998).

Tragedy struck the family again in 1897 with the death of Sargent's wife, Adelaide. Controversy surrounds her illness and eventual death, with speculation about Sargent's possible role therein. Whether Adelaide Sargent suffered a lengthy and debilitating illness or broke her leg is impossible to know. Sargent was variously described as too proud, too unfeeling and brutish, or too ignorant of the severity of the illness/break to fetch help (Diem 1986). Eventually, Jackson Hole residents moved the ill Mrs. Sargent from Marymere to D.C. Nowlin's ranch on the present Elk Refuge where she remained until her death two weeks later. Sargent was tried for second degree murder in the death of his wife, though the judge dismissed the case for lack of evidence. The court of public opinion, however, had no doubt that Sargent was an eccentric character at best and a two-time murderer at worst. Sargent's father took custody of the children and severed all ties to John Sargent.

Sargent himself fled east, not returning to Marymere until 1899. He remained largely alone at the ranch for the next six years, operating his small store for supplemental income. He also served as an agent for the Victor Talking Machine Company around 1910 (Diem, 1986:26). Sargent's multiple sources of income are typical of the early homesteader; "a number of homesteaders survived economically by diversifying their sources of income" (Caywood, 1997:22). Sargent mortgaged his ranch for $1,300 in 1905 in order to purchase a new herd of milk cows and to marry a woman he met in New York in 1899 during his eastern sojourn (Diem 1986:29).

Edith Drake Sargent, John's second wife, would bring no end to the mysteries and suspicion surrounding Sargent and Marymere. "After the wedding, rumors persisted that Edith was mentally ill and that Sargent was being paid by her family to take care of her" (Diem, 1986:29). Money did pass between Sargent and the Drake family. Edith's brother, Herbert Drake, paid off the $1,300 mortgage and loaned the couple money. In 1910, Sargent signed the ranch over to Drake (Diem, 1986:29).

Rumors circulated of strange behavior on the ranch. Edith made periodic appearances in the nude and this, coupled with her talent as a violinist, led to one of the more colorful stories associated with the ranch. Three hundred yards northwest of the homestead cabin, a spruce tree with a perfect curve to sit in, grew above a cliff overlooking the lake. Presently known as the "violin tree," this was Edith's favorite spot to come and play the violin. A nail protrudes from the tree where Edith used to hang her bow. Rumor has it that Edith played the violin in the nude, either by preference or because John took her clothes to keep her from straying off the peninsula.

The isolation brought on by the physical remoteness of the ranch and the long, harsh winters may have intensified any mental illness suffered by John or Edith. Edith commented on her husband's condition: "he was never unbalanced except by melancholia…This trait was inherited and made him live the life of a recluse on his ranch…living alone as he did, so long before our marriage was sufficient to render him, or any man unbalanced" (as quoted in Diem, 1986:31). In a possible effort to erase ties to the past, Sargent changed the name of the ranch from Marymere to Pinetree Ranch and took to using his mother's maiden name, Hemenway, instead of Sargent (Diem, 1986:31).

Edith, having left the ranch in 1912 for California, worried about Sargent's depression and loneliness. These fears proved well founded in the summer of 1913. A party of riders found Sargent dead in his cabin after having shot himself with his rifle some days earlier. Several men buried Sargent in a grave south of his cabin, now surrounded by a log fence. Slim Lawrence constructed this fence in the 1930s and carved a rock to act as a grave marker for Sargent's burial. Edith eventually died poor in New York City, having spent the last three years of her life hospitalized in the Manhattan State Hospital. Much to Edith's dismay, her brother Herbert Drake was the sole beneficiary of Sargent's estate.

After Drake failed to pay property taxes on the ranch, the County Treasurer sold the property. Between 1918 and 1926, the ranch passed through five different owners. Trappers, including William Cecil "Slim" Lawrence (the eventual caretaker), camped out in Sargent's cabin where they sometimes encountered itinerant livestock. William Lewis Johnson, an executive of the Hoover Company, bought the property in 1926 "for $1 'and other good and valuable considerations'" (Diem 39).

Although the homestead and other buildings that Sargent built during his tenure on the land are no longer extant, the Sargent era is an important and well documented foundation of the history of the ranch. In evaluating the property as a cultural landscape, it is impossible to ignore Sargent's contributions. In the most basic sense, the AMK Ranch as seen today would not exist if Sargent had not homesteaded this particular 160-acre property. Had it not been for Sargent, this peninsula would have come under federal ownership in 1891, and would not have been developed by private property owners.

Furthermore, Sargent's grave, the approximate location of the homestead, the "violin tree" where Sargent's second wife Edith played the violin and the old military road to Yellowstone, which passed by Sargent's homestead, are features of the cultural landscape, providing a visual link to this era of the peninsula's history.

William Johnson Begins the Vacation Home Era (1926 – 1931)

The arrival of William Lewis Johnson marked the beginning of the vacation home era at what had been Sargent's homestead. "After World War I, increased publicity of the Grand Teton region, escalating national appreciation for wilderness recreation, improved transportation, and increased leisure hours led to construction of a number of private vacation homes on lands leased from the United States Forest Service. The choicest sites were those near Jackson Lake and the perimeter of the 1929 Grand Teton National Park" (Caywood, 1997:30). Sargent's homestead was an exceptional site, not only for the views it afforded, but also because it was a privately owned holding within the eventual park boundaries.

Johnson, orphaned at the age of ten, had been sent to live at the Miller Manual Labor School in Batesville, Virginia. The school offered free education to a small number of students, many poor or orphaned. The pupils, all male, were also trained in wood and ironwork, the use of steam, and technical drawing (Diem, 1986:35). Though expelled for hazing at the age of sixteen, Johnson apparently felt no ill will towards the school and vowed to "repay the school for all the great things it had done for him" (Diem, 1986:37).

After leaving Miller School, Johnson worked for Bausch and Lomb Optical Company in Syracuse, New York. He left this position at the beginning of World War I to take a job as division manager at Hoover Suction Sweeper Company where he made his fortune. Johnson married Mae Eastman in 1915 and continued to work for Hoover until his retirement in 1926.

Johnson first saw Jackson Hole while vacationing at Brooks Lake Lodge near Dubois, Wyoming, in the summer of 1923. He fell in love with the area, and stayed in Moran every summer from that point until he bought the Sargent homestead in 1926. Sargent's ranch, "the only private land in the northern end of Jackson Hole," became the site for Johnson's second home (Daugherty, 1999:264).

Between 1927 and 1931, Johnson improved his property with numerous log structures. In addition to the main lodge (extended to two stories at the request of Mrs. Johnson, who was afraid of bears) with an attached barn and garage, Johnson bought three structures from a nearby homestead to serve as outbuildings. The Sunroom cabin, the Three Room/Director's cabin, and the Two Room cabin all came from the Hogan homestead and were each purchased for between twenty and fifty dollars. Johnson built a chicken house, woodshed, workshop, smokehouse, boathouse/icehouse and a small log generator house, all of which remain today.

Slim Lawrence and his wife, Verba, caretakers for the Johnsons beginning in 1930, lived in the east section of the Johnson Lodge, which contained its own kitchen, living area, bedroom, and bathroom. The east section has since been converted to house two kitchens, a dining area (formerly the Lawrences' living room), two bedrooms and two bathrooms.

The Johnsons named the property Mae-Lou-Lodge, a combination of Mrs. Johnson's first name and William's middle name. Johnson was passionate about outdoor activities and took advantage of the location of his second home to pursue hunting and fishing. He enjoyed riding and kept about seven horses at the ranch. Arriving in early spring and staying until November allowed Johnson to hunt elk, sage grouse, bighorn sheep, and mule deer. Johnson, often guided by Slim, traveled all over Teton County to hunt. Two Ocean Pass proved good elk hunting ground, and Granite Canyon was home to bighorn sheep. "In between big game trips, Johnson would hunt blue grouse, ruffed grouse and waterfowl around the Jackson Lake area. [Johnson and Slim Lawrence] had blinds set up near Berry Creek where they primarily shot Canada Geese and Canvasback ducks" (Diem, 1986:43). Johnson especially enjoyed bear hunting and made use of Slim's bait stations around Arizona Lake. Johnson placed many of his hunting trophies in the lodge.

Mae Johnson always accompanied her husband to the ranch. Unfortunately, she was only able to enjoy the property for a brief time as her health deteriorated in the late 1920s. Mrs. Johnson died of cancer at a private hospital in Ohio in the fall of 1930 (Diem, 1986z; 44). Johnson did not live much past his wife. On his way home after a big game hunting trip along the Salmon River with Slim, Johnson fell ill due to a heart disorder. He passed away a month later, on December 8th, 1931 (Diem, 1986:44).

In his will, Johnson left $400,000 of his nearly one million dollar estate to the Miller Manual Labor School. The Irving Trust Company administered this bequest, as well as the rest of Johnson's estate. In gratitude for all that Johnson had done for them throughout the years, the Miller School dedicated a stone memorial containing the ashes of Mr. and Mrs. Johnson. This memorial, which was dedicated on July 31, 1932, sits just west of the site of Sargent's homestead and north of Sargent's grave (Diem, 1986:44).

The Irving Trust Company held the property from 1931 to 1936, retaining Lawrence as caretaker. During this period, acting on the orders of the Irving Trust and the threat of being fired, Slim Lawrence dismantled and burned the Sargent homestead cabin. "It was the feeling of the Irving Trust that the cabin detracted from the appearance of the site they had selected for the Johnson grave" (Diem, 1986:45).

Slim Lawrence and his wife Verba were the only long-term, year-round residents of the peninsula. Born in 1899, Lawrence grew up in Laramie, Wyoming, helping his father who drove a section of the Laramie-to-Walden stage line. A job with the Lander-Yellowstone Transportation Company brought him to the Jackson Hole area. Slim drove tourists and mail all over Jackson Hole and worked numerous other odd jobs in the off-season until 1930 when he and Verba went to live and work at Mae-Lou-Lodge as caretakers under the Johnsons.

Slim and Verba spent the next forty years at the ranch on the shores of Jackson Lake, their lifestyle more akin to Sargent's during his homesteading years than that of later owners Johnson and Berol. Year-round living on the remote peninsula presented challenges. The early years, 1930-42, were especially difficult, "characterized by marked winter isolation and heavy physical exertion" (Diem, 1986:70). After turning off the water in December, the Lawrences had to melt snow or haul lake water to provide their water supply. It was not until Berol reworked and winterized the water system in 1936 that indoor plumbing became a year-round option.

The couple often traveled fifteen to twenty miles every day on skis or snowshoes to haul supplies, pick up and receive mail, and trap animals. As travel to town was such a laborious chore, the Lawrences hunted, canned their own food, and chopped ice from the lake for refrigeration. Jackson Hole had not yet achieved the immense popularity as a tourist destination that it would after World War II, and there were few residents and visitors, especially at the north end of Jackson Lake. The Lawrences enjoyed the isolation afforded by the ranch and the sparse population, but this would soon change.

The Berol Era (1936 – 1974)

In 1936, Alfred Berolzheimer (changed to Berol during World War II) purchased the 142-acre ranch from the Irving Trust for $24,300 (Diem, 1986:47). Berol made his fortune in the family business, the Eagle Pencil Company, and brought a life of upscale parties and recreation to the property. Berol and his wife, Madeline, spent vacations in Wyoming and Montana and enjoyed hunting and wilderness activities. "During one of Alfred's visits to the Montana Miller Ranch, he learned that the Sargent-Johnson property was for sale" and soon purchased it (Diem, 1986:47). The Berols called their new property AMK Ranch, selecting the first letter of each of their names (Alfred, Madeline, and their son, Kenneth).

Both Alfred and Madeline grew up accustomed to a life with servants and prestigious prep schools, and brought certain expectations with them to Jackson Hole. Upon acquiring the peninsula, the Berols immediately hired an architect, George Kosmak of New York, and began plans for an impressive lodge. Construction of the Berol Lodge began in the spring of 1937 and was finished the following fall. Logs came from Arizona Lake meadows, just east of the property. Most of the fireplace rocks came from the Gros Ventre Canyon, with the exception being the master bedroom fireplace, constructed with pink volcanic rock from Idaho.

The 5,200-square-foot Berol Lodge was designed for entertaining, with a large living room with a soaring cathedral ceiling supported by heavy logs, and a long dining room terminating in a polygonal bay, an idea Berol got from a lodge in Canada. Dramatic views of Jackson Lake and Mt. Moran are visible through the large picture windows on the west side of the lodge. Berol Lodge furniture maintained a Western and Southwestern feel. Pine furnishings and American Indian rugs and pottery predominated, and big game trophies hung on the walls. The wing to the north of the living room contained bedrooms for the family members, while a wing extending to the east from the dining room housed the kitchen and servants' quarters. Caretakers looked after the ranch year-round while a cook, two or three maids and a chauffeur-handyman were employed for the summer.

The Berols established a new era of sophistication at the ranch, and a change in emphasis from recreation to entertaining. The family entertained friends and visitors from July to the first of October each year. Guests stayed in the Mae-Lou-Lodge or in the remodeled space above the garage, and then walked, possibly over a boardwalk to protect clothing, to the Berol Lodge for meals and parties. The early years at the ranch were a busy time, with "six to eight parties per month with 12 – 22 people in attendance" (Diem, 1986:53).

The Berols added other ranch buildings in the mid 1930s to accommodate their recreation needs. A new pole and frame barn and a log tack cabin were built for the many horses kept for the Berols and their guests. Berol acquired a horse grazing permit in Teton National Forest, just south of Arizona Lake in order to pasture his ten to fifteen horses. In order to provide more accommodations for his hired help and guests, Berol remodeled the upper floor of the Johnson garage and the caretaker's quarters in the Johnson Lodge. Berol added a rolling dock and remodeled the boat house, then built an additional rolling boat dock on Sargents Bay.

Storms on Jackson Lake often eroded sections of shoreline. One such storm occurred just before the completion of the Berol Lodge, instigating a long battle between Berol and the Bureau of Reclamation. Berol wanted the Bureau to lower the maximum level of the lake or to construct cribbing to prevent further erosion; the Bureau and the National Park Service refused. Instead, Berol spent thousands to construct riprap devices along the west shoreline, many of which washed away in a severe storm. "The erosion problem was never resolved but only deferred to the future" (Diem, 1986:51).

Berol pursued his love of hunting in Wyoming and on the AMK Ranch itself. He had a trap shooting range built in the clearing east of Sargent's grave and the Johnson memorial and a rifle range built down by the east dock on Sargents Bay. Berol and his guests made extensive use of these ranges until Berol joined the Jackson Hole Trap Club in the 1960s. Big game hunting also appealed to Berol, and Slim Lawrence would often take him to hunt in the same places he had taken Johnson.

The nature of the Lawrences' work as caretakers changed with the arrival of the Berol family. Slim and Verba still spent the off-season trapping, hunting, horseback riding, searching for American Indian artifacts, and fishing, but summers were taken up with catering the parties at the Berol Lodge and taking care of the Berols' guests. With the 1950 enlargement of Grand Teton National Park, roads were plowed year-round, eliminating much of the hard winter labor. The Lawrences' years of service to the Berols were rewarded with a house and an acre of land at the ranch. Located southwest of the Director's and Sunroom cabins, the Lawrence house was built in 1968. "Slim and Verba worked hard clearing out trees and brush at their homesite in the spring [of] 1968" (Diem, 1986:86).

Unfortunately, Verba did not live in the house for long. She suffered a stroke in that same year and was afflicted with cancer. When she became too weak to take her favorite walks down to the lakeshore, Slim built Verba a series of benches enabling her to rest along the way. Unable to cope with the debilitating disease, Verba shot herself in the bedroom of the Lawrence house in July of 1970. She is buried next to her husband, who passed away in 1986, by the Johnson memorial, on the ranch they loved and lived on for forty years.

After 38 years of continuous summer residency at the ranch, Alfred Berol died in 1974. Kenneth, as executor of his father's estate, sold AMK Ranch to the National Park Service in 1976 for $3.3 million. Kenneth Berol still vacations in the area as of the writing of this nomination, though he no longer stays at AMK, which is now a research station.

Architecture at AMK Ranch

In addition to its historical significance, AMK Ranch is an important example of rustic architecture in Grand Teton National Park. The Rocky Mountain Rustic style evolved from the pioneer vernacular, and is characterized by the use of native timber and stone, crafted by local craftsman using traditional techniques. "Rustic architecture represented the deliberate attempt – usually an architect's deliberate attempt – to convey historical images and to meld man-made resources with their wilderness environment" (Caywood, 1997:41).

Western log architecture is characterized by diverse construction techniques originating in several European countries including Germany, England, France, and Sweden. Settlers carried traditional building techniques with them from Europe and the East Coast of the United States. The most common adaptations to the arid Western climate were the gable entrance and increased roof slope. These alterations accommodated the large snowfalls. Because the majority of settlers arrived in the West in the late nineteenth and early twentieth centuries, the iron stove, which was widely available after the mid-1800s, almost completely replaced the fireplace for heating and cooking.

Log homestead architecture, meant to be replaced by more durable and elaborate dwellings, soon came to symbolize the nascent and transitory qualities of life in the American West. With wilderness fast disappearing through homesteading, railroad, and land deals, Americans viewed the log cabin through the lens of nostalgia, connecting it with simpler times and a vanishing way of life. The literal connection to the environment through tree and stone as well as the nostalgic qualities of log architecture led to the domination of this style throughout the West.

Between 1927 and 1931, William Johnson improved his property with numerous log structures. His log home was built by local contractor Charlie Fox in the Rocky Mountain Rustic style. Round logs with saddle notched corners and tapered log ends, massive stone fireplaces, knotty pine paneling, burled log brackets and stair banisters and wrought iron hardware are all elements of this popular style.

In addition to the Johnson Lodge and its attached barn and garage, Johnson bought three structures, the Sunroom cabin, the Three Room/Director's cabin, and the Two Room cabin from the nearby Hogan homestead, a practice that was common throughout the Jackson Hole valley. "Vernacular buildings from the early period were also preserved out of practical concerns. Log cabins in particular have often been 'recycled' for other uses…A cabin once lived in might become a saddle house, a chicken coop, or a storage shed" (Caywood, 1997:39-40). Johnson also built a chicken house, woodshed, workshop, smokehouse, and boathouse/icehouse, all of which remain today. These vernacular additions to the ranch, all of them similar in architectural style to the Johnson Lodge, create a visually cohesive complex.

The Berol's added other ranch buildings to accommodate their recreation needs. A new pole and frame barn was built for the many horses kept for the Berol's and their guests, as well as a log tack cabin. In order to provide more accommodations for his hired help and guests, Berol remodeled the upper floor of the Johnson garage and the caretaker's quarters in the Johnson Lodge. Berol added a rolling dock and remodeled the boathouse, then built an additional rolling boat dock on Sargents Bay. The vernacular log buildings that Berol added to the complex blend so well with the Johnson-era buildings that it is difficult to tell them apart.

The most opulent and luxurious architectural touches were reserved for the Berol Lodge. Berol, used to the comforts of an upper-class lifestyle, built a lodge to reflect his status. Though only one story in height, the lodge contains 5,200 square feet and maintains a rustic yet airy atmosphere to capture the beauty of the setting. The living room impresses the visitor with towering ceilings supported by heavy logs and large picture windows overlooking Jackson Lake and Mt. Moran. Abiding by the dictates of formal Rustic architecture, the Berol Lodge uses materials both natural and local. Logs came from Arizona Lake meadows, just east of the property. Fireplace rocks were local as well, coming from the Gros Ventre Canyon. The logs represent a visual connection to the vernacular past, recalling the log cabins of early homesteaders. Imitating the building restrictions of early settlers, Rustic architecture highlights local materials, supplementing them with more luxurious items, such as indoor plumbing. Through Rustic architecture, "comfort and luxury coexisted with a vague concept of 'roughing it'" (Caywood, 1997:41). Massive stone fireplaces, the enormous logs at the entrance, and detailed wrought-iron work express the Rocky Mountain Rustic ideal. The Berol Lodge interprets "western elements in sophisticated ways,…through integration of architecture, interior design, and furnishings" (Caywood, 1997:42).

✦ CONCLUSION

The AMK Ranch is eligible for listing in the National Register of Historic Places with significance in settlement and architecture. The district's period of significance extends from John Sargent's original homestead in 1890 to the 1950s when it was used as a vacation home for the Berol family. Significant dates include 1926, when William Lewis Johnson acquired the property and built his own log home at the southern end of the peninsula, and 1936, when Alfred Berol bought the property and began planning an elaborate rusticated log vacation home. In 1976, the Berol family sold AMK Ranch to the National Park Service and it was dedicated as the University of Wyoming-National Park Service Research Station in July, 1978.

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Grand Teton National Park Archaeologist's Office, Moose, Wyoming.

Grand Teton National Park Historian's Office, Moose, Wyoming.

Jackson Hole Historical Society, Jackson, Wyoming.

Teton County Assessor's Office, Jackson, Wyoming.

Figure 1. The violin tree located on Sargents peninsula.

Figure 2. The Berol lodge viewed from the south.

Figure3. The Berol lodge entrance viewed from the north end.

Figure 4. The Johnson (Mae-Lou) Lodge viewed from the south with detail of stone fireplace

Figure 5. The living room of the Berol lodge.

Figure 6. The resting bench built by Slim Lawrence for Verba's walks along the lake shore.

Figure 7. Johnson (Mae-Lou) lodge porch showing detail of log detailing.

Figure 8. The Shop Cabin and Twin Room Cabin viewed from the west.

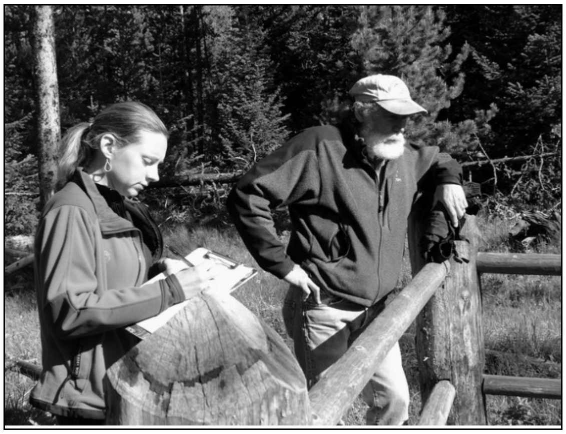

Figure 9. Visitors at John Sargent's grave.

Figure 10. Tack Cabin and Smokehouse on the left, pole barn on the right, wood shed in the far central viewed from the east.

NITROGEN FIXATION IN STREAMS IN JACSKON HOLE, WY

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Nitrogen fixation, the conversion of unreactive N_2 gas from the atmosphere into a biologically usable form NH_3, is the least studied process of the N cycle in stream ecology (Grimm and Petrone 1997). Tapping into the atmospheric N pool can only be accomplished naturally by N-fixers. These diazotrophic organisms can contribute significantly to the autochthonous inputs of nitrogen into streams (Grimm and Petrone 1997). Without further investigations into N-fixation we would ignore a potentially major N flux and transformation. Not only do we need to quantify this process, but also examine what factors control N-fixation in streams.

Nitrogen fixation has been measured in only a few streams (Horne 1975, Horne and Carmiggelt 1975, Naiman and Melillo 1984, Triska et al. 1984, Grimm and Petrone 1997, Henry and Fisher 2003, Marcarelli and Wurtsbaugh 2006), although there are some other ongoing studies (Marcarelli and Wurtsbaugh, Ulseth and Flecker, Gettel, unpublished data). A forested stream in Oregon had N-fixation, associated with woody debris and moss, which was estimated to be 5% of the total N input (Triska et al. 1984). A nitrogen budget was established for a subarctic stream in Quebec, Canada with influence from beaver and associated woody debris, N-fixation was <1% (Naiman and Melillo 1984). From the above forested stream experiments N-fixation does not appear to be an important contributor to the N budget of streams. However, N fixation accounted for 85% of all inputs to the benthic community in Sycamore Creek, Arizona (Grimm and Petrone 1997). Dodds (1989) examined *Nostoc parmelioides* collected from McRae Creek, Oregon and Halite Creek, Montana and compared nitrogen fixation of spherical (no influence by midge larva) and ear-shaped (containing midge larva, *Cricotopus nostocicola* or *C. fuscatus*) morphologies finding increased nitrogen fixation in midge containing *Nostoc*. Contributions of N-fixation to the stream N budgets vary among stream types and species of N-fixing organisms, but there is no theory explaining which streams.

Nitrogen (N) fixation is among the least studied processes of the N cycle in streams, despite its potentially dominant role in N-limited systems. Many streams in NW Wyoming are N limited (J.L. Tank and R.O. Hall, unpublished data). We hypothesize that N-fixation contributes to the N budgets of some streams. Cyanobacteria control the extent to which N uptake or transport occurs and may be important suppliers of N to downstream areas within these watersheds.

We measured nitrogen fixation rates using the acetylene reduction method in nine streams in three different land-use types in Grand Teton National Park and Jackson, WY (Reference-relatively unimpacted streams, Urban-in urban areas, and Agricultural-streams located on a ranch) (Figure 1). Reference and urban streams were not different, but this may be highly skewed due to high N-fixation occurring in the Golf course stream. The agricultural streams may not be low due to N concentrations, but rather the alteration of stream flow and fine sediments.

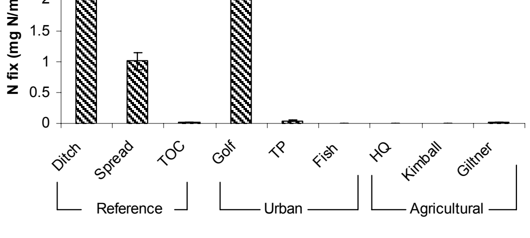

Figure 1. Mean stream nitrogen fixation rates (n ≥18). The results from summer 2005 nitrogen fixation measured using the acetylene reduction technique on 9 streams. Error bars represent standard error. TOC= Two Ocean Creek; TP= Teton Pines Waterway; HQ= Headquarters.

Intermittent flow patterns and fine sediments may not be suitable habitat for N-fixing assemblages. The higher rates we measured are comparable to Sycamore Creek, Arizona (Grimm and Petrone 1997) and tropical systems(A.S. Flecker and A.J. Ulseth, unpublished) which are much higher than most lake, marine and estuarine systems (Howarth et al. 1988). Various ambient nitrate concentrations (Figure 2) are associated with the 9 streams (Figure 1). Ambient stream nitrate concentrations exceeding 10μgN/L inhibit nitrogen fixation.

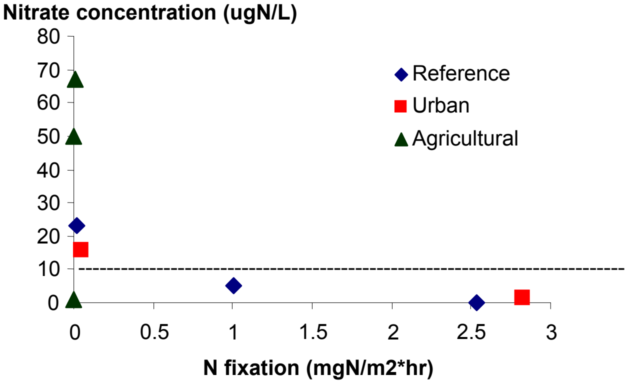

Figure 2. Ambient stream nitrate concentrations exceeding 10μgN/L have low nitrogen fixation rates. The only exception from this study would be Headquarters which has 0.7 μgNO_3-N/L and 0.002mg N m^{-2} h^{-1} nitrogen fixation rate. Headquarters has predominately silt substrate and intermittent flow.

Nitrogen can limit primary production even though there are organisms capable of fixing nitrogen (Vitousek and Howarth 1991). Nutrient limitation experiments have shown streams in many areas across multiple biomes to be N limited (Tank and Dodds 2003, Marcarelli and Wurtsbaugh 2006). Limiting nutrients on algal and phytoplankton community growth have been examined, but not specifically nitrogen fixing organisms. Examining effects of nutrient addition on N-fixation rates will expand knowledge of how nutrient limitation relates to the N-fixation process in streams.

To examine nutrient limitation on N-fixing assemblages, nutrient releasing substrates were incubated in Two Ocean Lake Creek at five sites. Four treatments (control, N, P, N+P) were implemented according to Tank and Dodds (2003). Nitrogen fixation was significantly inhibited by the addition of nitrate (Figure 3). It appears as if phosphorus addition stimulates nitrogen fixation, but it is not statistically significant. This stream had low stream nitrogen fixation rates and results from streams with the highest nitrogen fixation rates may show larger increases in N- fixation due to phosphorus stimulation.

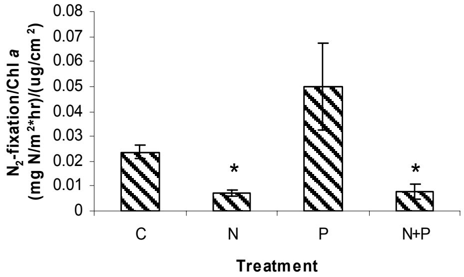

Figure 3. Mean treatment nitrogen fixation rates (n=5). Error bars represent standard error. Addition of nitrogen inhibits N-fixation, while addition of phosphorus may stimulate N-fixation.

Nitrogen fixation is an understudied process in streams. Further research is needed to better understand the rates and controls of nitrogen fixation in Wyoming streams because the contribution of nitrogen fixation to stream nitrogen cycling can be large. We will continue to pursue these questions.

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THE INVASIVE NEW ZEALAND MUDSNAIL, *POTAMOPYRGUS ANTIPODARUM*, REDUCES GROWTH OF THE NATIVE SNAIL, *FOSSARIA SP.*

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✦ INTRODUCTION

Invasive species are one of the greatest threats to global biodiversity. Hence, understanding the role of invasive species is of grave importance to managing and minimizing the impact of biological invasions. To date, the ecological impacts of biological invasions have received significant attention, but little effort has been made to address the evolutionary impact (Sakai *et al.* 2001, Cox 2004). This is despite the fact that evolutionary impacts are likely to be widespread; invasive species have been shown to alter patterns of natural selection or gene flow within native populations (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). We have begun to address some of the evolutionary consequences of the invasion of the New Zealand mud snail, (*Potamopyrgus antipodarum*) on a species of native snail in the Greater Yellowstone Area (GYA).

Potamopyrgus antipodarum are a likely selective agent on native snails because they have 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 dominate these communities (Kerans *et al.* 2005, Hall *et al.* 2006). These densities translate into a strong impact on the biotic and abiotic environment. For example, Hall and colleagues (2003) showed that *P. antipodarum* consumed 75% of gross primary productivity, and Riley and colleagues(*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. Hence, one way *P. antipodarum* may be impacting native snails and other benthic herbivores is by reducing their evolutionary fitness through consumption of resources. 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.

Indeed, consumption of resources by *P. antipodarum* has been shown to cause exploitative competition with a native snail. In experimental chambers, *P. antipodarum* reduced the growth rate of the native hydrobid *Pyrgulopsis robusta* in two streams in the GYA (Riley *et al.* in review). We used two methods to determine whether *P.antipodarum* are competing with another native snail (*Fossaria* sp.). First, we sampled every 150 m along a 900 m stretch of Polecat Creek to determine whether the densities of the two species are correlated. If competition is occurring and reducing their population sizes, the densities of the invasive snail should be negatively correlated with densities of the native snail. Second, we conducted an experiment to determine whether interspecific or intraspecific competition reduces growth and reproduction of the native *Fossaria* and the non-native *P. antipodarum.* Although *P.antipodarum* may be competing with native invertebrates for either food or space (Kerans *et al.* 2005), our experiment only addressed competition for food. We only report on the results of the competition experiment because the data on the relationship between densities of the invasive and the native snail in Polecat Creek are still being collected.

We conducted an experiment to examine growth and reproductive output in interspecific and intraspecific competition treatments at two different densities. To address intraspecific competition, we used experimental chambers with high or low densities of one species. To address interspecific competition, we mixed both species at high or low densities. For each species, we asked whether interactions with conspecifics or the other species had a greater effect on growth and reproduction.

✦ METHODS

Experimental design

We performed a field experiment in the summer of 2005 in Polecat Creek (Roosevelt National Parkway) to assess the competitive interactions between the invasive *P.antipodarum* and the native snail *Fossaria* sp*.,* in terms of on growth and reproduction. For each species, there were two levels of density (low and high) and two types of competition (intraspecific and interspecific). We determined the biomass for the density treatments by measuring the densities of both species in four random samples from the site of the experiment. Low density (1x, 550 mg AFDM/m2) was within the range of ambient density for both species. High density was eight times the ambient density (8x, 4400 mg AFDM/m2). We varied densities to determine whether competition occurred under current conditions (low density) or only when resources are very limited (high densities). Intraspecific competition was addressed in half of the experimental chambers containing only one species (all *Fossaria* or all *Potamopyrgus*). Interspecific competition was addressed in the rest of the chambers containing a mixture of both species.

To examine the impact of competition on the growth of each species, we designated 15 target snails in each experimental chamber. These animals were marked by placing a dab of water-proof paint on their shell. We measured the length of the shell of each target snail at the beginning of the experiment and at the end of the experiment (two weeks later). Since the growth of *P.antipodarum* decreases markedly after sexual maturity (Jokela and Lively 1995), we selected small snails that were likely to be immature for the target snails of this species. For *P. antipodarum*, the mean size of the target snails was 2.17 mm (min. = 1.61 mm, max. = 3.02 mm). Likewise, small *Fossaria* were marked as target snails. These snails were sorted by hand from the random samples that we collected. The mean size of the target *Fossaria* was 6.54 mm (min. = 2.59 mm, max. = 7.97 mm).Although little is known about the life history of this species, in the congener *Fossaria cubensis*, size at maturity is between 10 and 12 mm (Gutierrez *et al.* 2000).

We controlled for biomass in each experimental chamber by converting the length of the snails to ash free dry mass (AFDM) using length-mass regressions for *Fossaria* (Riley, unpublished) and *P. antipodarum* (Hall, unpublished). Then, we placed equal amounts of AFDM for each density (550 mg AFDM/m2 for low density and 4400 mg AFDM/m2 for high density) into the experimental chambers. This also serves to control for differences in body size since adult *Fossaria* are much larger than *P. antipodarum*. For the interspecific competition treatment, the differences in density were achieved by altering the non-target (other) species; the numbers (AFDM) of the target species (target and reproductive snails) were the same for both densities (Table 1).

To examine the impact of competition on the reproduction of each species, we included reproductive snails in addition to the target snails. To match the biomass across experimental chambers of the same density treatment, the AFDM of the target snails was subtracted from the total biomass needed and we then added the appropriate number of reproductive snails to yield the treatment biomass for that species. Hence for the experimental chambers with interspecific competition, there were 15 target individuals of species A, reproductive adults of species A (number varies by density treatment, Table 1), and a variable number of snails of species B to equal the total biomass of that density treatment (mg of AFDM for each density given above). Overall, there were 8 treatments, low and high density for intraspecific and interspecific competition for both species (2 density x 2 competition x 2 species = 8), with three replicates per treatment.

Competition Treatment	Density	Target species	N target	N reproductives	N (other species)
Intraspecific	Lo	Fossaria	15	18	0
Intraspecific	Hi	Fossaria	15	80	0
Interspecific	Lo	Fossaria	15	9	86
Interspecific	Hi	Fossaria	15	9	692
Intraspecific	Lo	Potamopyrgus	15	172	0
Intraspecific	Hi	Potamopyrgus	15	778	0
Interspecific	Lo	Potamopyrgus	15	86	16
Interspecific	Hi	Potamopyrgus	15	86	127

Table 1. Number of snails placed in each experimental chamber by treatment. Because we controlled for biomass across treatments, the total biomass in each experimental chamber for a given density are equivalent, whether the biomass is composed of a single species (intraspecific competition) or mixed species (interspecific competition). Since the two species of snails differ in size, the numbers of each species vary. N refers to the sample size of the target snails, the reproductive snails (same species as target snails), and number of snails of the other species.

Experimental cages were constructed from 0.0182 m^2 plastic storage containers. We cut out the plastic from each side and from the top and replaced it with 122 µm mesh Nytex screen. The screen allowed water to flow through the chambers but kept the egg masses of *Fossaria* and the newly hatched juveniles of *P. antipodarum* inside.

To assemble the experimental chambers, we attached each plastic chamber to a 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. Next, we placed between five and six rocks from the surrounding stream in each experimental chamber. These rocks, which had been cleaned of benthic invertebrates, possess periphyton and provide nutrients for the snails. Snails were added to each chamber according to the appropriate biomass and species combination. Then, we placed the chambers in the stream to a depth that covered the rocks in the chamber but also allowed some air at the top of the cage. The air pocket was required because *Fossaria* possess lungs and breathe air.

The experiment was set-up on July 1 and 2, 2005. Every two days during the duration of the experiment, we visited the site of the experiment to check the depth of the experimental chambers and to remove detached algae from the mesh. The experimental chambers were removed from the creek on 15 and 16 July; each experimental chamber remained in the creek for 14 days. At the end of the experiment all of the contents of the chambers (snails, egg masses, algae), except the rocks, were rinsed through a 250 µm metal sieve and preserved in 70% ethanol. Each of the rocks were scrubbed for analysis of chlorphyll *a*.

Measurements of resource use

We also measured use of algal resources by measuring the concentration of chlorophyll *a* for each rock. In addition to the experimental chambers containing snails, we also had three experimental chambers that had no snails in them. These chambers served as controls to compare the grazing effect among the treatments. The controls also allow us to determine whether one species utilizes the resource more completely and whether resource use was the cause of competition.

We scraped the periphyton off of each rock with toothbrushes and then collected a volume of the slurry on a glass fiber filter (Gelman AE) using vacuum filtration. We calculated chorophyll *a* concentrations with a 90% acetone extraction and spectrophotometric analysis of the extract (APHA 1998). We estimated the exposed surface area of each of the rocks using paper tracing. Hence, we will be able to calculate the concentration of chlorophyll *a* per unit area. These results are not reported here because they are not yet complete.

Statistical analyses

We omitted one replicate from each treatment because some of the experimental chambers failed (the Nytex mesh did not remain attached on one or more of the “windows”). In these replicates, the number of snails in the chamber was either higher or lower than the starting number (escapees and émigrés). Therefore, we analyzed the remaining two replicates per treatment.

To determine the effect of the experimental conditions on growth, we converted the length measurements to biomass (AFDM) and compared the biomass measurements at the beginning and end of the experiment among groups. We used a two-way ANOVA with biomass (mg of AFDM) as the dependent variable and with the categorical independent variables, density (low or high) and type of competition (intraspecific and interspecific). We did not use repeated measures ANOVA because snails were marked so that they could be distinguished from the reproductive adults, but not marked individually. Therefore, we have biomass measurements for the group at the beginning and at the end of the experiment.

The rate of reproduction in each chamber was calculated as rate of reproduction = $o / (r - m)$ where o is the total number of offspring (juvenile *P. antipodarum*, and juvenile and egg masses of *Fossaria*) in each container, r is the total number of reproductive adults, and m is the total number of snails of the target species that died in each container. Since the timing of mortality is unknown, excluding the dead animals may underestimate the number of animals contributing to reproduction. Despite this potential risk, we excluded the dead animals because of high mortality of *Fossaria* in the high density treatments. Reproductive rates were also analyzed with a two-way ANOVA. Again the categorical, independent variables were density and type of interaction. All statistics were conducted using the R statistical package (R Development Core Team, 2005).

✦ RESULTS AND DISCUSSION

Growth

Both density and type of competition had significant effects on biomass in the native *Fossaria sp.* (Table 2A). Not surprisingly, *Fossaria* showed a significantly higher increase in biomass in the low density treatment than in high density (Table 2A, Fig. 1). This result indicates that a high density of individuals lead to decreased growth, probably because of reduced resources. Importantly*, Fossaria* also gained significantly less biomass in the interspecific competition treatment than in the intraspecific treatment (Table 2, Fig.1). This result indicates that the invasive snail, *P. antipodarum* had a more detrimental effect on *Fossaria's* growth than conspecifics. A significant interaction term between density and type of competition was caused by a larger gain in biomass in the intraspecific treatments at low density that at high density (Fig. 1).

In contrast to the native *Fossaria*, only density had a significant effect on biomass in the invasive *P. antipodarum* (Table 2B); there was no effect of type of competition and no significant interaction term. Similar to *Fossaria*, the gain in biomass was significantly higher in the low density treatment (Table 2B, Fig. 2). Again, this result suggests that in the high density treatment, the presence of many individuals decreased resources which led to decreased growth. Although an accumulation of nitrogenous wastes may also stunt growth, this explanation is unlikely in this experiment because fresh water flowed constantly through the experimental chambers.

A. *Fossaria*

Source	d.f.	M.S.	F value	P
Density	1	30.30	14.66	**0.0002**
Competition	1	17.80	8.61	**0.0038**
Density * Competition	1	10.99	5.32	**0.0222**
error	187	2.07		

B. *Potamopyrgus*

Source	d.f.	M.S.	F value	P
Density	1	0.0576	4.53	**0.0347**
Competition	1	0.0003	0.02	0.8886
Density * Competition	1	0.0058	0.45	0.5011
error	189	0.0127		

Table 2. The results of a two-way ANOVA of the effects of density (low and high) and type of competition (intraspecific and interspecific) on the AFDM (mg) of the target snails before and after the experiment. Separate analyses were conducted for *Fossaria* (A.) and *Potamopyrgus* (B.) Statistically significant effects are bolded.

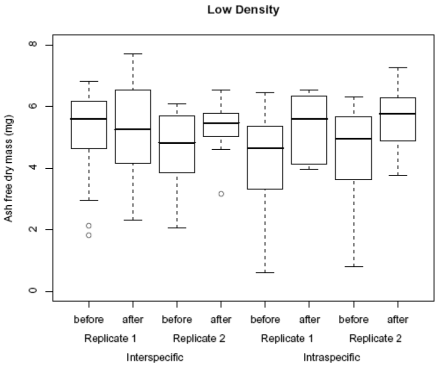

Figure 1 A

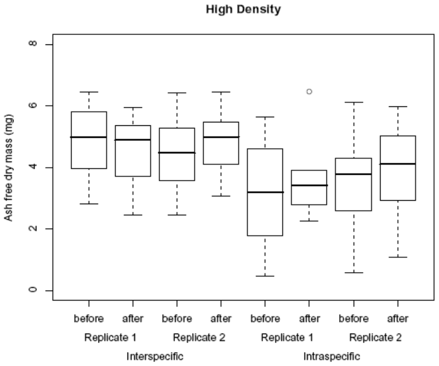

Figure 1 B

Figure 1. The change in biomass (AFDM in mg) of *Fossaria* between the beginning of the experiment (before) and two weeks later at the end of the experiment (after), for each replicate for interspecific and intraspecific competition treatments. In these boxplots, the dark, horizontal line is the median, the box bounds the 75th and 25th percentiles, and the whiskers bound the 90th and 10th percentiles. Any outliers are plotted as open circles. The low density treatments are shown in A) and the high density in B).

Despite the fact that conspecifics can have identical resource needs, interspecific interactions had a greater impact on the growth rate of *Fossaria* than did intraspecific interactions. This result is surprising and suggests that *P. antipodarum* may be depressing the periphyton resource to a greater extent than *Fossaria*. This explanation would also explain why there was no effect of competition type in *P. antipodarum* (intraspecific and interspecific competition treatments had an equivalent effect on growth). We will be able to address this hypothesis with the data on concentrations of chlorophyll *a*.

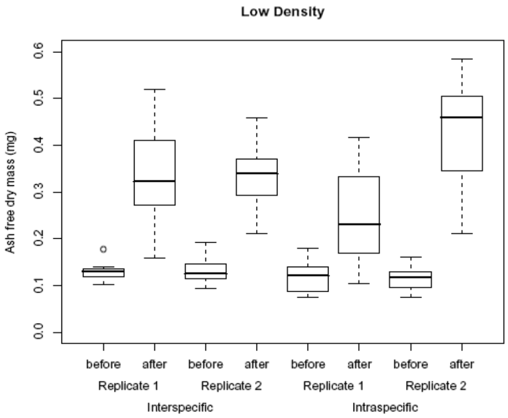

Figure 2A

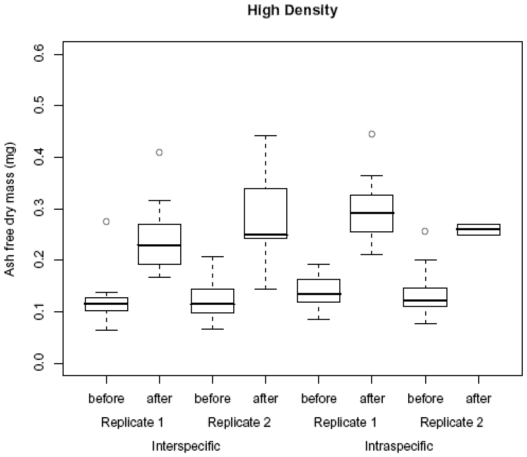

Figure 2 B

Figure 2. The change in biomass (AFDM in mg) of *Potamopyrgus antipodarum* between the beginning of the experiment (before) and two weeks later at the end of the experiment (after), for each replicate for interspecific and intraspecific competition treatments. In these boxplots, the dark, horizontal line is the median, the box bounds the 75th and 25th percentiles, and the whiskers bound the 90th and 10th percentiles. Any outliers are plotted as open circles. The low density treatments are shown in A) and the high density in B).

Reproduction

Overall, reproductive rate was less affected than growth. In the native *Fossaria*, there were no significant effects on reproductive rate by either density or type of competition (Table 3A, Table 4A). These results suggest that allocation to reproduction is prioritized over growth; when environmental conditions were poor (e.g. under competition in high density) growth was compromised but not reproductive rate. Another possible explanation is that fourteen days is not long enough to detect a response in reproduction.

A. *Fossaria*				
Source	d.f.	M.S.	F value	P
Density	1	6.42	0.92	0.3907
Competition	1	24.09	3.47	0.1361
Density * Competition	1	4.83	0.69	0.4514
error	4	6.95		
B. *Potamopyrgus*				
Source	d.f.	M.S.	F value	P
Density	1	0.765	2.41	0.1954
Competition	1	0.004	0.01	0.9180
Density *Competition	1	2.556	8.07	**0.0469**
error	4	0.317		

Table 3. The results of a two-way ANOVA of the effects of density (low and high) and type of competition (intraspecific and interspecific) on the reproductive rate of the target snails. Separate analyses were conducted for *Fossaria* (A.) and *Potamopyrgus* (B.) Statistically significant effects are bolded.

Results for the invasive *P. antipodarum* were similar. Reproductive rate of *P. antipodarum* was not affected by either density or type of competition (Table 3B, Table 4B). However, there was a significant interaction between density and competition; in the interspecific competition treatment, reproduction was highest in the high density treatments. In contrast, in the intraspecific competition treatment, reproductive rate was highest in the low density treatments (Table 4B).

✦ CONCLUSIONS

The two species differed in their responses to the experimental conditions. In *Fossaria*, growth was negatively affected by density and by *P. antipodarum* but not by conspecifics. Reproduction in this species was not affected at all. In contrast, growth of *P. antipodarum* was only affected by density and there was no difference in growth between the intraspecific and interspecific competition treatments. Similar to *Fossaria*, reproduction in *P. antipodarum* was not significantly affected by the experimental conditions. These results suggest that *P. antipodarum* is the stronger competitor. This asymmetrical relationship actually suggests that the interaction between the two species might best be described as amensal (Begon *et al.* 1990). Competition involves two species that have negative effects on each other. Inconsistent with this definition, *P. antipodarum* has a negative effect on *Fossaria*, but *Fossaria* does not have a significantly negative effect on *P. antipodarum*. An asymmetrical relationship was also found between *P. antipodarum* and *P. robusta* (Riley *et al*. in review).

Regardless of whether the interspecific interaction is best termed competition or amensalism, in an experimental setting, *P. antipodarum* had a negative effect on the growth of the native snail, *Fossaria*. The reduction in growth of the native *Fossaria* can lead to reduced population sizes, eventual population declines and possibly local extirpation. If these demographic consequences are not severe, the decrease in fitness of the native caused by reduced growth might lead to selection. For example, selection might favor traits in *Fossaria* that reduce the overlap in resource use. With sufficient genetic variation and time, this selection can result in evolutionary change in heritable traits. Alternatively, if competition causes age-specific mortality, it might lead to evolution in life-history traits. The possibility that invasive species can have an evolutionary impact within native communities has often been neglected (Sakai *et al.* 2001).

A. *Fossaria* Competition treatment	Density	replicate	Reproductive rate
Intraspecific	Low	1	4.57
Intraspecific	Low	2	3.07
Intraspecific	High	1	0.48
Intraspecific	High	2	0.48
Interspecific	Low	1	3.08
Interspecific	Low	2	8.40
Interspecific	High	1	3.00
Interspecific	High	2	8.00

B. *Potamopyrgus* Competition treatment	Density	replicate	Reproductive rate
Intraspecific	Low	1	1.63
Intraspecific	Low	2	1.26
Intraspecific	High	1	1.26
Intraspecific	High	2	2.66
Interspecific	Low	1	2.47
Interspecific	Low	2	2.76
Interspecific	High	1	0.57
Interspecific	High	2	1.67

Table 4. Reproductive rate for each replicate in each treatment. The rate of reproduction in each chamber was calculated as $o / (r - m)$, where o is the total number of offspring (juvenile *P. antipodarum*, and juvenile and egg masses of *Fossaria*) in each replicate, r is the total number of reproductive adults, and m is the total mortality of the target species in each container.

The reduction in growth in the native species most likely resulted from exploitative competition for algal resources. Both of these species consume periphyton and periphyton-covered rocks were the only resource available to the snails in the experimental chambers. The data on chlorophyll *a* will indicate whether competition occurred over resources.

Whether or not exploitative competition is also occurring in the natural environment depends on whether aquatic algivores are typically limited by the abundance of periphyton. Although we do not have these data, several pieces of evidence suggest that algivores probably are limited by the abundance of periphyton. First, several studies have shown that *P. antipodarum* significantly reduce the biomass of periphyton in experimental conditions (Riley *et al.* in review, Winterbourn and Fegley, 1989). Second, Kolher and Wiley (1997) showed that population sizes of many aquatic insect taxa were maintained at low levels because of limited periphyton. Third, several studies have suggested that growth of benthic algivores is limited by algal abundance (reviewed by Lamberti 1996). Therefore, while individual streams may vary, it is likely that periphyton is a limiting resource and hence competition over periphyton limits growth and population size of aquatic grazing species.

These results verify that the mud snail invasion should be a concern to biologists and managers. This and other studies (Riley *et al.* in review) suggest that the mudsnail is having a negative effect on native species. These negative impacts could lead to population declines of natives, local extirpation, or an evolutionary response in the natives. Our results also suggest that density dependent effects on growth and reproduction of *P.antipodarum* are much smaller than those of the natives (Tables 2 and 3). These results suggest that *P. antipodarum* is a superior competitor and further spread of this species is unlikely to be halted by competitive interactions with native organisms.

Studies of severe population declines of a strong grazing competitor in streams, showed the importance of competition in both the composition of aquatic benthic communities and the population dynamics of individual species in the communities (Kohler and Wiley 1997). Hence, the strong competitive interactions by *P. antipodarum* in this study, suggest that they too could change the composition of stream communities and population sizes of species in the communities. In addition, reduced fitness in the native snail in the presence of mudsnails also makes evolutionary change in the native species possible. Hence, the impact of the mudsnail on native communities and species is likely to be widespread and detrimental.

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CLIMATIC FACTORS, REPRODUCTIVE SUCCESS AND POPULATION 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 (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 2005 *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 the summer of 2005 montane voles *(Microtus montanus*) declined to approximately 50% of the population densities recorded in 2004. The decline had occurred during the winter of 2004-2005 since at the onset of the spring study period there was very little sign (cuttings, droppings) of vole activity. However, during the spring study period it also became apparent that early reproduction would be extremely successful. In 2005 the onset of spring (i.e., meltoff, growth of new herbaceous vegetation) was uncommonly early and, as expected, vole reproduction also began unusually early. Indeed, at the onset of the spring study period (last two weeks in May some females were already pregnant with their second litter (i.e., palpable embryos in lactating females). Such early breeding indicates that the first as well as the second litter would definitely breed in the year of their birth. In other words, a very large number of breeders was being added to the population and all observations suggested that vole populations should increase in density in Grand Teton National Park. However, the importance of green vegetation to vole reproduction was dramatically demonstrated in the summer of 2005.Vole populations tend to fluctuate synchronously over remarkably wide geographic regions although asynchrony can occur among populations separated by only a few kilometers. During the summer study period a dramatic difference became apparent between two local populations, based apparently on microhabitat differences. Whereas one (in a relatively xeric environment) had declined in density as compared to 2004, the other (in a more mesic area) increased dramatically over the 2004 levels. Furthermore, as reproduction had virtually ceased by the end of the summer study period in the former, it continued in the latter. The continued reproductive activity was characterized not only by the large percentage of breeding females but also by the production of large litter sizes. Consequently, by the end of the 2005 field study period two populations, separated by less than twenty kilometers, exhibited diametrically opposing patterns of population dynamics. Such observations indicate that, whereas climatic conditions over large geographic areas can synchronize population dynamics of voles, microclimate and microhabitat (Negus, Berger and Pinter 1992) can override the effects of large-scale weather patterns.

Microclimate and microhabitat may exert an effect on vole populations in a number of ways. For example, they may influence the degree and severity of parasitism experienced by *Microtus montanus*. It now appears that microclimate within burrow may determine the rates at which an endoparasite (*Hepatozoon* sp.) infects these rodents (Watkins, Moshier and Pinter 2006).

✦ CONCLUSTIONS

The data collected in the 2005 field season exemplify the extreme sensitivity of *M. montanus* to environmental vicissitudes and reinforce the point that climatic variables play an extremely important role in their reproductive processes. Furthermore, these data also demonstrate the surprising speed with which climatic change can shape the population dynamics of these animals. In turn, population dynamics of voles result in major consequences for the ecosystem. Montane voles constitute a major prey base for a variety of predators. Unexpected shifts in the reproductive responses and population dynamics of these rodents must therefore also have significant repercussions on population parameters of their predators.

✦ ACKNOWLEDGMENTS

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YELLOWSTONE NATIONAL PARK

CARBON CYCLING AT THE LANDSCAPE SCALE: THE EFFECT OF CHANGES IN CLIMATE AND FIRE FREQUENCY ON AGE DISTRIBUTION, STAND STRUCTURE AND NET ECOSYSTEM PRODUCTION

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✦ BACKGROUND AND OBJECTIVES

Climate, fire frequency and intensity, and forest structure and development are strongly linked, and predicting potential changes in carbon storage depends on understanding these links. However, we lack the ability to make robust predictions about how changes in climate will alter these interactions and change the carbon balance of a landscape. Forests contain as much as 80% of the total carbon stored aboveground and 40% of that stored belowground in terrestrial ecosystems (Dixon et al. 1994, Harmon 2001). Disturbances such as fires or insect outbreaks – controlled largely by climate - may shift a forested area from a net sink to a net source of carbon to the atmosphere, and increasing the frequency of large disturbances may affect the global carbon budget. Complex interactions among climate, disturbance regimes, and stand-level ecosystem processes, however, preclude predicting the importance of climate change for forest landscapes.

Carbon cycling in forests is a complex process affected by many factors. Carbon storage on landscapes is controlled by the balance between carbon accumulating in live biomass and the forest floor and carbon being lost though decay of dead wood (Kasischke et al. 1995); the distribution of stand ages on a landscape, since carbon stored in live and dead pools varies with stand development (Harmon 2001); and the distribution of stand structures on landscapes (Kashian et al. in review). Disturbance severity and frequency affect the proportional distribution of carbon among various pools, and may affect the distributions of stand ages on a landscape (Schoennagel et al. 2003). Moreover, rates of carbon accumulation may differ strongly following wildfires depending on fire severity (Wirth et al. 2002). Any change in climate that increases fire frequency or severity, and any change in fire regimes that alters the stand and structure distributions on landscapes, may therefore result in a shift of the landscape towards becoming a long-term carbon source.

Our current work in Yellowstone is examining how initial post-fire structural heterogeneity controls carbon dynamics over the full cycle of individual forest stands, and how climate-mediated changes in the fire regime could potentially alter the behavior of the entire Yellowstone ecosystem as a net sink of net source in the global carbon cycle. Our main objective is to estimate how changes in fire frequency, pattern, and intensity will alter the distribution of forest age and structure across a landscape and how these changes, in turn, will affect the landscape carbon balance.

✦ METHODS

Our research will provide a detailed case study of carbon dynamics from the scale of individual forest stands to a large coniferous landscape. To meet this objective, we are describing changes in all of the major pools and fluxes of the carbon cycle at temporal scales ranging from years to centuries, as influenced by periodic fires and successional patterns within a landscape where fire frequency will likely accompany changes in global climate, and can potentially alter carbon cycling dramatically. By directly and indirectly quantifying all of the stocks and rates of change in the major components of the carbon cycle in the Yellowstone subalpine landscape, we will contribute to understanding how changes in disturbance regimes may produce qualitatively different patterns of carbon release and storage in coniferous forests worldwide.

Field sampling

Near-complete sampling of a complex and extensive field sampling plan that includes 77 stands across Yellowstone National Park was accomplished in 2004 and 2005. Three separate, replicated chronosequences were identified in the field. Each chronosequence included 3-5 stands sampled in five age classes: < 25 years (stands sampled in Litton et al. 2004), 40-70, 80-130, 170-230, and >250. Chronosequences were constructed for low, medium, and high-density stands; stands >170 years old were sampled based on their recent history of bark beetles attacks rather than density. Thirty-one of the stands > 40 years old were sampled previously by Kashian et al. (2005). All but four of the 77 stands were located within Yellowstone National Park; two were located in the Targhee National Forest, and two in Grand Teton National Park. Data were collected to quantify carbon pools in each stand in live biomass (using allometric equations developed in Yellowstone in 2004), dead wood, forest floor, soil, understory vegetation, and annual litterfall.

Each stand was sampled using three 10 x 50 m plots, with plots located at equal distances along a baseline. Belt transects in each plot were used to measure standing live and dead trees, stumps, and saplings, with transect width differing for overstory trees and saplings based on density. The center line of each plot was used to select trees and saplings for allometric measurement and to select locations for sampling soil and forest floor. Twenty-five randomly selected saplings in each plot were measured at the base. Ten mature trees were randomly selected for further sampling in each plot along the center line of each plot. For each tree, an increment core was extracted at breast height and the sapwood marked on the core, and tree height, height to crown base, and crown depth was measured. Finally, three dominant (oldest) live overstory trees were selected in each plot and an increment core extracted at the base for age determination.

Dead wood was measured using eight 50-foot transects run due east from each plot; dead wood was tallied in five size classes, and classified for decay for the largest size class. Five forest floor samples approximately 900 cm^2 in area were collected along the center line of each plot; all forest floor material was collected to the top of the mineral soil and composited by plot. A soil core was extracted to 30 cm from the top of the mineral soil within the area the forest floor was collected and separated into a 0-15 cm sample and a 15-30 cm sample. In 2004, twelve litter traps were deployed per stand to estimate annual litterfall, and ion-exchange resin bags were deployed five per plot. Resin bags and litterfall were collected in July 2005; a second year of litterfall will be collected in July 2006.

Sampling of stands burned in 1988 follows the methods established by Litton et al. (2004). Coarse woody debris was sampled in all plots, including the 12 previously sampled by Litton et al. (2004). We also collected approximately 900 foliage samples from lodgepole pine in 42 stands in 2005 with the help of tree climbers for analysis of the variability of foliar nitrogen within and among trees and stands.

Sample processing

For each soil sample, fine roots were separated from soil, classified into live and dead roots, and weighed. A subsample of soil was then taken, rocks and non-root organic matter removed, and weighed, dried, and weighed again to determine bulk density. Live and dead roots were ground in a

Wiley mill and analyzed for percent carbon. Soil samples were ground on a roller mill and also analyzed for percent carbon. Foliage, forest floor litter subsamples, litterfall, and coarse wood samples were ground in Wiley mills and analyzed for percent carbon and/or nitrogen. Increment cores were mounted and sanded per standard techniques. Tree ages were determined from each increment core, and the average 10-year ring width (used to estimate growth and productivity) was determined for each core using a sliding bench micrometer. As of the end of the 2005 field season, all field samples have been collected except for the second year's litterfall (to be collected in 2006).

✦ PRELIMINARY RESULTS AND DISCUSSION

Eight work-study students were hired for the fall of 2005 and spring of 2006 to process samples in the lab. As of February 28, all field samples (soil, fine roots, forest floor, coarse wood samples, and litterfall samples) have been processed and ground for analysis and about 50% of these samples have been analyzed for carbon and nitrogen.

The success of a project based on replicated chronosequences depends on the similarity of replicate stands within age classes and density classes in terms of total ecosystem carbon and the distribution of carbon among pools. The dead wood and forest floor pools exhibited higher variability than any other carbon pool (CV = 51-79%), and this variability was most extreme in stands younger than 130 years. The proportion of carbon found in dead wood was most variable among replicates along the dense chronosequence, but this proportion was not significantly different among density classes. The coefficient of variation for carbon proportions for all other age classes was < 50%.

Strong differences occur in carbon storage and distribution among pools with stand age and density. In all stands, total ecosystem carbon increases from ~ 5000 g C/m^2 in stands <25 years to a peak of about 14700 g C/m^2 in stands 80-130 years, then decreases thereafter. Such a trajectory suggests a rapid increase of carbon storage as forest growth exceeds decomposition of dead wood, then a loss of carbon as forest productivity slows and carbon lost through decomposition increases proportionately. The initial proportion of total carbon in live biomass is higher in stands < 25 years as density increases, and the peak carbon storage is also higher in denser stands ($p < 0.03$).

The proportion of total carbon in dead wood varied almost inversely with that found in live biomass. Dead wood represented significantly more total carbon in young stands (> 91%; $p < 0.05$) than those aged 40-130 years ($p < 0.02$), and dead wood represented the least amount of total carbon in the 80-130 class (7-12%), although more carbon is found in dead wood in old stands ($p < 0.05$). Dead wood represented less than 27% of total carbon in all stand age and density classes except for young stands and old stands attacked by bark beetles (38%). The proportion of total carbon in dead wood was significantly higher in low- and moderate-density stands than in dense stands ($p < 0.01$), probably because higher rates of carbon accumulation occur in denser stands due to a higher leaf area.

✦ CONCLUSIONS

Though preliminary, our results suggest that the balance between carbon gained through tree growth and carbon lost through decomposition of dead wood controls the ability of a stand to store carbon. This balance differs among stands of different ages and structures, and thus altering the distribution of stand ages and structures across a landscape – which may occur with changes in fire frequency - may result in a qualitative shift of the landscape between a carbon source or sink. We have not yet calculated the carbon *balance* of the stands we have sampled, focusing here only on carbon *stocks*. Relatively low levels of carbon stored in live biomass vs. deadwood in young stands, however, suggests that young stands are likely to lose more carbon through decomposition than they gain through photosynthesis (carbon sources), while middle-aged and older stands are likely to gain more carbon than they lose (carbon sinks). The current Yellowstone landscape, therefore, dominated by young stands following the 1988 fires, is probably a source of carbon to the atmosphere, though it will likely return to a carbon sink with time. An increase in the frequency of fires like those that occurred in 1988 is likely to reduce the amount of carbon stored on coniferous landscapes, however, which has strong implications for the global carbon budget.

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HOW DO DISTURBANCE GENERATED PATTERNS INFLUENCE THE SPATIAL DYNAMICS OF ECOSYSTEM PROCESSES?

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✦ BACKGROUND

Our studies following the 1988 Yellowstone fires demonstrated that succession was surprisingly more variable in space and time than even current theory would have suggested, and that initial spatial patterns of disturbance may persist to produce long-lasting changes in vegetation. Our focus now is on explaining the spatial and temporal patterns of succession and understanding how these patterns influence ecosystem function. The most interesting new questions revolve around the degree to which the spatial variation in postfire vegetation -- in particular, the six orders of magnitude variation in pine sapling density, ranging from 0 to greater than 500,000 saplings/ha --controls the spatial variability in ecosystem processes across the landscape. In our current research, we are conducting studies in both Grand Teton and Yellowstone National Parks to answer four major questions:

1. Does the spatial heterogeneity of processes such as ANPP, nitrogen mineralization, and decomposition change with time since fire? How quickly do spatial patterns in processes develop following a large fire?

2. How does the spatial pattern of coarse woody debris vary across the post-1988 landscape, and what is the importance of this variation for ecosystem function? Are patterns of coarse woody debris abundance related to both prefire stand structure and postfire sapling density?

3. Do the enormous differences in postfire tree density produce differences in carbon and nitrogen availability across the landscape? Or, is nutrient availability governed largely by broad-scale (i.e., 10 s of km) abiotic gradients (e.g., climate, substrate) and/or fine-scale (i.e., less than 10 cm) heterogeneity in resources or the microbial community, such that nutrient variability is not sensitive to the spatial variation in plant community structure?

4. Does the disturbance-created mosaic leave a persistent functional legacy? What mechanisms in vegetation development may contribute to convergence (or divergence) in

ecosystem structure and function across the landscape as succession proceeds?

✦ FINDINGS AND STATUS

We completed our field sampling for questions 2 and 4 in 2004. In 2005 we conducted field work to address components of questions 1 and 3 in both Grand Teton / Rockefeller parkway and Yellowstone National Parks.

Studies in Grand Teton National Park / Rockefeller Parkway

Question 1: In 2003, we initiated a pilot fertilization study in the 2000 Glade Fire, in which replicate plants of several target species received a modest fertilizer amendment. Although nitrogen is considered to be limiting to vegetation growth throughout the subalpine forests of the Rocky Mountains, studies have not empirically demonstrated this limitation in early successional postfire forests.

Initial plant cover was measured before treatment in 2003, then again in 2004, at which time fertilizer treatments were once more applied. In 2005 we made final measurements of plant cover, and also harvested the plants (above and below-ground portions) to determine whether there has been a response to the treatment.

Laboratory work was completed in the winter of 2005-2006, to measure dry-weight biomass and foliar nitrogen content of all the plants harvested in 2005. Statistical analysis is now underway, with manuscript preparation planned for spring of 2007.

Studies in Yellowstone National Park

Question 3. Elizabeth Levitt, graduate student in ecology at the University of Wisconsin, completed her M.S. thesis in which she asked whether the differences in stand characteristics observed in 17-yr old post-fire lodgepole pine (*Pinus contorta*) were associated with differences in inorganic soil nitrogen availability. She sampled 25 stands that burned in the 1988 fires. Free resin bags were used as an index of nitrogen availability during the growing season, distributed randomly in each stand in June 2005, retrieved in September 2005 and extracted for nitrate (NO3-) and ammonium (NH4+). Observed stand characteristics included vegetation, forest floor cover, litter quality and quantity and soils. Overall, vegetation explained 58% and litter explained 19% of the variability in soil N availability among 25 stands. Of these attributes, graminoid cover (grasses and sedges) explained 51%, while pine sapling density explained 7% of the variation in the model. Litter quantity and quality explained 14% and 5% of the variation, respectively. Pine sapling density was negatively related to N availability (R2=0.25; p=0.01). Within-stand heterogeneity of inorganic N availability as measured by coefficients of variation (CV) ranged from 47 to 284% among stands, and CVs were largely attributed to litter mass (partial R2=0.47, p<0.001). The results of this study showed that postfire differences in vegetation structure were associated with patterns of N availability almost 20 years after the 1988 fires in YNP.

Levitt also left resin bags in the same set of 25 stands for retrieval in 2006, to compare patterns in mineralization during the course of a summer (2005) and a year (2005-2006).

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GREATER YELLOWSTONE ECOSYSTEM

ASSESSMENT OF RECREATIONAL IMPACE ON BLACK BEAR HABITAT USE AND IMPLICATION OF GRIZZLY BEAR RANGE EXPANSION IN THE SOUTHERN TETONS

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✦ ABSTRACT

Grizzly bears have been moving slowly southward in the Tetons and increasing their abundance over the last 20 years. Their distribution is now expanding into areas previously occupied by black bears only that are heavily developed and receive proportionately more recreational use. At the same time, white pine blister rust and other human-caused factors may reduce bear food abundance in the near future. Grand Teton National Park is now positioned for an unprecedented interplay of bears, declining bear food sources, and humans in a relatively small temporal and spatial scale. In a new study designed to provide information critical to future black and grizzly bear conservation in this area, 6 spread spectrum technology (SST) GPS radio collars were deployed on black bears in the southern end of Grand Teton National Park in 2005. SST collars allow interrogation of the data in the GPS unit on a regular basis. GPS units were programmed to record positions every 90 to 190 minutes, and data were downloaded aerially on a weekly basis. Four female bears, two with cubs of the year, an adult male, and a subadult male provided the bulk of approximately 2700 positions obtained in 2005, about 150 of which were visited for detailed site analysis. Sites visited were based on a randomly selected 24 hour period for each bear each week, and all sites were visited within a week of the location's recording. Efforts in 2006 will focus more intensively on site visits and associated data collection and analyses.

✦ INTRODUCTION

Like most protected areas across the West, Grand Teton National Park (GTNP) has experienced the pressure of gradual but consistent increasing recreation use and development. This is particularly true in the south end of the park, where both front and backcountry use is intense, park development densities are highest, large blocks of Teton County private lands abut the park's borders and the town of Jackson is just a stone's throw away. With these increased pressures have come escalating black bear-human conflicts, well illustrated by the 14 bears killed in Teton County by Wyoming authorities in the year 2002 alone. Furthermore, ecological changes, particularly the recolonization of wolves in the park, whitebark pine (*Pinus albicaulis*) blister rust infection, potential changes in ungulate numbers and distribution due to disease or related intensive management programs, and the slow but steady march of the Yellowstone grizzly population southward, also figure prominently on the landscape. The additive properties of these changes in GTNP have exacerbated the need for complex, potentially unprecedented human and wildlife management strategies. Scientific knowledge in several key areas of black bear habitat use, interactions with other species, and relationships with human activities will be critical in the development of these strategies.

Grizzly bears have been moving slowly southward in the Tetons and increasing their abundance over the last 20 years (Pyare et al. 2004, Schwartz et al. 2002). In addition, their distribution is slowly but surely expanding into southern areas previously occupied by black bears only that are heavily developed and receive proportionately more recreational use. At the same time, white pine blister rust and other human-caused factors may reduce bear food abundance in the near future. Thus, the Park is now experiencing an unprecedented interplay of bears, declining bear food sources, and humans in a relatively small temporal and spatial scale. The distribution of black and grizzly bears in GTNP, the associated infestation of blister rust, the complex ungulate management system, and a broad spectrum of human influences provide a compelling incentive to investigate the effects of changing food abundance on both resident grizzly and black bear populations, and the associated impacts on the bear-human interface. From a management perspective, black bear movement and habitat use data from the southern Tetons are essential for predicting, documenting, and mitigating changes in the bear-human interface, both in terms of providing for long-term bear conservation and minimizing bear-human confrontations.

In an on-going study in the park's more remote northern half, GTNP and the Interagency Grizzly Bear Study Team (IGBST) are investigating relationships among recreation, grizzly and black bear habitat use, and the implications of potentially declining food sources. The northern study presents a unique opportunity to conduct this companion work in the southern end of the park on black bears, thus contrasting 1) high vs. low recreation use and development, and 2) grizzly- occupied vs. grizzly-free effects on how black bears use the landscape and interact with humans. The results of both studies will help us predict how bear-bear and bear-human relationships may change as grizzlies colonize the southern Tetons. This will aid National Park Service, U.S. Forest Service, state, county, and city managers in planning future recreation management appropriately, with long-term bear conservation as a primary component. Results of this study will also help land managers mitigate current effects of recreation on black bears and reduce human-bear conflicts.

As food resources become more limited, the competition between black and grizzly bears will amplify. Scenarios discussed above suggest an increase in bear-human confrontations as a result of declining foods and the potential influence of ungulate management practices. Accordingly, this study and the companion northern study will provide information on habitat use and foraging habits of these two overlapping bear populations, a more detailed understanding of how black bears use the ecosystem, how grizzly bears interface with black bears that share the landscape, how each of them interface with ungulate management programs and share the landscape with humans, and, finally, what changes might be expected as major bear foods decline and grizzly bears increase their use of the southern Tetons. This information is critical for providing a solid foundation to direct adaptive management policies for bears, ungulates, and human recreation within GRTE (Grand Teton National Park). This work, therefore, represents a compelling combination of research, management, and conservation interest.

✦ OBJECTIVES

The overriding objectives of this study are to:

1) Evaluate black bear movements, activity patterns, and habitat use in response to patterns of visitor use and development, and use of whitebark pine and other foods and habitat resources.
2) Evaluate consequences of future interspecific competition between grizzly and black bears in the southern Tetons and the potential effects on human-bear conflicts.

STUDY AREA

This research is being conducted in the southern Greater Yellowstone Ecosystem, specifically within the southern half of GTNP (Fig. 1) where grizzly bears are absent or occur infrequently and at low density. GTNP is located in northwest Wyoming, just south of Yellowstone National Park. The Teton Range runs north to south approximately 40 miles and is bordered to the west by Idaho's Teton

Valley, to the east by Jackson Hole, to the north by Yellowstone National Park, and to the south by the Snake River mountain range. Seven glacial lakes and associated drainages lie east of the range, creating numerous riparian corridors. The study area will focus from Leigh Canyon to the southern border of the park. The area is surrounded by National Forest to the East and West. The southern border is lined with several housing subdivisions, a ski resort and the National Elk Refuge. The study area encompasses the valley floor, riparian corridors along the Snake River, alpine lakes, and the peaks of the Teton Range. The habitat is very diverse, ranging from valley sagebrush-grassland meadows to whitebark pine and subalpine fir stands.

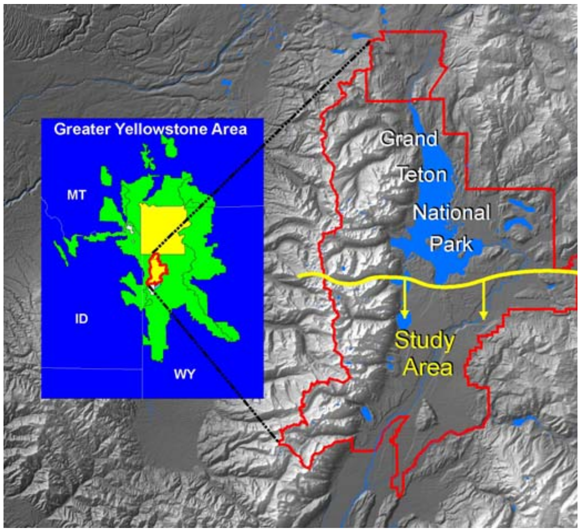

Fig. 1. Study area in Grand Teton National Park

✦ METHODS

Trapping and radio-collaring

All trapping was conducted with culvert traps at low elevations on or near the valley floor, in areas away from human activity. In 2005, trapping began 20 May and ended on 29 September. Traps were baited with meat from elk, moose, or deer roadkills within the park, and were set at 6 different locations for a total of 219 trap nights (Table 1). Captured bears were fitted with two ear tags and a pit tag, a vestigial pre-molar was taken for aging, hair and blood samples were obtained, and several measurements were taken. Those bears meeting sex, age and weight requirements were fitted with Telonics spread spectrum technology (SST) downloadable GPS radio collars. This technology allows for interrogation of the collar to collect stored GPS fixes on a regular schedule. All bears were released on site.

Site	Total Trap Nights	Successful Trap Nights
Whitegrass	26	0
Kaulfman JY	75	8
Jenny Lake	33	1
JY North	35	3
Lupine Meadows	26	0
Beaver Creek	24	0
Totals	**219**	**12**

Table 1. Black bear trap nights in Grand Teton National Park.

Female and male collars were programmed to record positions every 190 and 90 minutes, respectively. Telonics CR2-A collar decouplers were programmed to release collars from all individuals on October 1, 2006. The SST units were also programmed for downloading communication every Tuesday and Thursday from 0800hrs – 1200hrs MDT.

Generally, downloads occurred during weekly flights. From each week's data sets, a 24 hour period of locations was then chosen randomly for each bear, and all recorded positions were visited for detailed site analyses within a week's time of occupancy. Target sites were not visited when marked bears were nearby so as to not affect their movements.

Site Visits

Bear use of each site was determined by conducting searches within 15 meters of the locations. Each location was investigated for grazing, log rips, tree cambium tears, day beds, scats, digs, tree rubs, carcasses and several other feeding and non feeding activities (Appendix 1*). An established feeding site protocol developed by the IGBST (Mattson 1989, Mattson and Blasche 1990, Podruzny and Schwartz 2002) was followed. Detailed information included (1) physical site characteristics, (2) vegetation, and (3) black bear activity. Procedures included (1) a standard variable-radius forest overstory inventory plot, (2) cover and frequency of bear foods from microplots, (3) a plant species list with cover, abundance, and phenology ratings, (4) standard site parameters, and (5) feeding and bedding activity analysis (Mattson and Blasche 1990). We used Hitchcock and Cronquist (1973) as the definitive flora, Pfister et al. (1977) and Steele et al. (1983) for standard climax habitat types, and the classifications of Despain (1986) for forest cover types. All bear scats at feed sites and scats encountered during travels among sites were collected. Black bear food habits will be estimated from feeding site analyses and from laboratory analysis of scats. Bear species identification will be determined using polymerase chain reaction amplification and mitochondrial DNA determination following the procedures of Waits (1996). Evidence of various feeding activities is variably observable and persistent, and easily digestible food items can be under-documented in fecal analyses. By using both techniques, food items will be identified that one technique alone might miss. Collected scats will be air-dried and their volume measured by volumetric displacement. After softening by soaking in water, the scats will be washed through 2 screens (holes 0.125 and 0.0328 inches) to retain coarse and fine material. All items will be identified to species when possible and the percent volume for each item will be visually estimated (Mattson et al. 1991).

Forage items (>5%) identified in bear scats will be collected at bear feeding sites and random locations. Samples will be oven-dried at 40ºC for 48 hours and then stored in plastic bags in a freezer pending chemical analysis. If funding is available, dried samples will be analyzed for crude protein, dietary fiber, and ash (Pritchard and Robbins 1990). Root samples will also be analyzed for starch content. Because we did not know details of annual food habits prior to scat collection and analysis, we used previously published data (Barnes 1967, Graham 1978, Mealey 1980, Hammond 1983, Harting 1985, Mack 1988, Mattson et al. 1991, Holm 1998) to guide forage reference collections efforts the first year. In the following year, we will rely on results from scat analyses and published information. We anticipate that there will be approximately 12-15 major food items for the black bear.

✦ SOME PRELIMINARY RESULTS

Six female and 5 male black bears were trapped in 2005. Radio collars were deployed on 4 female and 3 male bears, although one male bear dropped its collar within a week of deployment (Table 2). Two females (22220 and 22212) had 2 cubs of the year each when captured. Collar downloading flights began on 21 June, after the first bear was collared, and continued weekly until 25 October. A total of nearly 2700 locations were gathered during this period (Table 2, Appendix 2*), about 150 of which were visited for detailed documentation of habitat, feed site, and behavioral attributes. Sites not visited will also eventually be analyzed through remote sensing techniques.

Two bears captured in 2005 had been captured previously. Bear 22046 was captured in July 2004 and fitted with a store-on-board GPS collar. She had been observed early in 2005 with a cub of the year, but was in estrus when caught in August, indicating her cub had died sometime previously. Bear 22212, a very old female, had been caught in the Tetons in August 2002 during an earlier black bear study led by the Wildlife Conservation Society, but was no longer wearing a radio collar when caught in 2005. The remaining nine bears had not been captured before.

On a somewhat subjective, body indexing scale, all bears appeared to be in good physical condition. More objectively, fat measurements showed gradual increases in fat content throughout the summer, as would be expected; none of the bears had outlying measurements (Fig 2). Age of bears caught ranged from 1 to 20 years, with only the oldest bear showing signs of severely worn teeth.

Capture	Bear					GPS	Habitat	
Date	ID	Sex	Age	Collar	Location	Position[1]	Plots[1]	Comment
19/6/05	22220	F	6	Y	Kaulfman	773	54	2 cubs of the year
02/7/05	22221	F	1	N	Kaulfman			
04/7/05	22222	M	2	N	Kaulfman			
16/7/05	22223	M	2	N	Kaulfman			Hunter killed in Idaho, 10/05
18/7/05	22224	M	2	Y	Kaulfman	560	12	
02/8/05	22046	F	5	Y	JY North	440	12	in estrus when captured
06/8/05	22225	M	5	Y	Kaulfman	78	4	Shed collar 8/11/05
12/8/05	22226	F	4	Y	JY North	362	16	
15/8/05	22227	F	2	N	Jenny L.			
21/9/05	22212	F	20	Y	JY North	20	0	2 cubs of the year
29/9/05	22228	M	8	Y	Kaulfman	207	25	
Totals		11				2483	123	

Table 2. Collar status, GPS positions, collection, and habitat plots documented for black bears, 2005

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*Appendixes are available upon request. Contact UW-NPS through our website www.uwyo.edu/uwnps

[1] positions collected and plots documented as of October 14, 2005

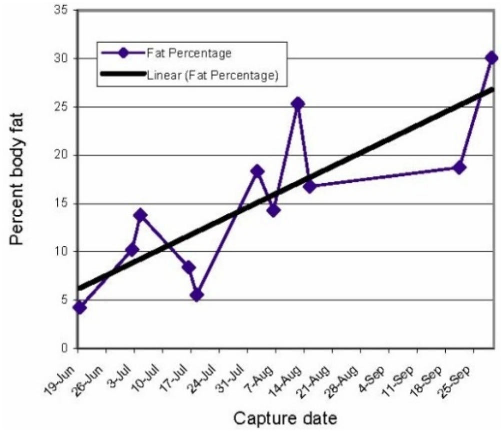

Fig. 2. Percent body fat of 11 individual black bears when captured.

As of the last flight on 25 October, all four collared females were denned in the Death Canyon area (Fig. 3). Bear 22228, an adult male, discovered 2 elk carcasses in mid to late October, and had not denned by this flight. Bear 22224, a subadult male, was northeast of the Gros Ventre Range's Green Mountain feeding on whitebark pine nuts in late October and had also not denned. Bear 22223, which was not collared, was harvested in Idaho by a hunter in October.

We documented bears using a wide variety of foods in 2005. Hawthorn (*Crataegus douglasii*) berries were an important food to three females in September and October (Fig. 4). An additional unmarked sow with 2 cubs of the year was also observed focusing on hawthorn berries during this time. Several of the females worked hawthorn thickets that were either along the Moose- Wilson road or in the general Moose-Wilson corridor area (Fig. 5). Hawthorn shrubs are not specific to this area but thrive in the southwestern part of the park. These preliminary data clearly illustrate the importance of this area and hawthorn to black bears.

Bear 22224, a two-year-old male, left the park and frequented a 4 mile stretch of the Fish Creek road to Teton Village corridor during July and August. This area shares many of the same excellent bear habitat features that occur in the southern end of the park, but has been somewhat of a mortality pit for park bears because of the many unsecured human food sources associated with residential development. In recent years, at least 3 park bears with no nuisance history in the park have been euthanized in this area by the Wyoming Game and Fish Department (WGFD). WGFD was

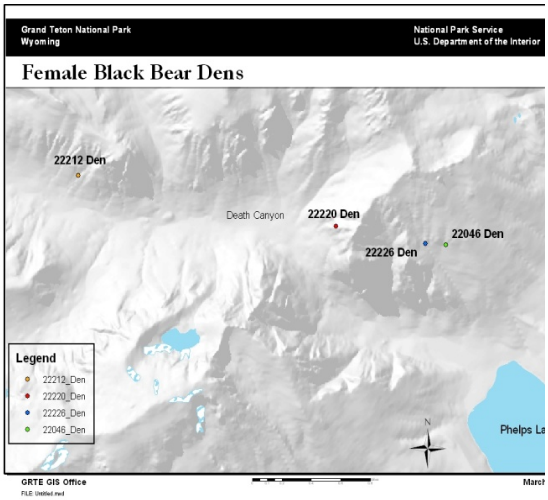

Figure 3. Den locations for 4 radio-marked female black bears.

Figure 4. Hawthorn berry

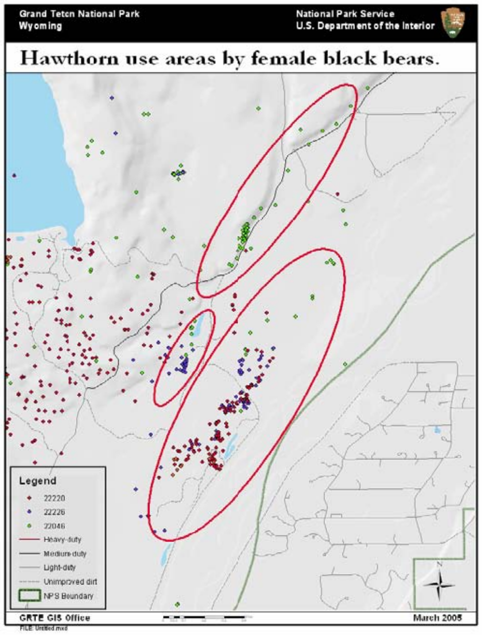

Fig. 5. Concentrated use of hawthorn by 3 black bears.

actively pursuing at least one nuisance bear during the period 22224 was in the area in 2005, but he was never trapped. He made a long, northeast movement to the Gros Ventre range by September (see Appendix 2*).

FUTURE DIRECTION

The 2006 field season will focus on conducting detailed habitat and feeding site inventories at sites downloaded from the bears currently radio-instrumented, as soon as they emerge from dens, and collaring additional bears to increase sample size as funding permits. In addition, high priority will be given to establishing an additional habitat field crew to increase our capacity for site visits and inventories.

✦ ACKNOWLEDGEMENTS

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MONTANE MEADOWS AS A MICROCOSM FOR PREDICTING GLOBAL CHANGE

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✦ INTRODUCTION

The last decade has witnessed intensifying, abrupt global climate change. Despite this impact, we know little about when, what, and how changes occur. Most climate research is limited to studies of the *abiotic* environment, focusing on atmospheric composition and carbon fluxes. These studies fail to provide adequate indicators of climate changes and their impact on habitats and species. Recent and intensifying ecological changes have generated interest in (Root et al. 2003, Thomas et al. 2004), and the need for tools that can help to prepare for global climate shifts. Changes in ecological (*biotic)* communities are excellent indicators of climate shifts, providing models to predict changes over time. Montane meadows, defined here as persistently non-forested habitats in mountain ecosystems, make up a small percentage of terrestrial habitats, but they are likely to exhibit changes much more rapidly than most other areas. These meadows are arrayed along a hydrological gradient (from hydric to mesic to xeric) and inhabited by short-lived plants and highly mobile animal species that can exhibit quick changes in distribution patterns relative to environmental changes. Thus, they can provide an early warning system for other ecosystems across the globe. Currently, the extent and range of climatic changes that will occur in montane meadows are unknown.

This research focuses on collection and analysis of long-term data to determine how climate variability affects species distribution patterns in the Greater Yellowstone Ecosystem. Specifically, I have been quantifying landscape-level and ecological variability in montane meadow communities across three trophic levels (plants, butterflies, and birds). The *central hypothesis* for the proposed research is that montane meadows and their associated species are particularly sensitive to climate variations and thus can serve as early indicators of regional climate change. I have formulated this hypothesis based upon preliminary findings suggesting that montane meadows exhibit variations in patch size and classification as a response to interannual variability of climate and that there are related changes in species distribution patterns. The major objective of the research is to document temporal changes in species distribution patterns relative to habitat changes. I am examining how interannual climate variability affects the bird, and butterfly communities. I hypothesize that species will show interannual shifts in distribution along the hydrological gradient that are correlated with habitat changes. For example, butterfly species normally associated with xeric meadows may move into more mesic sites in a hotter, drier year.

1996-2001 were extremely dry years in the Greater Yellowstone region (Fig. 1), so this is an excellent time period during which to examine interannual variations in species distribution patterns. Abiotic change is easy to quantify using satellite data (Fig. 2), and because the landscape is predominantly xeric, I expected that changes would manifest themselves quickly. The taxa examined each provide unique indications of how changes in climate affect the biotic community. I expected that changes in distribution for birds and butterflies would be quick and show high interannual variability, yet also show strong correlation with annual climatic changes. I expected changes in the plant community to take longer to manifest themselves, but to exhibit lower interannual variance. Here I focus on an examination of the interannual variation in bird and butterfly species distribution patterns. The importance of collecting and analyzing these data lies in providing both an understanding of interannual baseline variations and creating a long-term data archive for species distributions.

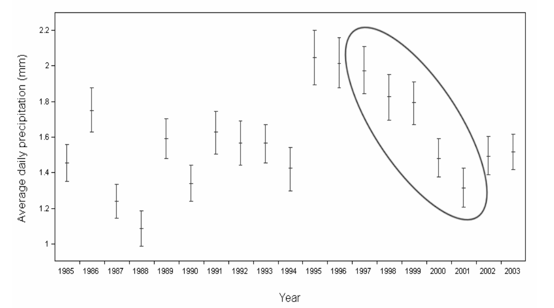

Figure 1. Average daily precipitation in Greater Yellowstone Ecosystem from 1985-2003 based on data from three National Climate Center weather stations (Stations 489905 (Yellowstone Park Mammoth), 485345 (Lake Yellowstone), and 486440 (Moran 5WNW)). Note drying trend from 1997-2001. (This figure is reprinted with publishers's permission from Debinski et al. 2006.)

✦ METHODS

Our sampling sites were identified using classification of remotely sensed multispectral imagery to identify a moisture gradient in montane meadows. Six meadow types were defined, ranging from extremely hydric sedge and willow (M1) to extremely xeric (M6) sagebrush meadows (Debinski et al., 2000). We sampled extensively starting in 1997 in two regions of the ecosystem: the northern region (Gallatin study area) that includes the Gallatin National Forest and the northwestern portion of Yellowstone National Park; and the southern region (Teton study area) that includes Grand Teton National Park and the Bridger-Teton National Forest. We established 55 sampling sites: 30 sites were located in the Gallatin study area (5 of each of the six meadow types), and 25 sites were located in the Teton study area (5 of each meadow type except for M4 meadows, which are not found there). We focused our work on low elevation meadows (2000-2500 m), to avoid introducing another environmental gradient (elevation) into our analysis. These sites were sampled annually for plants, butterflies, and birds until 2001, and surveys in the Teton region continued for birds and butterflies through 2005.

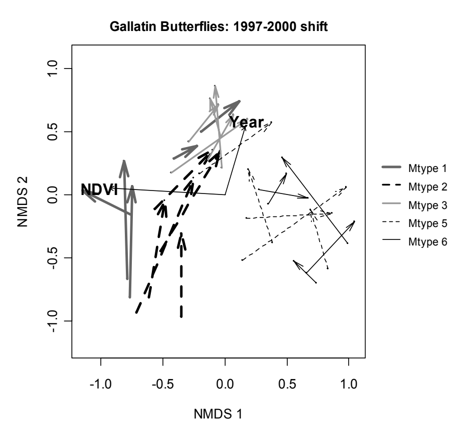

Figure 2. NMDS plot of Gallatin butterfly site-years for only 1997 and 2000 fitted with an NDVI and Year vector. Colored arrows point from 1997 to 2000 and the fitted Year vector summarizes the individual site-year shifts. The wet meadows (M-types 1, 2, and 3) appear to have a concurrent shift in the same direction, while the dry meadows (M-types 5 and 6) appear randomly oriented. (This figure is reprinted with publishers's permission from Debinski et al. 2006.)

Our research has shown that the meadow types do in fact have different ecological communities with respect to plants, butterflies, and birds (e.g., Debinski et al., 2002; Jakubauskas, 1998; Kindscher et al., 1998).

Species Characterization in Sample Sites

Bird data were collected from June to mid-July. Butterfly data were collected from mid-June to early-August. Birds and butterflies were surveyed two times during the field season at each of these sites. Birds (i.e., songbirds and woodpeckers) were surveyed between 0530-1030 hrs using 15 min. point counts in 50 m radius circular plots. Butterflies were surveyed between 0930-1630 hrs by two people netting for 20 minutes in 50 x 50 m plots at each sampling site (e.g., Debinski and Brussard, 1992). Surveys were limited to times when temperature is above 70 degrees F, wind is less than 16 km/hr, and the sun is not obscured by clouds. Butterfly sampling at each site was temporally spaced to cover the two major emergence periods during the summer.

Community Analysis

To detect trends in species composition over time, we used Non-metric multidimensional scaling (NMDS), an unconstrained ordination technique. NMDS can be used to ordinate sites in a two dimensional *similarity space* based on Bray-Curtis dissimilarity indices among sites. Each pair of points within the landscape represents a pair of replicates, and differences among times can be estimated by comparing the average temporal dissimilarity to the average replicates dissimilarity. Temporal trends can be described by the correlation of temporal dissimilarity with the length of time between samples. The closer sites are to each other in this plot, the more similar they are in species composition. The NMDS ordination is unconstrained in the sense that the spatial pattern of sites seen in the ordination plot is derived entirely from the structure of the species abundance data. Since each point in the ordination represents a *site-year* combination, among-year changes in species composition can be revealed. Environmental variables can then be overlayed onto the plot without disrupting the original ordination's integrity. Such variables can be represented by arrows or contour gradients, and the relative importance of each variable can be assessed. Specific species that have high loadings on one end of the gradient can also be identified, allowing for species-level assessments.

The rationale for comparing changes in species distribution across different taxonomic groups is that we expect each of the taxa to provide different, but important insights into how organisms with very different life history strategies respond to short-term variations in climate. We have developed a meadow habitat classification scheme and shown that plants, birds, and butterflies in this system show strong habitat affinities with specific meadow types (Kindscher *et al*., 1998, Jakubauskas *et al*., 1998, Debinski *et al*., 2002). Butterflies are capable of moving throughout the habitat matrix if conditions change, but they are also dependent upon the distribution of their host plants. Quantifying short-term distributional changes in each of these taxa, and comparing changes across taxa will provide a window into understanding how communities might be expected to change in distribution relative to longer-term (e.g., decadal) changes.

✦ RESULTS

Preliminary analysis of interannual meadow variation show some striking trends relative to climatic changes from a remotely sensed perspective (Debinski *et al*., 2000) and an ecological perspective. NMDS ordinations plot of butterfly, and bird communities have shown that similar M-types are closely grouped, indicating similar species compositions in those sites (Debinski et al., 2006). Because there was a significant drying trend in the region during 1997-2002, we decided to examine the data for temporal changes. There were no major changes over time for the bird data for either region or for the Teton butterfly data. However, Gallatin sites showed strong year effects for butterflies. Because year and short-term precipitation variables both showed significant correlations, we chose to examine these results graphically during a single time interval (1997-2000) when precipitation dropped drastically. We then connected only the 1997-2000 site-years with arrows (Fig. 2, Debinski et al., 2006). Nearly all of the mesic and hydric meadows (M1-M3) show a trend towards a drier state, whereas there is no such trend in the xeric sites. The species strongly showing year effects were *Phyciodes campestris*, *Speyeria atlantis hesperis*, *Pieris napi*, *Coenonympha haydenii*, *Boloria kriemheld* and *Oenius chryxus chryxus*. Most of these species show strong habitat affinities with mesic meadows. To further support the argument that mesic to hydic species are most vulnerable, two wetland species were missing from the Teton sites in 2004 --*Boloria frigga*, a relatively common wetland species and *Euphydryas gillettii*, a rare wetland habitat associate. These species had been observed annually in these sites since 1997, were not observed in any of the Teton sites in 2004, but were present in 2005. These changes may just be the random variation observed within one year, but they reinforce the emerging story that hydric and mesic meadows may be much more sensitive to short-term variations in climate such as droughts. It will be important to monitor these species during the next few years.

✦ SUMMARY

The Greater Yellowstone ecosystem is one of the largest "intact" ecosystems remaining in the temperate zones of the world (Keiter and Boyce, 1991), and thus provides an excellent opportunity to conduct natural experiments in a largely unmodified landscape. These long-term data and their analysis will be of critical significance given the projected warmer, drier conditions for montane environments in the Rocky Mountains. If smaller, more mesic to hydric meadows disappear, larger meadows will become more isolated and will serve as the only habitat source for demographic rescue effects (Brown and Kodric-Brown, 1977). It thus becomes important to monitor species distribution patterns over large spatial and temporal scales in order to unveil and predict some of these complex ecological interactions between climate variability, landscape, and biodiversity.

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EVIDENCE FOR SHOSHONEAN BIGHORN SHEEP TRAPPING AND EARLY HISTORIC OCCUPATION IN THE ABSAROKA MOUNTAINS OF NORTHWEST WYOMING

✦

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✦ INTRODUCTION

This report briefly summarizes 2004-2005 archaeological investigations at five sites located on Boulder Ridge in northwest Wyoming's Absaroka Range. Archaeological investigations on Boulder Ridge began in the 1970s when Frison (1978:258-262) documented site 48PA781, the Boulder Ridge Animal Trap (Figure 1C). In July 2003, a Northwest College (NWC) archaeological field school documented several additional sites on Boulder Ridge, including 48PA2646, a previously unrecorded feature interpreted as remains of a bighorn sheep trap (Finley and Finley 2004).

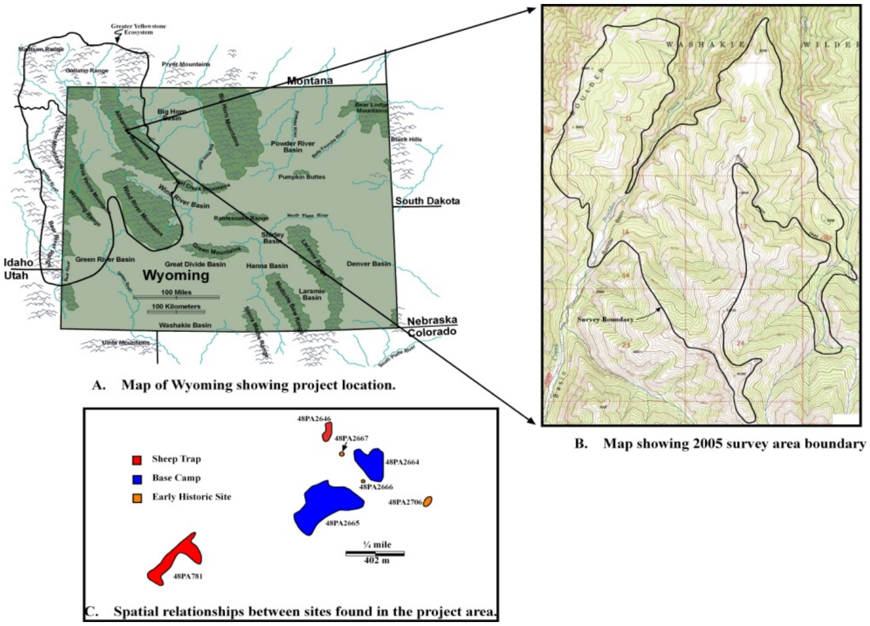
In August 2003 the Boulder Basin Wildfire burned more than 11,000 acres of Shoshone National Forest land including much of the study area. In 2004 a NWC field school re-visited the area to perform a fire damage assessment on the sites recorded the previous year. In close proximity to the feature recorded by the Finley's, the team found four sites that had escaped previous notice but had been exposed by the combustion of the forest duff layer. Two of the sites are believed to have resulted from occupation concurrent with sheep procurement activities; a site type never before documented in the archaeological record of Wyoming. The two other sites possessed unique artifact assemblages, including stone and metal tools and other Euro-American trade goods representing a very brief and poorly understood span of time known as the contact period. Efforts were made in 2005 to inventory a larger portion of the wildfire area and spend additional time investigating sites recorded in 2004. Several additional sites were located as a result of the 2005 investigations.

STUDY AREA

The study area is located in the Absaroka Mountains of northwest Wyoming (Figure 1A) and includes the mountainous and rugged terrain found in the middle reaches of Boulder and Castle creeks (Figure 1B). Prior to the 2003 fires the area was characterized by thick stands of spruce, fir and pine broken by open, grassy slopes and ridges. Elevation in the study area ranges between 2438m and 3050m.

✦ METHODS

Survey methods followed standard archaeological inventory procedures accepted by the State Historic Preservation Office (SHPO 2003) and the USFS. Areas of burned off duff having slopes under 30° were targeted and all identifiable spring and seep areas were sought out and inspected. Due to confidentiality issues, site locations are not shown in Figure 1B. Collected artifacts are now curated at the University of Wyoming Archaeological Repository, Laramie. Richard Hughes, Geochemical Research Laboratory, performed x-ray fluorescence analysis.



A. Map of Wyoming showing project location.

B. Map showing 2005 survey area boundary

C. Spatial relationships between sites found in the project area.

Figure 1. Map showing (A) location of study area in GYE; (B) Survey area boundaries, (C) Spatial relationships of sites discussed in this report.

Background

Although the project area lies within the traditional territory of both Crow and Shoshone Indians, several sites discussed below appear to be Shoshonean and for this reason, aspects of Shoshone ethnography, history, and archaeology are briefly reviewed. This is not to imply that the region was not used by the Crow as well as other Native American groups (Nabokov and Lorendorf 2004).

Within the historic period the Bighorn River was often considered the northeast boundary of Eastern Shoshone territory. Areas to the west, including the Yellowstone-Absaroka plateaus, upper Snake, Salmon, Missouri and Yellowstone rivers, the Wyoming Basin and peripheral northern Great Basin were used by several Shoshonean groups for subsistence, trade, and warfare (Shimkin 1986).

Ethnographic studies show that 19th century Shoshone social structure was based on dietary mainstays, which by virtue of local environment were a general reflection of group territory (Lowie 1909, Hultkrantz 1961). Because the names carried no political affiliation, and individuals or family groups cycled from one dietary region to another, it was not uncommon for movement to lead to dietary change and a change of group name. A few commonly cited Northern Shoshone groups are: Salmon Eaters of the Snake River; Groundhog (marmot) Eaters around Boise; and the Sheep Eaters (Tukudeka) of the Idaho Sawtooths (Murphy and Murphy 1986:287). From his work with the Eastern Shoshone, Shimkin (1986: 309) discusses two groups, the Buffalo Eaters (Sage Brush People) of the Green and Wind River valleys and plains, and the Mountain Sheep Eaters (Mountaineers) of eastern Idaho, southern Montana and the GYE of northwest Wyoming. While ethnographic sources provide various amounts of information on the above groups that for the Sheep Eaters is somewhat scanty, with unclear distinctions between the Northern and Eastern Shoshone groups, and no mention of sheep trap use.

A similar situation is found in the early exploration period literature. No first or even second hand trapper or trader account mentions sheep trapping. The few references to “Sheep Eaters” or “Mountain Snakes” from these sources provide, at best, limited and inconclusive information regarding material culture, group size and range (Hughes 2000). Hopefully, the associations discussed in the following report will provide a better understanding of at least some of the high elevation animal procurement features in the GYE and the poorly understood groups responsible for their construction.

Larson and Kornfeld (1994:200-210) have reviewed the theoretical issues related to associating archaeological sites or artifact assemblages with a cultural group. They argue for recognition of a suite of “culturally diagnostic” artifacts indicative of prehistoric/early historic Shoshonean occupation in western Wyoming. The association is based on the repetitious occurrence of several artifact types, some of which are traceable southwestward to Shoshonean sites in the Great Basin. The artifact types include: side-and-base-notched (tri-notched) and Cottonwood triangular projectile points (see Jennings 1986:113-119), Intermountain ceramic vessels (Mulloy 1958), bilaterally re-sharpened bifaces known as "Shoshone knives" (Frison 1971:269), steatite vessels and or pipes (Frison 1982), wooden structural remains including bighorn sheep and antelope traps, cribbed log structures, and conical pole lodges or "wickiups". Although some of the artifact types may be more common to some geographic areas than others, the overall artifact suite is employed here to infer Shoshonean occupation (Figure 2).

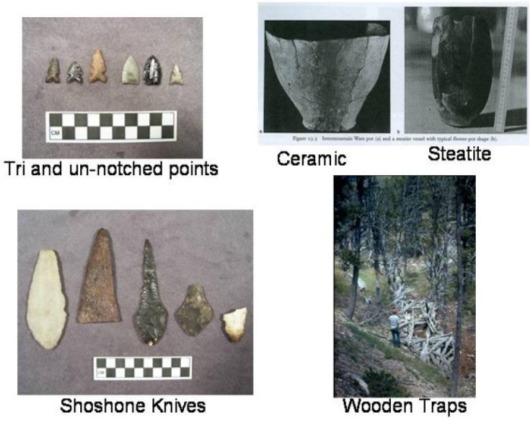


Figure 2. Artifacts diagnostic of Shoshonean occupation (After Larson and Kornfeld, 1994).

Several examples of a poorly understood artifact known as *teshoa* (an unhafted Shoshone woman's knife) were found at four of the five sites discussed below and may be of some importance to cultural and temporal interpretation. Shoshone women were observed using teshoa in 1872 by Joseph Leidy (1873) while on paleontological reconnaissance near Fort Bridger, Wyoming (Figure 3). Shimkin (1986:322) also mentions a "split cobble" scraper used by the Eastern Shoshone to process hides. Butler (1978) briefly mentions and provides an illustration of teshoa, but does not provide a cultural or temporal context. Eyman (1968) discusses teshoa in some detail and provides evidence that the basic design is represented as a common tool type worldwide. Perhaps more importantly teshoa are not reported from other late period Shoshonean sites in the region (Eden-Farson AD 1720±100, Frison 1971; Level 1 of Mummy Cave AD 1610±90,Husted and Edgar 2002, Bugas-Holding AD 1510±100, Marcel Kornfeld, personal communication). In the following context teshoa may have been briefly used in a limited geographic area and could reflect an early historic or historic need for a simple, though effective and expedient tool, possibly due to an increased demand for tanned hides.

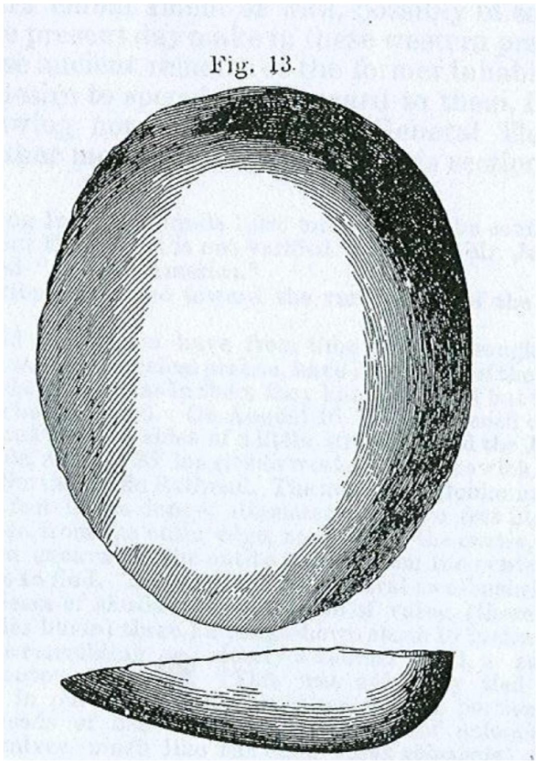


Figure 3. Illustration of a teshoa, from Leidy 1873. Caption reads "A modern stone implement of gray quartzite; a simple flake from a drift –pebble of the Uintahs. Called by the Shoshone Indians a "teshoa," and used by them as a scraper in dressing skins. Tow views: one-half size. One of half dozen similar specimens obtained from the Shoshones."

Trade items found at several sites discussed below lead to questions involving the timing of the replacement of stone tools by metal ones of Native or Euro-American manufacture. It will become apparent to the reader that the timing of the initial arrival and spread of early historic trade goods into the Rocky Mountains is poorly understood.

Bighorn Sheep Traps

Bighorn sheep traps, hunting blinds, and game fences in and around Yellowstone National Park were described as early as the 1880s (Norris 1880) but have continued as a focus of interest up to the present day (Clayton 1926, Honess and Frost 1942, Dominick 1964, Frison 1978, Frison et al 1990, Frison 2004). Sheep traps and related features occupy a number of topographic settings and it is highly likely that their positioning was deliberate and exploited both physical features of the landscape and the behavioral characteristics of the animals they were designed to harvest (Frison 2004). In the only systematic study to date Frison et al (1990) found that traps are typically made from standing or deadfall timber and rocks and have no evidence for metal tool use in their manufacture. They describe two basic designs; a possible earlier design of a simple V shape, and a later design that is a modified V or hook shape that may have employed a terminal curve to exploit the animal's tendency to flee down slope. Both types have constricting wings leading to a catch pen (Figure 4).

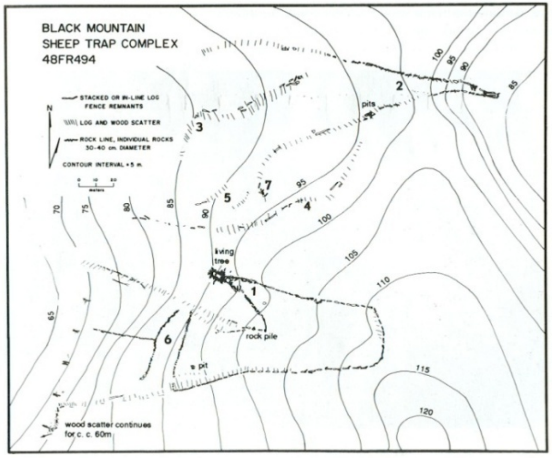


Figure 4. Sketch map, Black Mountain bighorn sheep traps. Taken from Frison et al. 1990.

Catch pens are almost always constructed from logs because of the strength necessary to hold one or two animals prior to killing. Frison (2004:158) argues that a small rise or ramp located just before the catch pen could be a diagnostic characteristic as it may have lessened the animals' tendency to spook and turn prior to jumping into the structure. Approximately 100 km north of the study area, in Sunlight Basin, an animal procurement feature believed to be a sheep trap was recently found (2006) that exploited a large cleft in the surrounding bedrock as a catch pen (Figure 5).

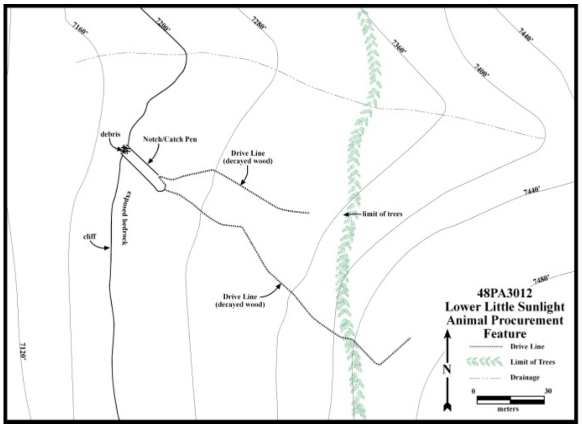


Figure 5. Map of trap that exploits bedrock cleft as catch-pen.

Frison et.al (1990) used deteriorated trap features found at high elevations represented by rock alignments and pitch-log remnants to infer a time depth of up to 500 years for this procurement strategy. In the same study, Charles Reher conducted dendrochronologic assessment of younger and better-preserved traps from the upper Wind River Valley and estimated their age at between AD 1770 and 1820. The procurement feature closest to the Boulder Ridge base camps (48PA2646, Figure 1C) is probably of this younger age, as portions of it are not totally weathered away and still visible (Figure 6).

Figure 6. Photo of wing section at site 48PA2646.

Little cultural material has been found in association with bighorn sheep traps. A few ram skulls exist in museums and private collections that were evidently placed in tree branches at several traps, while one or two clubs reportedly found near traps and possibly used for dispatching animals, have also been reported (Frison 2004:161). An unknown number of bighorn sheep traps are still in existence today. The outlines of these now highly weathered and deteriorating structures probably do not convey the amount of time, effort and know-how necessary to construct and successfully operate such a feature. All are associated with old growth forest and the timber from which they are constructed is entering advanced stages of decay.

✦ FINDINGS

Approximately 1000 acres of burned area was inventoried (Figure 1B). Eight additional sites were recorded, seven of which are small, limited activity areas and are discussed in the main report of investigations. The five sites in close proximity to 48PA2646 are described here. All of these sites are considered eligible for nomination to the National Register of Historic Places.

Site: 48PA2664

This site is a 200 m x 300 m campsite/processing area situated on a hill slope adjacent to a small spring. Artifacts consist of chipped stone and bone scatters as well as multiple hearth locations. Areas of high density chipped stone were initially encountered on the site but these disappeared within the first season of exposure, probably from unauthorized artifact collection. Artifacts of note consist of tri-notched and un-notched projectile points, bifaces, scrapers and other chipped stone tools, both complete and fragmentary teshoa, shaft abraders and carved bone disks (Figure 7). One Rose Spring point and one probable Late Archaic point indicate the site was occupied prior to the most recent episode marked by the tri-notched and un-notched projectile points. No trade items were found at this site indicating that occupations may have ceased prior to the contact period. Obsidian artifacts have been sourced to several localities including Grassy Lake (n=1), Obsidian Cliff (n=3) in Yellowstone Park, and the Crescent H source (n=1) in Jackson Hole.

Thousands of bone fragments littered the surface of the site. Identified species include bighorn sheep, elk, medium and large artiodactyl. Part of the faunal assemblage is comprised of eight badly burned sheep crania found in close proximity to the base of a large tree, a context suggesting they were deliberately cached (Figure 8). A similar pattern involving cached skulls has been described by Frison (2004:160) from a site located on a tributary of the upper Greybull River in northwest Wyoming. The two carved bone disks were found in direct association with the sheep crania.

Figure 7. Selected artifacts from 48PA2664; a-d tri-notched projectile points, e-f un-notched projectile points, g Rose Spring point, h-i archaic points, j-r stone tools, s teshoa, t-u shaft abraders, v unknown tool with highly polished edge, w notched bone, x-y carved bone disks.

Figure 8. Three of eight badly burned bighorn sheep skulls found near the base of a large tree at 48PA2664.

Site: 48PA2665

Site 48PA2665 is a campsite about 200 x 200 m in size situated on both flat and sloped topography adjacent to a spring. Several areas containing flake, tool, or bone concentrations were observed and multiple tool caches and fire hearths were noted. High-density bone concentrations at several locations indicate probable processing areas. Other features likely represent lodge localities. A total of 142 chipped stone tools were recovered along with ground and carved stone objects, ceramics, rim fragments from a steatite vessel, and a bone flesher. Some examples of these items are shown in Figure 9.

Nearly 800 identified faunal remains represent only a fraction of the total, initially estimated in the thousands. Bighorn sheep (n=70), bison (n=16) and elk (n=4) are represented with the most common remains being medium (n=666) and large (n=26) artiodactyl.

Three localities were identified as sites where lodges once existed. One of these, known as the cut-fill lodge, was created by cutting into an 18°-20° hillside and spreading the displaced sediment on the downhill side to create a bermed, flattened floor suitable for habitation. A similar construction pattern has been documented in the Upper Green River Basin where prehistoric Shoshonean lodges were found in association with evidence for a communal antelope kill (Frison 1971). Artifacts recovered from the cut-fill lodge include a shaft abrader, a teshoa, chipped-stone debitage, butchered sheep bone, a tri-notched projectile point and a broken trade bead. A second lodge locality is marked by a several meter wide circular outline of stones (Figure 10). Projectile points and a number of other tools were found within the outline while other artifacts, a flint knappers pile, and a complete Intermountain ceramic vessel were found just outside.

Figure 9. Selected artifacts from 48PA2665: a-g tri-notched and h-l Cottonwood Triangular projectile points, m-o point pre-forms, p Shoshone knife, q-s teshoa, t biface, u-z, end and side-scrapers, aa drill, bb-dd utilized flakes, ee-gg large retouched blades, hh-ii steatite vessel fragments, jj flat-bottomed Intermountain ceramic vessel, kk shaft abrader.

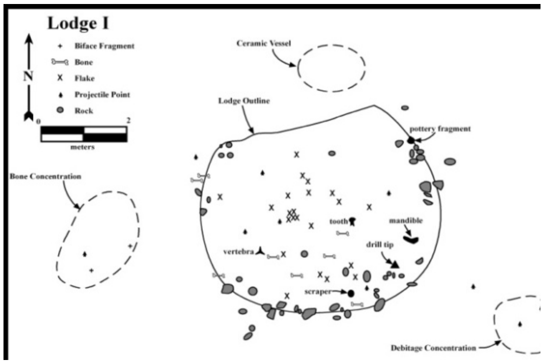


Figure 10. Plan view of Lodge I at 48PA2665.

Obsidian artifacts from 48PA2665 have been sourced to Obsidian Cliff (n=14), two sources in Jackson Hole (n=16), Bear Gulch (n=2) in eastern Idaho, and Beatys Butte (n=1) in southern Oregon, approximately 800 km west.

Although all common artifacts found at 48PA2665 are made of stone, a small number of trade items were also present. These occurred as isolated concentrations and include the above mentioned trade bead in the lodge, two trade bead scatters (each under 10x10 m area) and another small area with several pieces of badly rusted sheet-iron and a uniquely edge abraded cobble. The overall distribution of features, artifact groupings and concentrations might suggest either 1) a pre-contact setting, as artifact classes (i.e., points, drills, scrapers, knives) are represented by stone technology, with a more limited post contact occupation superimposed later in time; or 2) an early post-contact setting when stone technology was still predominant and only limited amounts of trade goods were available in the region. The single obsidian artifact sourced to Beatys Butte Oregon may imply the use of horses.

Site: 48PA2666

This site is a small campsite approximately 10 x 10 m in size and located on a low inter-stream divide. Artifacts include tri-notched and cottonwood triangular projectile points, a teshoa, a bent wire object believed to be an awl, trade beads, a “glob” of trade vermillion, a probable gun flint, a machine screw identical to types used in late 18th and early 19th century gunlocks, and butchered bighorn sheep bone Figure 11. The site is less than 1 km from 48PA2646 (Figure 1C) but there is no basis to relate the two. Although a suite of culturally diagnostic artifacts is not present, the three projectile points and the teshoa might suggest an early historic Shoshonean association. All three of the obsidian projectile points from this site have been sourced to Obsidian Cliff. Bighorn sheep bone remaining at the site can provide information pertaining to diet as well as carcass processing and treatment. The small size of the activity area may indicate use of a temporary structure. Sites of this age are rare in the region and provide information about a poorly understood period in Native American history.

Figure 11. Selected artifacts from 48PA2666: a-c tri-notched and un-notched projectile points, d teshoa, e-f trade beads, g gunflint, h machine screw, i bent wire object.

Site: 48PA2667

This is a campsite and bighorn sheep processing area about 20 x 20 m in size, situated on a 20-degree slope within about 250 m of site

48PA2646 (Figure 1C). Cultural material includes hundreds of obsidian flakes, an un-notched projectile point sourced to Obsidian Cliff, four types of trade beads, sheet iron, butchered bighorn sheep (n=20) and medium artiodactyl (n=63) bone, and up to 200 pieces of additional unidentifiable bone of the same size class (Figure 12). Six late-term or newborn long bone shaft fragments indicate occupation coincident with the late spring lambing period. The metal items are unique as one (Figure 12b), characterized by an angular edge, could be discard generated during metal arrow point manufacture (Hansen 1972). Another (Figure 12d) could have resulted from deliberate bending or the manner in which it was cut, possibly with a chisel or shears. Together these artifacts indicate an early historic, Native American cultural context. Slope wash processes are currently re-burying the site.

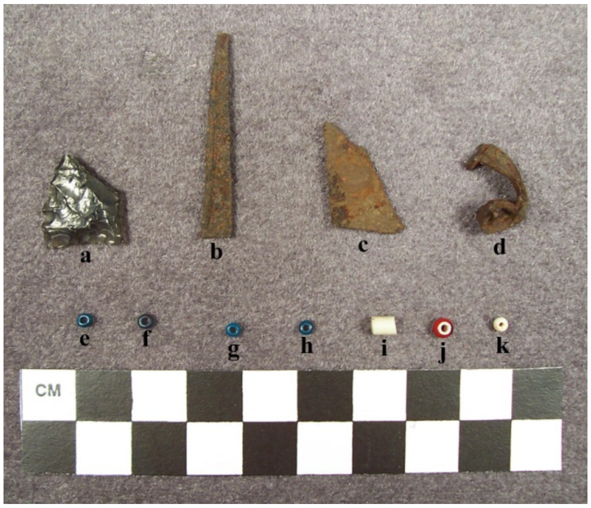


Figure 12. Selected artifacts from 48PA2667; a un-notched projectile point fragment, b-d cut and twisted metal, e-k trade beads.

Site: 48PA2706

This is a multi-component surface site approximately 30 x 120 m in size, situated on a remote and inaccessible flat between the base of a 50°+ slope and the edge of a vertical canyon. Three distinct activity areas characterize the site: a lodge/artifact scatter, a chipped stone/metal-working area, and a probable dump. The Area 1 lodge is marked by a 3x4 m outline of large tabular stones. Within the outline was found trade beads (Figure 13a) a tri-notched projectile point (Figure 13b) and a brass button (Figure 13c), along with chipped stone flakes and other stone tools. The brass button is about 7/8 inch in diameter, has a smooth face, and is of the footless shank variety with no re-strike anvil seam. An embossed eagle insignia is at top center, below this and slightly off center left are stars and dots on either side of the word "BEST." The manufacturing technique of this button dates from between 1785-1800 (Olsen 1963).

Area 2 is about 12m^2 in extent and provides evidence for early historic Native American metalworking. Artifacts (Figure 13d-k) include trade beads, an un-notched projectile point, gunflint, sheet copper, three heavily edge ground and battered cobbles, approximately 10 pieces of sheet iron, chipped stone flakes and butchered sheep bone. One of these cobbles (k) shows signs of heavy abrasion, battering and divoting, indicating it was used to deliver heavy blows to a resistant cylindrical object such as an iron chisel.

Figure 13. Selected artifacts from 48PA2706. Area 1: a trade beads, b tri-notched projectile point, c brass button, Area 2: d trade beads, e un-notched projectile point, f gun flint, g trade beads, h sheet copper, i-k edge-abraded and battered cobbles.

Area 4 is a tear-shaped, 4.5x4m^2 artifact concentration located on an 18° slope adjacent to an ephemeral stream cut. The shape of the concentration indicates the artifacts may have either been deliberately dumped or were in a container and were subsequently affected by slope wash processes after the container deteriorated. In addition to artifacts shown in Figure 14, about 500 trade beads, 200 chert and obsidian flakes, several vermillion globs, 30 pieces of sheet iron and wire scrap, and several additional brass tacks were found.

Figure 14. Selected artifacts from Area 4 48PA2706; a-c stone projectile points, d-g stone projectile point pre-forms, i-j teshoa, k-l pipe pre-form, m-n shaft abraders, o trade beads, p lock bridle, q sear return spring, r fishhook, s awl, t possible trade knife handle, u flesher bit, v brass tack, w punched tin plate, x – aa metal projectile points, bb metal projectile point pre-form.

Several trade items provide tentative age estimates. The brass tacks are square-cut with a reinforced shank/dome junction, indicating pre-1850 British manufacture (Engages 1982, Hanson 1984). Fishhooks were popular trade items from an early date (Astoria Inventories of 1813). Those manufactured prior to 1850 were similar to modern types though the shank was not eyed for line attachment (Engages 1980). Such a large hook may seem out of place in this particular setting, but as an account from a fur trader (Ross 1956) in what is today Washington state shows, Native Americans sometimes used trade items in non-traditional but creative ways..... "Wolf hunting as well as bear hunting occasionally occupies the attention of the natives…the wolf is far more difficult to decoy or entrap, being shy, guarded and suspicious. For this purpose, three cod hooks are generally tied together back to back, baited, and then fixed with a line to the branch of a tree so that the hooks are suspended in the air at the distance of four or five feet from the ground. To get hold of the bait the animal has to leap up, and the moment the hooks catch their hold it finds itself either in a standing or suspended position, which deprives the animal of its strength, neither can it in that posture cut the line; it is generally caught, sometimes dead, sometimes alive...." Alexander Ross, Spokane House, 1817 in Ross (1956).

The awl is not the common square stock, double pointed, offset trade awl (Engages 1971), but instead is circular in cross-section, pointed at one end and flattened at the other. The lock bridle and sear return spring are parts of a common side-action or bar style flint or percussion lock used from about 1800 to the 1870s, with replacement parts still available as late as 1907 (Engages 1986). The gunflint is Indian-made from Absaroka green chert but provides little information other than that flintlocks were in use (Kenmotsu 1990). The flesher bit is about one and three-quarters inch wide and is identical to iron bits typically used in elk-horn fleshers (Hanson 1970, Shimkin 1986). The punched tin plate appears to be of non-Indian manufacture and could have originated from a number of sources. The cut edges of the tin plate and lighter-gauge metal arrow points have sharp intersecting angles consistent with those cut by scissors, a common early trade item (Astoria inventories 1813, St. Louis Mercantile Library Association 2006). The carved stone object is most likely a pipe pre-form and possesses markings consistent with having been shaped with a file. The stone may have originated locally from the contact zone between the Wiggins Formation and the Trout Peak Trachyandesite (Love and Christiansen 1985).

Artifacts recovered from 48PA2706 represent a brief period in history when the ability to work stone had not yet disappeared and the gun had not yet replaced the bow and arrow. Preliminary age estimates indicate site occupation between the early- and mid- 1800s. The trade items certainly indicate access to a supply of Euro-American trade goods, perhaps during the Rocky Mountain fur trade period that lasted from about 1820 to 1840. Although side and base-notched projectile points - and eight teshoa – are present, this site clearly post-dates those used by Larson and Kornfeld to illustrate their case for a diagnostic suite of Shoshonean artifacts. For this reason it may be more appropriate to classify it as early historic Native American, with Shoshonean indicators. Obsidian artifacts from the site have been sourced to Obsidian Cliff (n=8) and Jackson Hole (n=1), as well as Packsaddle Creek (n=1) in the Big Hole Mountains of eastern Idaho.

✦ CONCLUSIONS

The archaeological discoveries within the Boulder Basin burn area bring to light a number of concerns for both archaeologists and land managers.

1) Sheep traps are the *visible component of a site complex* (Figure 15). The site complex can consist of an animal procurement feature, processing area, and base camp. The concept of site complex, is not new (Frison 1991:160), but is important when considering the impact of various land management practices. The Boulder Ridge sites demonstrate a high potential for processing areas or base camps not

far from where animal procurement features are known to exist.

Climatic patterns believed related to an increase in wildfire frequency since the 1980s in the western U.S. may lead to continued declines in forest health (Westerling et al 2006). The lack of post-fire cultural resource investigation in wildfire areas has probably resulted in a loss of information related to prehistoric use of high-elevation environments and may result in more loss in the future. Post-burn cultural resource inventories can provide a basis to amend land management policy to reflect the long-term obligation of management agencies.

2) Forest floor duff, otherwise known as the *O horizon* (Birkeland 1984), is a viable burial medium for archaeological sites in forested environments. Ground visibility in forested environments is problematic for archaeologists because vegetation and the O horizon conceal artifacts and features that form the basis of archaeological site identification. Site visibility in forested environments influences management decisions related to timber harvesting, controlled burns, and post-fire management of natural burns.

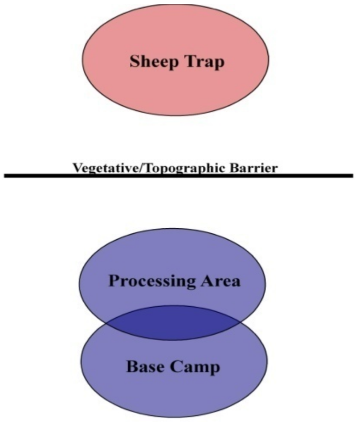


Figure 15. Model of bighorn sheep trap site complex.

3) The suite of culturally diagnostic artifacts from 48PA2664 and 48PA2665 strengthen arguments for the Shoshonean origin of wooden animal procurement features on Boulder Ridge and other areas. Although their place in the material culture remains unclear, the teshoa described in this report are associated with a generally accepted suite of artifacts that indicate a Shoshonean affiliation. The ties may be reinforced by Leidy's 1870s observation in the upper Green River Basin, as well as Shimkin's reported use by the "Plains" Shoshone. For the Boulder Ridge sites the presence of teshoa in a protohistoric/pre-contact association and an early historic/post contact association suggests their use was very late and short-lived.

4) Artifact assemblages from the two base campsites indicate Shoshonean groups living in high-elevation, warm-season settings shared a closely related material culture - including identical projectile point and Shoshone knife styles, Intermountain ceramics and steatite use - with Shoshonean groups living in lower-elevation settings at other times of the year. In addition, the geographic range implied by the Boulder Ridge obsidian sourcing, sheep trap occurrences, steatite, and teshoa indicate that Shoshonean "Sheep Eater" groups shared common cultural traits and subsistence strategies encompassing a wide area. Over the course of several seasons these groups would have exploited food types that would potentially identify them with other group names (Figure 16). This pattern is consistent with the ethno-historically based models of a relatively homogeneous inter-regional Shoshonean adaptation (Murphy and Murphy 1986, Shimkin 1986) and may outline pre-contact group ranges that became disrupted after historic contact.

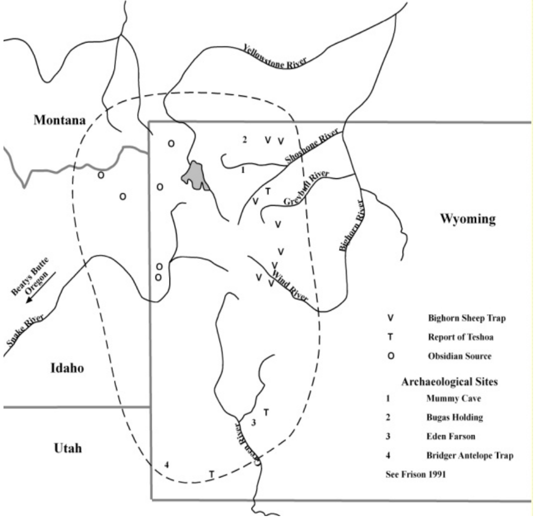


Figure 16. Schematic map showing obsidian sources, wooden traps, and selected archaeological sites mentioned in this report. Dashed line shows inferred range of groups sharing similar subsistence practices.

5) The three early historic sites (PA2666, PA2667, PA2706) represent rare occurrences in the archaeological record of the Central Rocky Mountains. Based on this brief analysis, they could date from as early as the late 1700s to as late as 1850. Native American archaeological sites representing the early 19th century are few; with finds often from poor contexts such as a grass-roots zone, or the churned floor of a cave or rock shelter. Although it is well accepted that trade goods were diffused in advance of the first Euro-American traders and

explorers, very few primary accounts describe the early contact-period native culture of the Rocky Mountains. Lewis and Clark's account is one of the best, in light of the above cultural and temporal contexts, as they chronicle a surprising number of Euro-American items in possession of a group of Upper Salmon River (Lemhi) Shoshone at a time (August 23, 1805) well before the heyday of the Rocky Mountain fur trade:

"The metal which we found in possession of these people consi[s]ted of a few indifferent knives, a few brass kettles some arm bands of iron and brass, a few buttons, woarn (sic) as ornaments in their hair, a spear or two of a foot in length and some iron and brass arrow points which they imformed (sic) me they obtained in exchange for horses from the Crow or Rocky Mountain Indians on the yellowstone River. the bridlebits and stirreps (sic) they obtained from the Spanyards (sic), tho these were but few. many of them made use of flint for knives, and with this instrument, skined (sic) the animals they killed, dressed their fish and made their arrows; in short they used it fir (sic) every purpose to which the knife is applied. this flint is of no regular form, and if they can only obtain a part of it, an inch or two in length that will cut they are satisfied. they renew the edge by flecking off the flint by means of the point of an Elk's or deer's horn. with the point of a deer or Elk's horn they also form their arrow points of the flint, with a quickness and neatness that is really astonishing. we found no axes or hatches among them; what wood they cut was done either with a stone or Elk's horn.the latter they use always to rive or split their wood. their culinary eutensils (sic) exclusive of the brass kettle before mentioned consist of pots in the form of a jar made either of earth [ceramic], or of a white soft stone [steatite] which becomes black and very hard by birning (sic), and is found in the hills near the three forks of the Missouri between Madison's and Gallitin's (sic) rivers" (Thwaites 1905:19).

6) Native metal working, including hand-hammering metal and smoothing with stone tools to produce lance or projectile points, has been inferred from surface finds (Frison 1991:123, Crabtree 1968). Three of the five sites discussed above possess either direct or indirect evidence for such activity, indicating that it was a relatively common practice, although a short-lived one, which contributed to the ultimate replacement of stone technology.

7) Relationships between the two animal procurement features on Boulder Ridge and the two base camp occupations may never be firmly understood. The three small, early historic camps are located away from and appear to post-date the larger base camps. When combined, the occupations may imply multi-generational familiarity with the area, as possibly learned through descent, and represent re-occupation of a favored area, whose use, perhaps within a certain band, extended into the Prehistoric period.

✦ EPILOGUE

Through a grant from Indiana University's New Frontiers in the Arts and Humanities, archaeological research continued on Boulder Ridge during the summer of 2006. Under a cooperative agreement between the Shoshone National Forest and the Office of the Wyoming State Archaeologist, Dr. Laura Scheiber (Indiana University) and Judson Finley (Washington State University) led a team of students from Indiana University, Northwest College (Powell, Wyoming), the Universities of Utah, Oregon, Montana, and the American University in Washington D.C. The fieldwork combined survey-grade EDM and GPS equipment and in-field attribute-based artifact analysis to map more than 1500 artifact clusters at 48PA2665 and over 800 surface artifacts at 48PA2706.

Mapping and recording artifacts at 48PA2706. Left to Right: Jake Enk, Laura Scheiber, Sara Newman, Gina Zavala, Judson Finley, Ashley Howder; photo by Dan Eakin

✦ ACKNOWLEDGMENTS

A debt of gratitude is owed to a number of organizations for their assistance thus far in the Boulder Ridge area. These include the University of Wyoming/National Park Service Research Center, Wyoming Department of State Parks and Cultural Resources/Office of the Wyoming State Archaeologist, Shoshone National Forest, Northwest College, Bighorn Canyon National Recreation Area,

National Park Service, Wyoming Archaeological Society, and Lee Livingston Outfitters. Individuals contributing time to the project include Chris Finley, Vickie Finley, Forrest Green, George Frison, Julie Eakin, Ann Johnson, Crystal Hazen, Tim Brown, Brandi Jessup, Richard Adams, John Laughlin, Ardeth Hahn, Jud Finley, Laura Scheiber, Marcel Kornfeld, Allen Madril, John Allen, Roger Green, Steve Potter, and Steve Rhonne.

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TECTONIC EVOLUTION OF THE HIGH PRESSURE GRANULITES IN THE TETONS; THE EARLIEST RECORD FOR HIMALAYAN-STYLE TECTONICS IN THE WORLD

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Our field season in August 2005 consisted of mapping an area from Hidden Corral in the S. Fork Bitch Creek (which is not in the Grand Teton National Park) to Moose Basin. In addition to mapping and sampling in Moose Basin area we made an important traverse along the head of the cirque around Camp Lake (which lies just west of the Park).

As the result of our fieldwork in 2004 and 2005 we now recognize four distinct units in the basement gneiss of the Northern Teton Range (Fig. 1). One unit, which we call the Moose Basin gneiss, consists of intensely interfolded pelitic and mafic gneisses that locally retain evidence of high-pressure, high-temperature metamorphism. The Moose Basin gneiss lies upon the leucogranitic Webb Canyon gneiss, which lacks any sign of this high-pressure metamorphism. The other two units in the northern Teton Range are the layered gneiss and the augen gneiss. Both of these are quartzo-feldspathic gneisses. The augen gneiss is distinctive in that it clearly retains evidence of an igneous parent. Such evidence is cryptic in the layered gneiss. Neither unit shows evidence for the high-P metamorphism seen in the Moose Basin gneiss.

During our 2005 fieldwork we collected petrologic samples of the Moose Basin gneiss in upper Moose basin and measured structural features in the Moose Basin gneiss in a traverse from Moose Basin to west of Camp Lake. This involved measuring the orientation of planar features, linear features, and small-scale folds within the gneiss. We discovered that the Moose Basin gneiss occupies in a broad synform, the axis of which lies less than a kilometer west of Camp Lake (Fig 1). The Webb Canyon

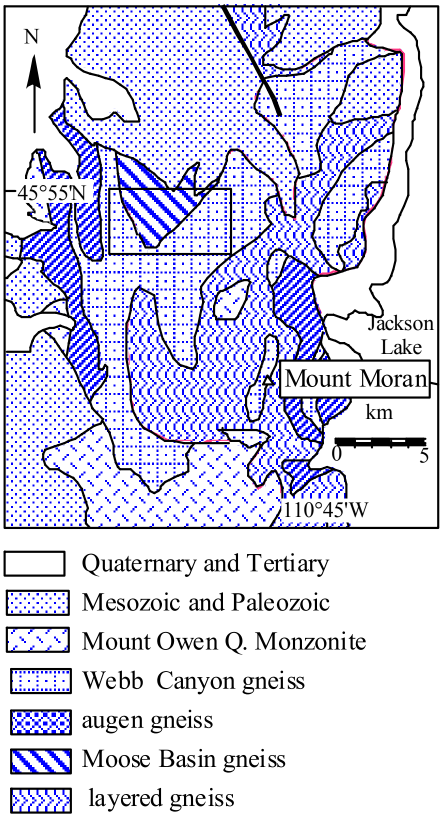

Figure 1. Geologic map of the Northern Teton range revised after Reed (1973). Small box shows the approximate location of the block diagram in Figure 2.

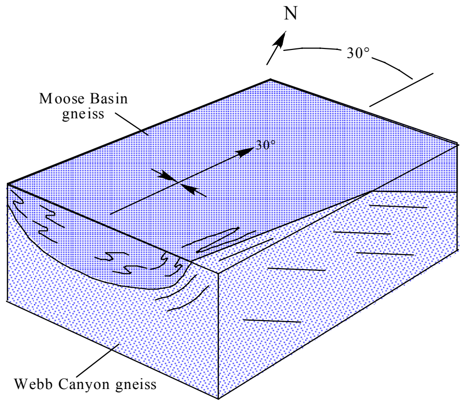

Figure 2. Block diagram showing the relation between the Moose Basin gneiss and the Webb Canyon gneiss.

gneiss abuts the Moose Basin gneiss on both the east (along the upper stretches of Webb Creek) and the west (on the west side of South Bitch Creek) of this fold. In both areas the Webb Canyon gneiss dips beneath the Moose Basin gneiss (Fig. 2). These relations suggest that the Webb Canyon gneiss lies beneath the Moose Basin gneiss and separates it from the layered gneiss and augen gneiss.

Petrology

Our petrologic observations indicate that the peak metamorphism in the Moose Basin gneiss occurred at $T > 900$°C and $P \sim 12$ kilobars (Figure 3). Very little is left of these peak mineral assemblages because the rock underwent extensive deformation and re-equilibration during uplift. Relict features we have found include evidence of partial melting in the mafic rocks that produced garnet, high Zr rutile in the pelitic rocks as well as sillimanite needles in garnet. The major deformations affecting the Moose basin gneiss took place as the rock cooled and decompressed from these peak conditions. Fluids were able to gain access to the rock during these deformation events, causing hornblende to form from the pyroxenes in the mafic rocks and biotite and kyanite to grow in the pelitic rocks. The presence of late staurolite, sillimanite, and cordierite indicate that the pelitic rocks underwent considerable decompression on cooling (dashed arrow on Figure 3).

Implications and Further work

The structural relations discovered in the summer of 2005 lend credence to our theory that the high-pressure Moose Basin gneiss was thrust onto the rest of the gneisses in the Tetons 2.67 billion years ago and that the Webb Canyon gneiss later intruded the thrust fault. High-pressure metamorphism such as recorded in the Tetons is rare in rocks older than 2.5 billion years old and is found today only in continent-continent collisions such as the Himalaya. This means that the gneisses in the Tetons record one of the oldest Himalayan-type mountain building events on Earth.

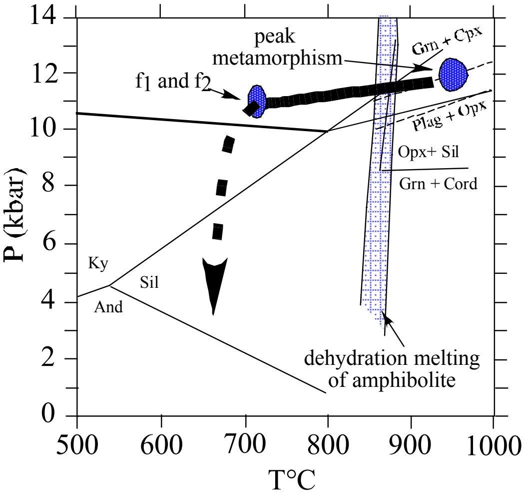

Figure 3. Inferred P-T path for the Moose Basin gneiss.

In December of 2005 we learned that NSF was going to provide us with $216,000 to continue our study of the basement granulites in the Tetons. Studies we intend to pursue with this grant include:

1) We will determine the structural relations between the Webb canyon gneiss and the underlying layered gneiss. In particular we wish to learn whether these rocks record evidence of the tectonic emplacement of the Moose Basin gneiss

2) We hope to determine the structural, metamorphism, and plutonic history of the layered gneiss. The layered gneiss is the rock upon which the Moose Basin gneiss was thrust. We wish to find if there is a “basement” to this complex or whether it consists of an accretionary prism. If so it would have formed as an agglomeration of rocks that at ca. 2.68 billion years ago, lay ocean-ward of an island arc.

3) We intend to undertake the detailed geochronological studies of the rocks in the Tetons to determine the age of the various structural and metamorphic events within the Moose Basin gneiss, Webb Canyon gneiss, and the layered gneiss.

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TROPHIC CASCADES AND HISTORIC ASPEN RECRUITMENT IN THE GALLATIN ELK WINTER RANGE OF SOUTHWEST MONTANA

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ABSTRACT

The extirpation of the gray wolf (*Canis lupus)* by 1930 in Yellowstone National Park (YNP) provided us with an opportunity to study historic aspen (*Populus tremuloides*) recruitment with and without a top carnivore predator present. Herbivory, climate trends, fire records, and current conifer invasion were also examined within the context of aspen recruitment. We obtained tree cores and diameter at breast height measurements to create an aspen age-diameter relationship which we used to approximate aspen origination dates. One elk (*Cervus elaphus*) exclosure, erected in 1945 within the same elk winter range, was compared to the rest of the winter range. Consistent recruitment inside the exclosure began in the 1940s and has continued into the present. Outside of the exclosure, aspen recruitment began decreasing in the 1930s and ceased in the 1950s. Within the scope of the study, we found little correlative evidence between aspen decline and climate trends, conifer invasion, or fire suppression. The results are suggestive of a trophic cascade between aspen recruitment, and historical elk browsing activities as affected by the absence or presence of wolf predation.

INTRODUCTION

The decline of quaking aspen in the Greater Yellowstone Ecosystem (GYE) and YNP has been documented for decades (Warren 1926, Grimm 1939, Barmore 1965, Houston 1982) and continues to be of concern to scientists and natural resource managers (Romme *et al.* 1995, NPS 1997, Meagher and Houston 1998, NRC 2002). Concern over aspen recruitment is due to frequent observations of deteriorating aspen stand structures characterized by mostly mature trees. Due to its widespread decline in YNP, understanding the historical processes that have lead to a decline in aspen is needed to enhance future aspen survival.

Aspen largely reproduce vegetatively (Jones and DeByle 1985), producing genetically identical stems known as ramets. Aspen can also reproduce by seed, but seeding events in the YNP are rare due to the infrequent fire events that promote aspen seed regeneration (Romme *et al.* 1995) and the exacting conditions necessary for successful germination (Jones and DeByle 1985). Thus, because seeding is such a rare event and many aspen have not successfully reproduced vegetatively, the future of aspen persistence in the YNP is unknown.

Aspen decline has been variously attributed to fire suppression, natural stand dynamics, climate trends, and ungulate browsing (Houston 1973, Loope and Gruell 1973, Romme *et al.* 1995, Meagher and Houston 1998, Singer *et al.* 1998). It is also possible that large carnivore presence can influence both ungulate population size and behavior, and in doing so, affect aspen population dynamics (White *et al.* 1998, Ripple and Larsen 2000, Ripple *et al.* 2001, Mao 2003, Hebblewhite *et al.* 2005, Fortin *et al.*

2005, Binkley *et al.* 2006). In YNP, it is therefore possible that the extirpation of the gray wolf in the 1920s lead to changes in both elk browsing behavior and elk density, thus impacting aspen recruitment (Ripple and Larsen 2000). This ability of a carnivore to indirectly impact vegetation is known as a trophic cascade.

Ripple and Larsen (2000) conducted a comprehensive historical aspen study in the park's northern range, the location of the park's largest wintering elk herd. The study concluded that a decline in aspen recruitment inside the park coincided with wolf extirpation. Other studies within the park examining willow and cottonwood have also found associations between low recruitment, wolf extirpation, and elk browsing (Beschta 2003, Ripple and Beschta 2003, Beschta 2005). Though these studies have not found direct evidence that wolves influence elk, other studies have more directly found an association between wolf reintroduction and changes in elk densities and behavior in the park (Childress and Lung 2003, Laundré *et al.* 2001, Mao 2003, White and Garrott 2005).

To understand future aspen dynamics, a first and necessary step is to comprehend historical aspen dynamics. Therefore, the objective of the present study was to examine historical aspen recruitment within the framework of trophic cascades theory in the Gallatin elk winter range, an area to our knowledge where aspen had not previously been studied. The *a priori* hypothesis of this study was that the decline and extirpation of the gray wolf in the 1920s resulted in increased elk herbivory and a subsequent decline in aspen recruitment. Conifer invasion, fire suppression, and climate were also examined as alternative explanations for aspen decline. An elk exclosure, erected in 1945 and located within the same winter range, provided an opportunity to study aspen decline while disentangling the influence of ungulate herbivory and climate. Historical aspen conditions were studied by creating an aspen age-diameter relationship. Long-term climate records, conifer basal area, and historical documents were all examined to study other potential factors that may influence aspen decline.

STUDY AREA

The Gallatin is the main wintering area of the Gallatin elk herd (Lovaas 1970). Elevation ranges between 2400-3000m. Winter precipitation normally occurs as snow and annual precipitation ranges from 50 cm at low elevations, to 150 cm at high elevations (NRCS 1996). Heavy, deep snows in the fall and winter force the elk herd to move to lower elevations that include both the Daly Creek and Black Butte watersheds, a core winter range for the Gallatin elk herd (Lovaas 1970). In the current study, all aspen stands within the Daly Creek and the northern half of the Black Butte watersheds were examined (Figure 1).

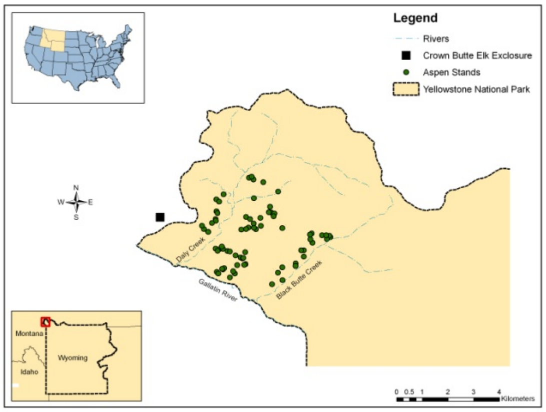

Figure 1. Study location. All data were collected within the Gallatin elk winter range southwestern Montana.

The coniferous vegetation of the Gallatin is comprised of pure stands of lodgepole pine (*Pinus contorta*) or mixed stands of lodgepole pine, Douglas-fir (*Pseudotsuga menziesii*), and Engelmann spruce (*Picea engelmanni*), with willow (*Salix* spp.) the most prevalent hardwood in the Gallatin valley bottom, and aspen the dominant hardwood at higher elevations. Both willow and aspen are minor components in comparison to the conifer species. On open hill slopes, sagebrush (*Artemisia* spp.), rabbitbrushes (*Chrysothamnus* spp.), Idaho fescue grass (*Festuca idahoensis*), wheatgrasses (*Agropyron* spp.), and bluegrasses (*Poa* spp.) are commonly found. Due to their higher nutritional content, preferred elk forage in the winter range include willow and aspen. Elk typically browse coniferous species in the winter range once they have depleted more nutritious forage.

METHODS

During the summer of 2004, we enumerated and visited all aspen stands within the study area with 1:24000 aerial photography and field reconnaissance. We defined a stand as a minimum of three aspen stems with each stem less than 30m away from any other stem. When available, nine diameter at breast height (DBH) measurements representing a range of tree diameters were collected in each stand. Increment cores were similarly taken from the full range of diameters present in the stand.

To examine current aspen reproduction levels, we established a 2x20 m belt transect in every third aspen. Each transect ran from the stand edge toward the stand centroid and the direction of the belt transect was randomly selected with a random number table. Within each transect we collected aspen sprout information, defining aspen sprouts as immature aspen less than 200 cm in height. For all aspen sprouts within each transect, we recorded the total number, height, and previous year browsing (yes/no). We collected conifer basal area data using a basal area gauge (basal area factor = 5) to assess current conifer encroachment. We obtained fire information from historic documents and looked for the presence or absence of fire scars on Douglas-fir while in the field.

Within the same elk winter range, additional data on aspen was gathered within a 2ha fenced elk exclosure erected in 1945. We collected DBH measurements on all aspen stems greater than 1 cm in DBH and extracted increment cores from stems > 5 cm in DBH.

We used standard dendrochronological procedures (Stokes and Smiley 1968) to dry, mount, and sand each core. Rings on each core were counted with a dissecting microscope. Cross-dating was unsuccessful due to ring complacency. We created an aspen age-diameter relationship from 31 aspen cores and corresponding DBH's. The age-diameter equation was: $\text{Age} = 2004 - (2.50{*}\text{DBH}^{\wedge 1.036} + 5)$. We placed the remaining aspen DBH's into the regression equation to approximate aspen age and year of origination.

We downloaded Palmer Drought Severity indices (PDSI) from the International Tree Ring Databank website to examine climate trends http://www.ncdc.noaa.gov/paleo/treering.html. Created by Cook *et al.* (2004), this long-term climate record is based on climatically sensitive tree-ring chronologies. Average PDSI values have a value of zero. Negative values are indicative of drought conditions (moderate (-2), severe (-3), extreme (-4)), whereas positive values are associated with above average precipitation. We averaged PDSI values from the two nearest records available.

✦ RESULTS

Aspen Stands

From the 71 aspen stands located in the winter range, we collected 462 DBH measurements and an additional 353 DBH measurements within the elk exclosure (Fig. 2). Outside of the exclosure, the decline in aspen began in the late 1930s and completely ceased in the 1950s (Fig. 3), illustrating a large gap in tree recruitment from the 1950s through 1999. In contrast, aspen numbers originating within the exclosure began to increase following fence construction and has continued inside the exclosure through 1999, (Fig. 3).

Figure 2 A.

Figure 2 B.

Figure 2. A typical winter range stand (A), and aspen in the Crown Butte Exclosure (B). Note our ability to see through the typical winter range stand and lack of aspen recruitment. Note the lack of recruitment outside of the Crown Butte exclosure and the greater aspen stem density inside the exlcosure.

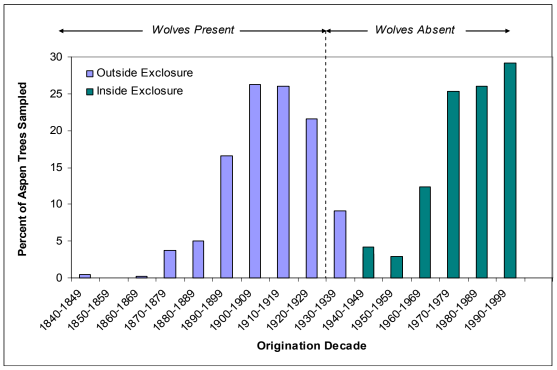

Figure 3. Winter range aspen origination within and ouside the elk exclosure. Outside of the exclosure, no aspen were found originating after the 1950's. Consistent recruitment was found inside the exclosure after its erection.

Conifer Encroachment

We found a total of 262 aspen sprouts within the 23 transects situated in aspen stands, with a mean sprout density of 2,837 per ha (Lower CL = 1571, Upper CL = 4102). Mean conifer basal area was 14.74 m^2/ha (Lower CL = 10.0, Upper CL = 19.5), and mean live aspen basal area was 21.3 m^2/ha (Lower CL = 14.8, Upper CL = 27.7) in the 23 stands (Fig. 4). We found little association between the proportion of conifer basal area in a stand and current sprout numbers ($F_{1,21}$ = 1.52, p-value = 0.23, R^2 = 0.07).

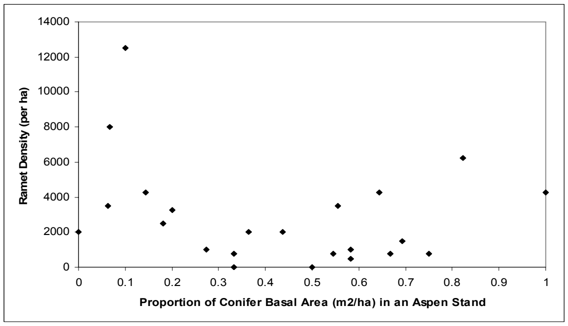

Figure 4. Conifer invasion and aspen recruitment in 23 aspen stands. No relationship was found between current conifer basal area and the density of aspen sprouts ($F_{1,\ 21}$ + 1.52, p-value +0.27, R^2=0.07).

Fire

In his history of the Gallatin elk herd, Lovaas (1970) did not document any fires in the Gallatin elk winter range. We did not observe fire scars on any Douglas-fir trees we opportunistically located in the study area. We therefore concluded there was a low likelihood of high severity fires in the study area since at least the late 1800s.

Climate

A scatter plot of raw annual PDSI values indicated periods of above and below average wetness before and after wolf extirpation (Fig. 5).

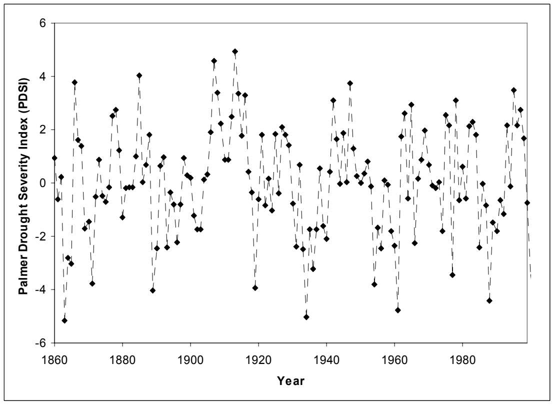

Figure 5. Average Palmer Drought Serveity Index (PDSI).

Herbivory

Of the 262 aspen sprouts measured in the winter range, 94.6% had been browsed within the last year and had a mean height of 26.3 cm (Lower CL = 24.3, Upper CL = 28.4). Within the exclosure, 91.3% of the aspen originated after the exclosure was erected in 1945 (Fig. 2). Outside of the exclosure, we found no aspen trees less than 17 cm in DBH (Fig. 3).

DISCUSSION

Conifer Encroachment

As stands change from aspen to conifer dominated, aspen sprout numbers could decline because conifer trees limit available sunlight to the shade intolerant aspen sprouts (Jones and DeByle, 1985). It would therefore be predicted that aspen stands with greater conifer basal area should have fewer aspen sprouts than those aspen stands with lower conifer basal area. Yet with a mean sprout density of 2837 aspen per ha (Lower CL = 1571, Upper CL = 4102) aspen growth and mortality currently appear to be more problematic than the actual number of aspen sprouts. However, as conifer basal area increases, future aspen sprout numbers could eventually be negatively impact.

Fire Suppression

If fire suppression was the predominant process causing a decline in aspen numbers, few aspen should recruit without fire. However, aspen recruited into the 1950s in the winter range despite no fires reported in historic documents since at least the late 1800s. In addition, the high density of aspen in the elk exclosure illustrates fire is probably not a necessary requirement for aspen to recruit in this area.

Climate

Climate can influence forage production and the ability of plants to successfully regenerate. Researchers have therefore suggested the decline in aspen is attributable to a changing climate (Houston 1982, Singer *et al*. 1994, Romme *et al*. 1995, NPS 1997, Singer *et al*. 1998). Thus, the lack of aspen since the 1950s in the winter range would be consistent with a drying climate. However, with aspen continuously recruiting into mature stems inside the exclosure since its construction during periods of above and below average wetness (Fig. 5), the climate hypothesis becomes more inconsistent. Specifically, since the exclosure is in the same winter range as the other measured aspen stands, we would expect climate, and therefore its impact on aspen recruitment, to be similar within and outside of the exclosure. Other researchers have similarly found weak associations between climate and aspen, willow, and cottonwood growth in other parts of the Rocky Mountains (Wagner *et al*. 1995, Baker *et al*. 1997, White *et al*. 1998, Hessl and Graumlich 2002, Barmore 2003, Beschta 2003, 2005, Ripple and Larsen 2000, Ripple and Beschta 2004).

Herbivory

For herbivory to impact aspen numbers, recruitment should be minimal within the elk winter range and extensive within the elk exclosure. This assertion is supported by the data (Fig. 3). The only multi-aged aspen stands currently recruiting in the entire winter range study area lie inside the elk exclosure. Aspen have only successfully recruited in large numbers within the exclosure since the 1940s, corresponding to the installation of the exclosure fence in 1945 (Fig. 3). It is only inside the exclosure the distribution of aspen origination ages follows the expected J-shaped distribution of a healthy reproducing plant population. The unimodal distribution of aspen origination outside the exclosure is more indicative of a declining aspen population.

Trophic Cascades

In the current study, no aspen <17 cm in DBH were found outside of the elk exclosure. On Isle Royale, Michigan, McLaren and Peterson (1994) observed that as wolf numbers declined, moose numbers increased causing a suppression of balsam fir. Within the northern range of YNP, a decline in aspen recruitment since the 1930s was reported in the park's northern range (Ripple and Larsen 2000). As with aspen, Beschta (2003, 2005) documented a decline in cottonwood (*Populus* spp.) beginning in the 1920s within YNP and did not find a correlation between cottonwood decline and climate. Thus two browse species growing under different conditions (riparian cottonwood versus upland aspen) concurrently declined during the time of wolf extirpation.

According to general top-down theory, in a two-level trophic system, herbivores directly impact vegetation by reducing plant biomass. Therefore, as herbivore numbers increase, plant biomass should decrease, indicating an inverse relationship between trophic levels. In a three-level trophic system of carnivores, herbivores, and plants, trophic theory predicts predators will lower herbivore numbers and/or alter herbivore behavior, which in turn increases plant biomass. Examination of aspen within the Gallatin elk winter range of YNP yielded little evidence of successful aspen recruitment outside of the elk exclosure following wolf extirpation. Thus, we observed a negative plant response to predator removal outside the exclosure, and a positive plant response under limited herbivory (inside the exclosure), consistent with top-down theory. At this time, uncertainty remains as to whether elk densities and/or behavior will change enough to enable aspen in the Gallatin winter range to persist outside of the exclosure. If elk herbivory patterns do not change, the loss of aspen will change the availability of resources on the landscape potentially resulting in an alternative stable state.

✦ CONCLUSIONS

Due to the loss of many top terrestrial carnivores, terrestrial trophic cascades studies involving large vertebrate mammals are rare. Because most terrestrial vertebrate systems are therefore not fully intact, the information gleaned from a time when the system was more complete becomes valuable. The correlative evidence presented in this study are consistent with a positive top-down influence of wolf presence on aspen via additive predation pressure and a negative top-down influence on aspen when wolves are absent. Therefore, the presence of wolves may be integral to the long-term recruitment of woody browse species in YNP.

✦ ACKNOWLEDGEMENTS

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GRAZING EFFECTS OF THE NEW ZEALAND MUD SNAIL ACROSS A PRODUCTIVITY GRADIENT IN THE GREATER YELLOWSTONE ECOSYSTEM

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✦ ABSTRACT

Accurately predicting the effects of introduced species on native communities and ecosystems is a challenge. Utilizing methods of food web ecology, we measured grazing effects of the invasive freshwater New Zealand mud snail, *Potamopyrgus antipodarum*, in streams within the Greater Yellowstone Ecosystem. Previous results indicate that *P. antipodarum* can significantly reduce algal standing stocks in less than one week, but it is not yet known if grazing effects vary across streams differing in benthic algae production. In this study, we measured the strength of *P. antipodarum* grazing on algal resources across six streams varying widely in ambient primary production. In field enclosure experiments within each stream, we estimated direct grazing effects of snails on algae by measuring chlorophyll *a*, gross primary production and chlorophyll *a*-specific primary production. In most streams, *P. antipodarum* decreased overall algal standing stocks, as measured by chlorophyll *a*, even though gross primary production was not affected. As a result, chlorophyll-*a* specific primary production increased in productive streams. Finally, standardized comparisons of *P. antipodarum*-algae interactions indicated that grazing effects were largest in the most productive streams. The overall impact of *P. antipodarum* on native stream communities will be greatest in the most productive streams if these assemblages are also capable of supporting dense *P. antipodarum* populations.

✦ INTRODUCTION

Invasive species have changed biodiversity (Wilcove et al. 1998, Mooney and Cleland 2001) and altered ecosystems in profound ways (Vitousek 1990). Population-level effects can be manifested through a multitude of community interactions, including competition (e.g. Petren and Case 1996, Juliano 1998, Byers 2000), predation (e.g.Grosholz et al. 2000), facilitation (e.g. Bruno and Kennedy 2000) and herbivory (e.g. Russell and Louda 2005). Invasive species can also affect ecosystem properties by altering nutrient fluxes or disrupting energy flow (e.g. Hall et al. 2003, Vitousek and Walker 1989). Yet despite the importance of introduced species in affecting native communities and ecosystems, the effects of many successful exotic species are variable or still unknown (Bruno et al. 2005, Strayer 1999) and little attempt has been made to standardize measures of effect with ecological theory (Shea and Chesson 2002).

A central goal of ecology is to determine factors that contribute to variation in species interactions across space. An important conservation implication of this goal is the increased ability to predict impact of invasive species in a variety of environments. To facilitate comparisons of introduced species effects across sites, Parker et al. (1999) proposed that overall impact could be related to the combination of three components: range, abundance and per unit effect (e.g. the effect of each individual or unit of biomass). In many instances, range and abundance can be estimated easily, while per unit effects are more difficult to measure. It is possible, though, to experimentally quantify the magnitude of per unit effects of one species on another in a community by calculating interaction strengths (e.g. Paine 1992). Measuring interaction strengths provides an appropriate framework to create standardized comparisons of introduced species effects. Estimates of population-level impacts can be calculated by multiplying interaction strengths by population biomass (Wootton 1997, Parker et al. 1999), assuming that per unit effects scale linearly with biomass (Pfister 1995, Wootton 1997, but see Ruesink 1998). Large effects occur when introduced species interact strongly in the invaded community and especially if they also are abundant.

We were interested in making standardized comparisons of grazing effects of the New Zealand mudsnail (*Potamopyrgus antipodarum,* Class Prosobranchia, Family Hydrobiidae) on benthic algae across streams varying in primary production levels. *P. antipodarum*, a worldwide invader, was first recorded in streams in the western U.S. in 1987, and now has a widespread, but patchy, distribution, including several areas of conservation significance (e.g. Yellowstone, Grand Teton and Grand Canyon National Parks). *P. antipodarum* grazes on periphytic algae in benthic stream communities and can significantly reduce algal standing stock in less than one week (Riley, Dybdahl and Hall, in review). Within the Greater Yellowstone Ecosystem (GYE), densities of *P. antipodarum* can exceed 500,000 individuals/m^2. Grazing by dense populations of introduced *P. antipodarum* are likely to affect entire stream communities given that benthic algae is energetically important to stream food webs (Lamberti 1996) and can constitute a significant portion of the total energy budget in small, sunny streams (Minshall 1995).

Effects of grazers in streams are not always easy to predict. While it is well-known that herbivorous grazers, especially snails, can significantly reduce periphytic algal standing stocks (e.g. Lamberti et al.1987, Steinman 1996, reviewed in Feminella and Hawkins 1995), the direction or magnitude of these impacts are not consistent across streams (Lamberti and Feminella 1996) and can differ according to the response variables that are measured (Feminella and Hawkins 1995). In general, heavy grazing reduces algal standing stocks (e.g. Hart 1985, Sumner and McIntire 1982, Lamberti 1989), but can increase rates of areal primary production or biomass-specific primary production (Lamberti and Resh 1983). Measuring only one response variable can lead to different conclusions regarding the impact of an invasive grazer on stream communities and ecosystem functions. Consistently, though, the magnitude of grazer effects are more pronounced in streams with higher periphyton biomass and/or primary production (Feminella and Hawkins 1995). If grazing varies predictably across productivity gradients, we can estimate the variation in impact *P. antipodarum* populations have on streams with different levels of benthic algal productivity.

Our study investigated grazing effects of *P. antipodarum* across six streams varying in periphyton abundance and primary production within the GYE. In the summer of 2005, we experimentally assessed the direct impact of *P. antipodarum* snails on standing stocks and production rates of periphytic algae. We then calculated grazing interaction strengths to standardize effect sizes to allow for comparisons across streams. Finally, we analyzed the relationship between primary production and grazing interaction strengths to understand if grazing effects vary predictably with stream production. We found negative grazing effects on algal standing stocks in most streams, with the largest effects in the most productive streams.

✦ METHODS

We experimentally measured grazing effects of *P. antipodarum* in caged experiments in six streams (Polecat, Spirea, Iron Springs, Little Firehole, Fairy and Sentinel) within the Greater Yellowstone Ecosystem. Controlled field experiments are best for determining effects of herbivory and other factors on periphyton (Lamberti and Feminella 1996). Within each stream, we set up ten cages, each containing three - four rocks from the surrounding stream. All other macroinvertebrates were removed from rocks. Five cages received *P. antipodarum* as grazers (15 g AFDM/m^2, equivalent to approximately 600 adult snails) while the other five cages did not receive grazers and served as controls. The biomass of snails used in this experiment fall within the ambient range of *P. antipodarum* in some of these streams (Hall et al. 2003, Kerans et al. 2006). We purposely used the same snail biomass in all experiments for a few reasons. First, we wanted to compare grazing effects across streams that vary in production regimes and needed snail biomass to stay constant. Second, as herbivore biomass is increased, periphyton biomass often decreases (Allan 1995). On the other hand, under heavy grazing pressure, productivity per unit of algal biomass can increase (Lamberti and Resh 1983). Testing benthic algal responses, under heavy, but realistic, grazing pressure, should maximize potential differences between production and standing stock responses (Allan 1995, Lamberti and Moore 1984).

At the start of each experiment, we collected benthic algae from nine rocks in the stream and measured ambient chlorophyll *a* (as an estimate of algal biomass) using standard methods for spectrophotometric analysis (APHA 1995). Each replicate combined algae from three rocks, creating three replicates for ambient initial algal biomass. This allowed us to test for cage effects in all experiments.

At the conclusion of each experiment (average: 5.3 days), chlorophyll *a* and gross primary production (GPP) were measured from each cage following standard procedures used in other grazing studies in the GYE (APHA 1995, Steinman and Lamberti 1996 and R. O. Hall, Jr. personal communication). We first measured GPP by incubating rocks from each cage in clear and dark PVC plastic tubes, with water continuously pumped in a closed circuit to mimic stream conditions. Oxygen concentrations were recorded with a dissolved oxygen meter (YSI; Yellow Springs, Ohio) at the start of the incubation and one hour later. The decrease in oxygen in the dark chamber represents community respiration (CR), while the change in oxygen in the clear chamber represents net primary production (NPP). NPP+|CR| = Gross Primary Production, which is the rate of photosynthesis. Next, we scraped periphyton from the rocks to create slurries of algae that we analyzed for chlorophyll *a* content using standard methods for spectrophotometric analysis (APHA 1995). All chlorophyll *a* measurements were pheophytin – corrected. Finally, rock area was estimated from each cage by tracing the exposed rock surface onto paper. We measured all response variables over two days for each stream because GPP measurements could not be finished in one day given the number of replicates. We calculated three estimates of algal biomass and/or productivity: 1) chlorophyll *a* (mg/m^2) as an estimate of algal standing stock, 2) GPP ((mg O$_2$/m^2)/h)) as an estimate of production rate per rock area and 3) chlorophyll *a* - specific GPP (mg O$_2$/mg chlorophyll *a*) as a measure of production per amount of algal standing stock.

We analyzed each response variable separately. First, we combined all streams and used a two-way ANCOVA to test for stream effects, grazing effects and an interaction between stream and grazing, with day of measurement as a covariate. A significant interaction term indicates that the response of benthic algae to grazing is different among streams (i.e. algae decreases in response to grazing in stream A, but increases in stream B). Second, we analyzed each stream individually, using a one-way ANCOVA to test for grazing effects on each of the response variables.

We then standardized grazing estimates in order to make comparisons across streams. Algal reduction by each species was measured as the difference between algal biomass (as estimated by chlorophyll *a*) when snails were present compared to the control treatment. We calculated interaction strengths from the following equation, adapted from Wootton (1997):

$$\frac{\ln\left(\frac{N_t, s > 0}{N_t, s = 0}\right)}{St} = -c$$

where N_t , $s>0$ is the concentration of chlorophyll *a* (μg chlorophyll a/cm^2) with snails present, N_t , $s=0$ is chlorophyll *a* (μg chlorophyll a/cm^2) with snails absent, S is snail biomass (g AFDM) for N_t , $s>0$, t is time (days) and $-c$ is per biomass interaction strength ((g AFDM/m^2)$^{-1}$d^{-1}). More negative values indicate that algal biomass is lowered to a greater extent per unit of snail biomass per unit of time. This index does not assume equilibrium conditions and works well for short-term experiments (Laska and Wootton 1998; Berlow et al.1999; Berlow et al. 2004). We used a one-way ANOVA to test if interaction strengths differed across streams. We then performed a linear regression to determine if interaction strengths were stronger (i.e. more negative) in streams with higher productivity. The predictor variable was the average GPP from control cages in each stream. Control cages did not experience grazing for the duration of the experiments. All statistics were performed on Systat 10 (SPSS Inc., 2000).

RESULTS

Initial chlorophyll *a* measured on rocks in each stream was not different from either control or grazing cages for that same stream (p = 0.515, p = 0.197 respectively). Therefore, cages were representative of ambient stream periphyton conditions. Within experimental cages, streams differed significantly in gross primary production (p = 0.000; Table 1). Streams also differed with respect to chlorophyll *a* and chlorophyll *a*-specific GPP although these results were only marginally significant (p=0.087 and p=0.071, respectively; Table 1, Figure 1

Response	Stream	Grazing	Stream x Grazing	Day (covariate)
GPP	**0.000****	0.114	0.920	0.310
Chl-*a*	0.087*	**0.000****	0.149	0.567
Chl-*a* specific GPP	0.071*	0.132	0.365	0.271

Table 1. Summary table of ANCOVA results for snail grazing across all streams.
Notes: Each response variable was analyzed in a separate two-way ANCOVA and is listed in the left-hand column. Factors included in each ANCOVA were: stream, grazing and day of measurement as the covariate. P-values for the corresponding response variables are listed in the cells in the table.
* Significant p-values at p<0.1.
** Significant p-values at p<0.05.

Overall, grazing trends were similar across streams. Across all streams, grazing did not affect GPP or chlorophyll *a*-specific GPP (p=0.114 and 0.132 respectively; Table 1). On the other hand, grazing significantly lowered chlorophyll *a* across all streams (p=0.000; Table 1). For all three response variables, no significant interaction existed between stream and grazing level (Table 1). This indicates that grazing effects were relatively consistent across all six experiments.

Grazing did not significantly affect GPP across all streams, but separate analyses for each stream revealed a significant effect of grazing on GPP in Iron Springs (p=0.047 for grazing; p=0.003 for day as the covariate; Table 2; Fig. 2). This result is likely due to significantly lower GPP measurements on day 1 compared to day 2, rather than a true effect of grazing. Primary production in all other streams was not affected by grazing (Table 2; Fig. 2).

While grazing did not affect GPP, grazing significantly lowered chlorophyll *a* across all streams (Table 1). Snails were effective at reducing the standing stock of periphyton even though overall production (i.e. GPP) was not affected (Table 2; Figs. 1 and 2). In separate analyses, grazing significantly lowered chlorophyll *a* in Polecat Creek and Spirea (p=0.008 and p=0.048, respectively; Table 2, Fig. 2). Grazing effects were also marginally significant in Little Firehole (p=0.096, Table 2, Fig. 2).

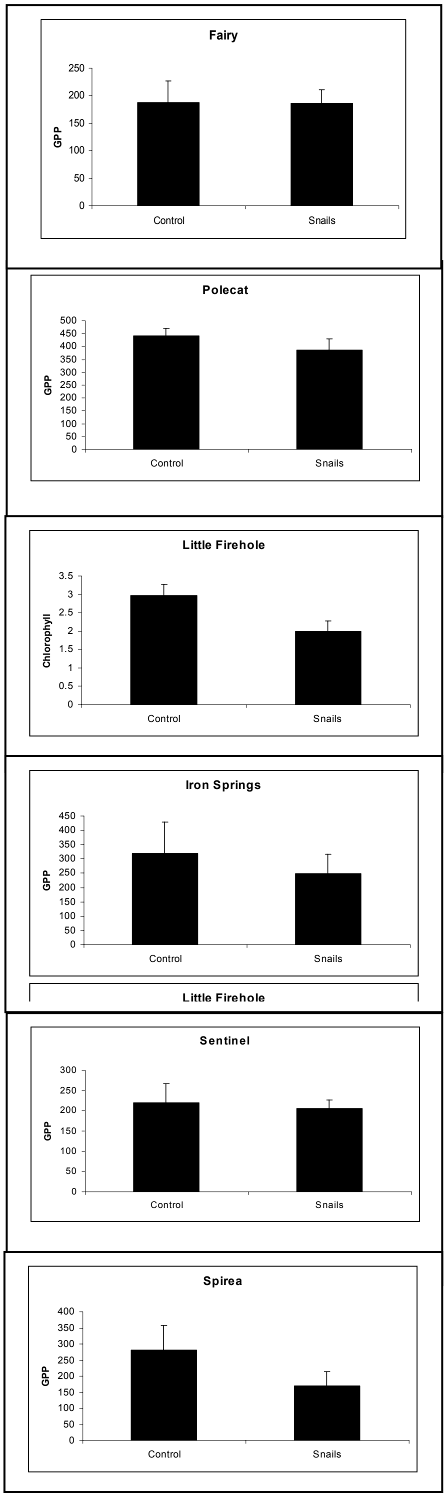

Figure 1. Snail grazing effects on primary production (GPP) in each stream. GPP is measured as mg $O_2/(m^2*h)$. Grazing only significantly lowered GPP in Iron Springs due to a significant effect of the covariate (day). Note that the y-axis varies among streams.

Stream	GPP	Chl-*a*	Chl-*a* specific GPP
Fairy	0.771 (0.244)	0.904 (0.533)	0.803 (0.895)
Iron Spring	**0.047 ** (0.003) §**	0.404 (0.218)	0.381 (0.108)
Little Firehole	0.959 (0.237)	0.096* (0.206)	0.363 (0.818)
Polecat	0.314 (0.375)	**0.008**** (0.129)	**0.026**** (0.981)
Spirea	0.304 (0.304)	**0.048**** (0.938)	0.175 (0.848)
Sentinel	0.678 (0.678)	0.359 (0.456)	0.598 (0.246)

Table 2. Summary table of ANCOVA results for snail grazing within each stream.

Notes: Each response variable was analyzed in a separate one-way ANCOVA for each stream. Streams are listed in the left-hand column and p-values for the corresponding response variables are listed in the cells in the table. P-values for day as the covariate are listed in parentheses.

** Significant p-values at p<0.05.

Significant p-values at p<0.1.

§ Significant effect of day as the covariate at p<0.05.

On the other hand, grazing caused slight increases in chlorophyll *a*-specific GPP across all streams, although this result is only significant for Polecat Creek (p=0.026; Table 2, Fig. 3). Chlorophyll *a*-specific GPP is likely to increase in some streams because snails can reduce the standing stock of periphyton (as estimated by chlorophyll *a*), while not affecting the overall rate of photosynthesis (as measured by GPP). This indicates that a smaller standing stock of algae can be responsible for the same amount of primary production.

To facilitate comparisons across streams and productivity regimes, interaction strengths were used to standardize effects of snails on algae and remove any bias that initial differences in algal standing stock might cause (Feminella and Hawkins 1995). Interaction strengths between snails and chlorophyll *a* differed across streams, with a 10-fold increase from the smallest to the largest interaction strengths (p=0.021; Fig. 4). In addition, GPP in control cages differed across streams, with more than a four-fold difference from the lowest to the highest productivity streams (p=0.000; Fig. 4). A regression between control GPP and interaction strengths revealed that interaction strengths were strongest (i.e. most negative) in the most productive streams ($R^2 = 0.156$, p = 0.045; Fig. 4). Snails were most effective at reducing algal standing stocks in highly productive streams

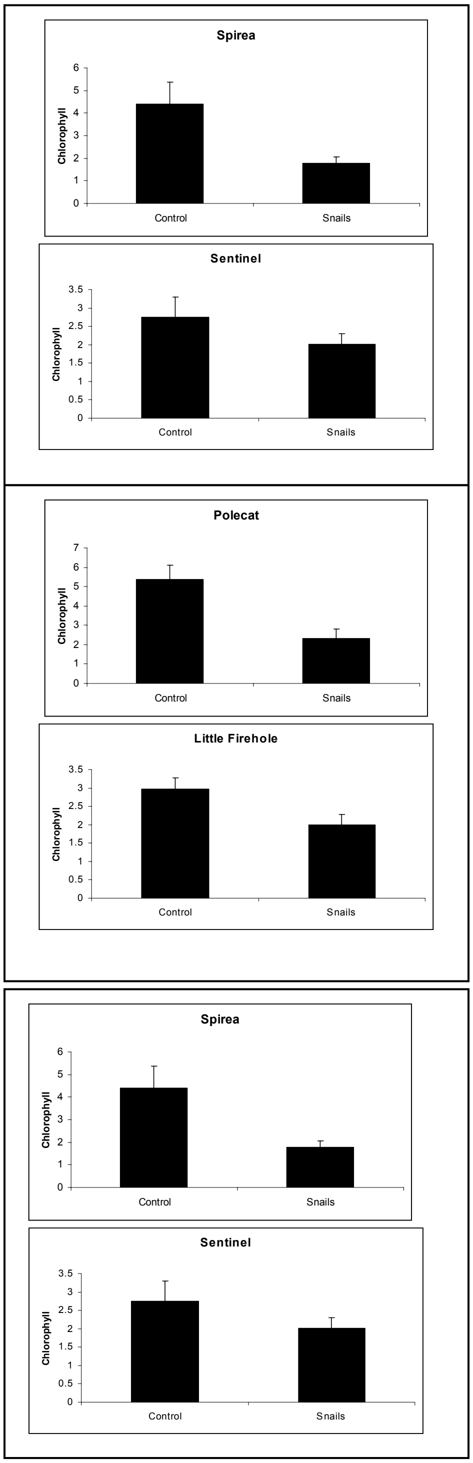

Figure 2. Snail grazing effects on chlorophyll *a* in each stream. Chlorophyll *a* is measured as mg/m^2. Grazing significantly lowered chlorophyll *a* in Polecat Creek and Spirea. At a significance level of p=0.1, grazing also significantly lowered chlorophyll *a* in Little Firehole. Note that the y-axis varies among streams.

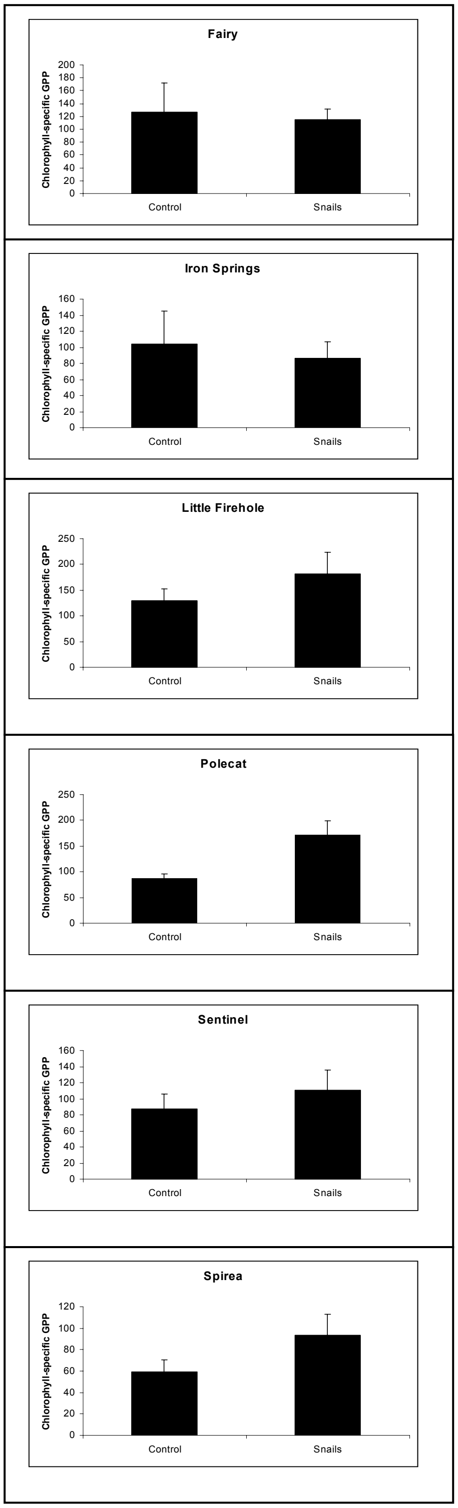

Figure 3. Snail grazing effects on chlorophyll *a*-specific GPP in each stream. Chlorophyll-specific GPP is measured as mg O_2/mg chlorophyll *a*. Grazing by snails significantly increased chlorophyll-specific GPP in Polecat Creek. Note that the y-axis varies among streams.

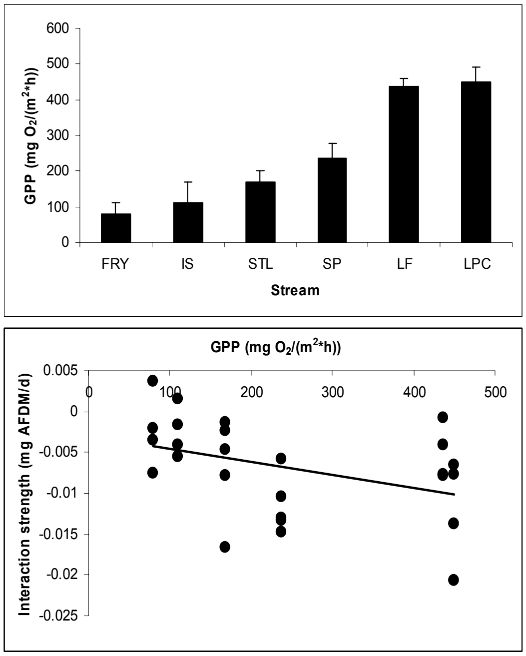

Figure 4. The relationship between GPP and interaction strengths across streams. The top panel represents GPP in control treatments for each stream. Abbreviations are as follows: FRY = Fairy, IS = Iron Springs, STL = Sentinel, SP = Spirea, LF = Little Firehole and LPC = Polecat Creek. The bottom panel represents the interaction strength between snails and algae, as measured by chlorophyll *a*. See text for explanation of interaction strength calculations. Snails have larger effects in more productive streams ($R^2 = 0.156$, $p = 0.045$).

✦ DISCUSSION

We studied grazing effects of an introduced species, *P. antipodarum*, across a productivity gradient that included six streams in the GYE. We show that intense grazing by *P. antipodarum* did not affect GPP and even had slight positive effects on chlorophyll *a*-specific GPP. On the other hand, *P. antipodarum* reduced standing stocks of algal periphyton in most streams. Grazing effects on periphyton standing stocks were strongest in the most productive streams even though snail biomass remained constant across all experiments. This pattern indicates that *P. antipodarum* has large impacts on basal resources in highly productive streams in the GYE. *P. antipodarum* grazing impacts might translate into increased growth and/or reproduction, leading to high snail densities in the most productive streams.

Based on the proven effectiveness of snails as grazers in streams (Allan 1995, Lamberti et al. 1987, Steinman 1996), we expected snails to reduce algal resources. We showed that *P. antipodarum* reduced algal standing stocks in most streams. However, *P. antipodarum* did not affect areal primary production, leading to increased primary production per unit of chlorophyll *a* in the most productive streams. This resulted from a reduced algal standing stock creating the same amount of primary production. This pattern is not surprising given that other studies have also reported similar grazing effects (Lamberti and Resh 1983, indirect evidence: Hill and Knight 1987). Potential mechanisms for increased production with a reduced algal standing stock might include (1) the removal of dominant overstory algae resulting in shade reduction for understory algae, (2) the removal of senescent algae with lower photosynthetic rates creating space for younger, more productive algae to flourish or (3) any combination of (1) and (2) along with increased rates of nutrient regeneration by grazer excretion (Lamberti et al. 1987). In all three scenarios, the grazing effect of the invader would reduce algal standing stocks but increase photosynthetic rates per unit of chlorophyll *a*.

While effects of *P. antipodarum* grazing were similar across all streams, the magnitude of grazing effects increased in the most productive streams. This result might seem counterintuitive at first, but is consistent with a recent meta-analysis examining grazing effects across 89 experimental studies (Feminella and Hawkins 1995). Two mechanisms for large grazing effects in productive streams were proposed by the authors. First, dominant grazer identity varied among streams. Grazers effective at reducing large standing crops are present in highly productive assemblages, but absent in low production streams. Grazers chosen for experimental studies would be more effective in streams with high production. This mechanism, however, cannot account for our results given that grazer identity remained constant across all streams. Second, densities of grazers might be higher in productive areas, resulting in high grazer densities used during experimental trials. Again, this mechanism does not explain the aforementioned results because snail biomass also remained constant across all experiments. A more plausible explanation for this study is that low initial standing stocks can only experience a small reduction. *P. antipodarum* is capable of larger reductions in more productive streams. If so, we expect that low production streams do not have enough algae to support high growth and/or reproductive rates of *P. antipodarum*. This would lead to low production streams having lower densities of *P. antipodarum*. We are currently examining this final mechanism.

Our approach using standardized measures of grazing effects has demonstrated the potential for the introduced *P. antipodarum* to impact resource availability across streams in the GYE. Intense grazing pressure by *P. antipodarum* reduced algal standing stocks and increased chlorophyll *a*-specific primary production in highly productive streams. The overall impact of *P. antipodarum* on algal resources will be magnified in these streams if highly productive assemblages are also capable of supporting dense populations of *P. antipodarum*. These results indicate that *P. antipodarum* has the potential to dramatically alter algal assemblages if intense grazing persists in productive streams.

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SPATIAL AND TEMPORAL VARIATION IN HYDROLOGIC CHANGE DUE TO REGULATION AND TRIBUTARY CONTRIBUTIONS ON THE SNAKE RIVER IN GRAND TETON NATIONAL PARK WY

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✦ INTRODUCTION

Channel and floodplain form are primarily determined by the flux of water through a reach and the associated transport of the sediment delivered from the upstream watershed. The dominant paradigm of fluvial geomorphology is that the size of the bankfull channel and the characteristics of the adjacent floodplain are maintained by the current hydrologic and sediment supply regimes (Wolman and Miller, 1960; Andrews, 1980; Leopold, 1994). The linkage among flow regime, sediment supply, and channel and floodplain form is well illustrated on regulated rivers where the flow regime and sediment supply are altered by dams. Bed incision under conditions of sediment deficit has been widely described (Mostafa, 1957; Komura and Simmons, 1967; Galay, 1983; Williams and Wolman, 1984). The longitudinal change from near-dam sediment deficit to sediment surplus further downstream has been described by Andrews (1984) and Grant et al. (2003), although local differences in bed texture, channel organization, and valley confinement affect the magnitude of channel and floodplain change in any specific reach (Lagasse, 1981; Grams and Schmidt, 2002, 2005).

Relatively few studies have described the characteristics of channel change under conditions of sediment surplus. The sequence of bed aggradation and narrowing has been described by Everitt (1993) for the Rio Grande along the Texas/Mexico border upstream from Presidio, TX, and by Church (1995) for the Peace River in British Columbia and Alberta, Canada. A significant length of the Trinity River in California is in sediment surplus, as described in numerous agency reports (e.g., U.S. Fish and Wildlife Service and Hoopa Valley Tribe, 1999).

The purpose of this paper is to describe patterns of hydrologic change downstream from Jackson Lake Dam (JLD) and to introduce channel change and bed mobility study methods for which analyses are not yet complete. Because this dam, originally constructed in 1908 and rebuilt in 1916, increased the elevation of an existing, glacially-scoured Pleistocene lake, the dam caused no change in the downstream supply of sediment. Thus, decreased flood magnitudes inevitably lead to sediment surplus, although the magnitude of this surplus is unknown. Though Mills (1991) and Marston et al. (2005) described large-scale changes caused by JLD on the same part of the Snake River described here, they failed to explicitly characterize the hydrology of most of the study area because they did not account for tributary inflows that alter the flow regime initially created by dam releases. Mills (1991) and Marston et al. (2005) also did not take advantage of estimates of the mean daily discharge in the absence of JLD that allow more precise characterization of stream flow alteration in most of the study area. Mills (1991) and Marston et al. (2005) analyzed aerial photographs as recent as 1989, and we supplemented their work by analyzing more recent photographs within an improved geographic information system (GIS) framework.

STUDY AREA

The study area extends 43 km between JLD and Moose, WY, and significant changes in stream flow and sediment supply occur over this distance (Figure 1). The contributing drainage area more than doubles from 2090 km^2 at the dam to 4343 km^2 at Moose, and much of this increase is related to two large tributaries. Pacific Creek and Buffalo Fork join the Snake River within 8 km of the dam, and their combined watershed area is one third of the total Snake River watershed upstream from Moose. Thus, the influence of dam operations on the flow regime of the Snake River is mitigated by these unregulated tributaries. Three smaller tributaries join the Snake River further downstream: Spread Creek at 14.5 km downstream from JLD, Cottonwood Creek at 40.5 km, and Ditch Creek at 41.6 km.

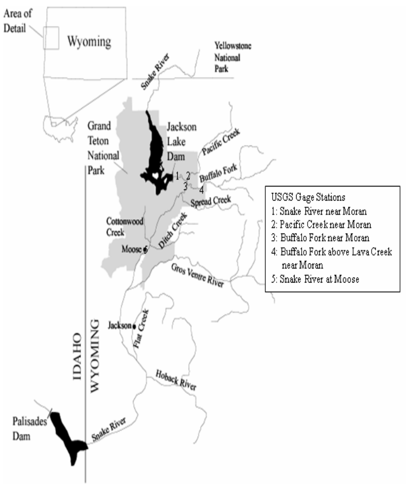

Figure 1: The Snake River as it flows from Yellowstone National Park to Palisades Reservoir. The study reach is from Jackson Lake Dam to Moose.

The Snake River is a braided channel and its adjacent floodplains and low terraces are best described as Class B, medium-energy, and non-cohesive, using the classification scheme of Nanson and Croke (1992). Channel organization alternates between single-threaded in a narrow Holocene alluvial valley and multi-threaded in a wider valley or immediately downstream from some tributaries (Marston et al., 2005). Using visual estimation methods along 372 transects, Mills (1991) and Marston et al. (2005) found that the gradient and proportion of large bed material and riffles and rapids increases downstream. Marston et al. (2005) divided the study area into 5 reaches based on location of tributaries, access points, and significant changes in channel morphology. Love et al. (2003) divided the same area into three reaches, based on the response of the river to its glacial history and changing gradient.

Prior to the completion of Palisades Dam on the Snake River in Idaho in 1958, the magnitudes of peak flows on the Snake River downstream from JLD resembled natural flows but were delayed 2 months (Marston et al., 2005). Winter base flows were nearly non-existent during these decades. Peak flows were restored to their natural timing (mid-May to mid-June) after Palisades Dam was completed, but the magnitude of peak dam releases was decreased and summer flows were increased to sustain the recreational boating industry. Marston et al. (2005) described changes in the Snake River hydrology by creating residual mass curves computed from the measured mean daily flows at the U. S. Geological Survey gauging station immediately downstream from the dam (Snake River near Moran, station number 13011000) and they estimated mean monthly unregulated flows based on changes in end-of-month reservoir storage data. We used estimated unregulated mean daily discharge values from 1910 to 2005, calculated by the U.S. Bureau of Reclamation for the Snake River downstream from JLD to more precisely compare regulated and estimated unregulated flows throughout the study area (<http://www.usbr.gov/pn/hydromet/arcread.html>).

Mills (1991) and Marston et al. (2005) determined that total sinuosity had increased during the 20th century, based on analysis of 7 topographic map or aerial photograph series between 1899 and 1989. They considered total sinuosity to be a surrogate metric of channel stability. They determined that total sinuosity was greatest near tributaries and where the alluvial valley was widest. A composite map of channel location, created in a raster-based GIS, indicated a large number of cells in the floodplain immediately downstream from tributaries that had been recently (as of 1989) active, suggesting that the channel was unstable near tributaries whose delivered sediment load could not be transported by the dam-regulated flood regime (Marston et al., 2005). These findings were based on an imprecise GIS whose raster cells had widths and lengths comparable to the average width of the Snake River channel at base flow – 80.5 m.

METHODS

Hydrology

The hydrology of the study area was estimated for four segments defined by the locations of tributaries: JLD to Pacific Creek (Segment 1), Pacific Creek to Buffalo Fork (Segment 2), Buffalo Fork to Ditch Creek (Segment 3), and Ditch Creek to Moose (Segment 4) (Figure 2). Gauging stations have directly measured stream flow at the dam since 1903 and at Moose (Snake River at Moose, station number 130136500) since 1995. Elsewhere, and for other periods, main-stem stream flow was estimated by adding measured tributary inflow or by correlation of measured periods and application of that correlation to unmeasured periods. Tributary inflow has been measured at Pacific Creek (Pacific Creek at Moran, station number 13011500) and at Buffalo Fork since 1944, although the gage was moved from the mouth (Buffalo Fork near Moran, station number 13012000) to upstream from Lava Creek (Buffalo Fork above Lava Creek near Moran, station number 13011900) in 1965. We estimated inflow from the entire Buffalo Fork watershed by multiplying the unit runoff for the upstream gage to the entire watershed area for the post-1965 period:

$$Q_{\mathrm{mouth}} = (Q_{\mathrm{above\ LC}}/A_{\mathrm{above\ LC}})\ A_{\mathrm{mouth}} \qquad (1)$$

where Q is mean daily discharge, A is drainage basin area, and the subscripts refer to the location of the gages at the mouth ($_{\mathrm{mouth}}$) and upstream from Lava Creek ($_{\mathrm{above\ LC}}$). Only sporadic and incomplete inflow data are available for other tributaries.

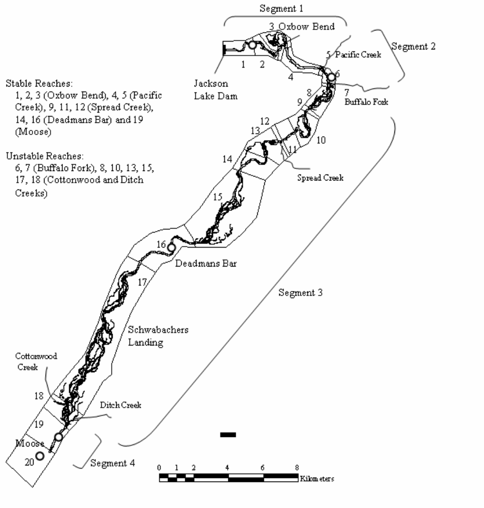

Figure 2. Map of the Snake River from JLD to Moose. The four segmats are the portions of the of the river analyzed for hydrologic change, numbers refer to reaches analyzed for channel change, outlined with think black lines, hollow circles are location of paited rock, the river channel is that of 2002. :

We added daily inflows from Pacific Creek and Buffalo Fork to daily data at the dam to estimate main-stem mean daily discharge since 1944 upstream from Ditch Creek. We calculated the least-square linear regression between the estimated flow upstream from Ditch Creek and that measured at Moose for the period since 1995 and estimated flows at Moose since 1944 by application of the regression equation. We established the correlation between flows at the dam and between Pacific Creek and Buffalo Fork for the period since 1944 and estimated flows in this segment since 1916 by application of this correlation to the mean daily discharge at the dam. We estimated flows further downstream in a similar fashion by correlation of estimates for an overlapping period and application of this correlation to the 1916-1944 estimates for the upstream segment. The R^2 values of each regression equation exceeded 0.93 (Table 1). We did not analyze flows prior to 1916 because the 13 years of record consisted of 5 years of natural flows, 3 years of flows regulated by a log-crib dam, and 5 years of flows during construction of the larger dam and did not represent a stable flow regime suitable for analysis.

Two data series used to create regression	Regression for Mean Daily Flows	R^2
Segments 1, 2	$y = 1.1083x + 105.19$	0.9441
Segments 2, 3	$y = 1.3005x + 91.855$	0.9306
Segments 3, 4	$y = 1.0987x + 280.97$	0.9877

Table 1: Linear regressions used to estimate flows for the Snake River for Segments 2-4.

Flood frequency was estimated for the maximum mean daily discharge. Calculation of maximum mean daily discharge for each segment provides comparable data not confounded by the addition of instantaneous and mean daily data, because the measured instantaneous annual peak flow immediately downstream from JLD rarely occurred on the same day as the annual instantaneous peak of the tributaries. Estimates of maximum mean daily discharge are also better compared with unregulated conditions, because estimates of annual instantaneous peak flow released from the dam have not been made. The difference between instantaneous and mean daily peak flows is small; the instantaneous annual peak flow was typically less than 5% greater than the maximum mean daily discharge for the Snake River at the dam and at Moose. Flood recurrences were calculated for the Log-Pearson Type III distribution (Linsley et al., 1982). Because bias and error influenced station estimates of the skew coefficient used in these calculations, especially as the number of observations in the series decreased, we calculated a weighted coefficient of skewness (IACWD, 1982). We obtained the regional skewness factor, -0.1, from a map of generalized skew coefficients for the United States and used the variance in regional skew, 0.302, estimated for the United States (IACWD 1982). The duration of mean daily flows for each segment were also determined.

Channel Change

Channel location and surface area were mapped on 4 aerial photographs or orthophotography (Table 2), and these data were entered into a GIS. We mapped the water surface and also estimated the area of the bankfull channel, because the surface area of the flow is partly dependent on discharge. The edges of the bankfull channel were defined as the boundary between vegetated surfaces and the water or between the floodplain and unvegetated deposits. Thus, the bankfull channel includes the mapped flow area at the time of photography and unvegetated, mid-channel and bank-attached gravel bars adjacent to the floodplain.

	Discharge (m^3/s)			
Image Date	Segment 1	Segment 2	Segment 3	Segment 4
7/1/1945	81.3	97.1	136.4	157.9
9/8/1969	73.9	75.4	82.7	98.8
8/7/1990	53.8	55.9	68.6	83.4
7/4/1991	56.1	63.0	121.6	141.6
7/10/2002	70.2	75.0	106.4	126.6

Table 2: Mean daily discharges for each segment of the Snake River below JLD for dates of photograph series

The aerial photographs were orthorectified by matching fixed locations such as road junctions, trees, buildings, and distinct landscape elements common to the aerial photographs and orthophotographs. Two main sources of error were inherent in orthorectification (Table 3). First, there was error associated with initial mapping and digitizing of the channel. This error was quantified by calculating the product of the half width of a pencil line (0.15 mm) and the scale of the aerial photograph. Second, there was error associated with orthorectifying the photographs. The root mean square (RMS) error of each tic for each photograph in each series was calculated. Average RMS errors were less than 1 m for each photograph series. The total linear error inherent in mapping the channel and orthorectifying the aerial photographs was determined by calculating the square root of the sum of the squares of each error (Geauman et al., 2003). For error calculations of channel width, the total linear error was doubled to account for linear error on both sides of the channel. These are conservative error calculations as other, smaller, sources of error not included in this analysis may be associated with digitizing and overlaying layers in a GIS (Geauman et al., 2003, 2005).

We integrated these data with the GIS data of Mills (1991) for 1975 and 1989. However, the data of the earlier studies could not be ortho-rectified into our data base with acceptable precision, and we compared the spatially averaged values with those that we computed.

Year of Aerial Photograph	Scale of Photograph	Mapping Error (m)	RMS Error (m)	Total Linear Error (m)
1945	1:56,000	8.4	0.94	8.45
1969	1:16,000	2.4	0.93	2.57
1990/1991	1:56,000	8.4	0.67	8.43
2002	1:12,000	1.8	0.00*	1.80

Table 3: Error associated with mapping the channel and orthorectifying the aerial photographs. RMS = root mean square. See text for details.

* There was no RMS error for 2002 because these photos were digital and mapping of the channel was completed solely on the computer.

We developed several metrics to describe channel change. These metrics included channel activity, bankfull channel width, and braid index. Channel activity is defined as the total area, per unit longitudinal distance, of channel erosion and deposition per year. Erosion and deposition were determined by overlay of channel position maps within the GIS and determining changes of floodplain to channel and channel to floodplain between different years. Bankfull channel width was defined as the bankfull channel area divided by the reach length. We also estimated the bankfull area from the Mills (1991) maps for 1975 and 1989, although the dimensions of the bankfull channel were not explicitly mapped. Bankfull area was estimated by scaling the Mills (1991) data by the ratio of water surface to bankfull area. We calculated this ratio for 1945 and 1990/1991, which were the two photograph series in which our data was based on the same (1945), or similar (1989 and 1990/91), data to those of Mills (1991) (Table 4). Since the braid index is the ratio of total channel length to main channel length (Church, 1995), no scaling was necessary to calculate the braid index from our data base or that of Marston et al. (2005).

Year of Aerial Photo	Marston et al. (water's edge)	This study (water's edge)	This study (bankfull)	Marston's water's edge vs. this study's bankfull	Marston et al. (recalculated for bankfull)
	Area (m^2)	Area (m^2)	Area (m^2)	% Difference	Area (m^2)
1945	4,501,786	5,107,579	5,930,512	31.74	5,857,142
1975	4,316,403	--	--	--	5,615,945
1989	4,398,948	--	--	--	5,723,342
1990/91	--	4,770,057	5,651,648	28.48	--
Average				30.11	

Table 4: Channel area data from Marston et al. (2005) recalculated to approximate bankfull channel area. See text for details.

Channel change metrics were calculated for 19 reaches in the study area (Figure 2). Reach boundaries were defined by the locations of tributary inflows, channel organization, and the degree of valley confinement. We calculated channel area for the four photo series of our data base for each reach and calculated braid index for each reach for the four series in our data base as well as the data of Mills (1991) and Marston et al. (2005).

Bed Mobility

We estimated bed mobility by marking tracer rocks on gravel bars and determining the flows when these particles moved. Tracers were marked by painting yellow stripes or circles on exposed bars or by placing painted rocks into the low flow channel prior to the 2005 runoff season. In the latter case, we placed rocks that represented the D_{16}, D_{50}, and D_{84} of the gravel bar. We placed 266 particles into the low flow channel and otherwise painted more than 4,800 clasts on exposed bars. Locations of tracers were between JLD and the Oxbow Bend, below Pacific Creek, at Deadmans Bar, and above and below the bridge at Moose (Figure 2). Photographs and surveys before and after the high flows helped relocate painted clasts and track changes in topography. The movement or absence of movement of tracers was recorded periodically during the rise of the spring flood. Once the flood receded and painted clasts were fully exposed, the locations of the clasts were identified and the distance and direction that each had moved was measured. In an effort to generalize the range of flows that initiate bed movement, boundary shear stress (τ_o) and dimensionless shear stress (τ^*) were calculated for the locations of tracer injection and the conditions where movement, or no movement, was observed

$$\tau_o = \rho g h S \qquad (2)$$

$$\tau^* = \tau_o / (\rho_s - \rho) g D_i \qquad (3)$$

where ρ_s, ρ, and g refer to sediment density, water density and gravitational acceleration respectively, h is the flow depth over the tracers, S is the local slope, and D_i is the b-axis diameter of the particles. Surveys of benchmarks and the water surface at flood flow were used to calculate the local slope and depth over the tracers. For each location of painted rocks, we calculated the active proportion of the bed using the classification of Haschenburger and Wilcock (2003). Active proportions less than 10% were considered immobile, between 10 and 90% partially mobile, and greater than 90% fully mobile. Thresholds of dimensionless critical shear stress were calculated for locations changing from one mobility category to another through the high flows.

✦ RESULTS

Hydrology

The hydrology of the Snake River at the dam during the past century includes 5 periods of relatively high runoff when the annual discharge exceeded the long-term average; this average for the period between 1904 and 2005 is 40.7 m^3/s. The longest consecutive periods of above average runoff occurred near the beginning and end of the measurement period -- between 1907 and 1918 when 10 of 12 years were above average and between 1996 and 2001 when there were 6 consecutive years above average. Other periods of high runoff occurred between 1944 and 1956 when there were 9 years of above average runoff, between 1970 and 1976 when there were 6 years above average, and between 1982 and 1986 when there were 5 consecutive years above average. These periods of high average runoff also occurred downstream from Pacific Creek and Buffalo Fork, because the cycles of high and low runoff of these tributaries were in phase with the runoff pattern from further upstream (Fig. 3).

Although the magnitude of the flood regime at the dam between 1916 and 1958 was not significantly different from that predicted for the unregulated flow regime (Fig. 4A, B), the timing of the flood was delayed approximately 2 months so that the largest amount of flows were delivered downstream when irrigation needs were greatest (Fig. 5A). The magnitude of the 2-year recurrence flood was 17% less than predicted for the unregulated flow regime, and the magnitude of the 10-year recurrence flood was approximately 14% less than that of the unregulated regime. The mismatch in timing of high dam releases with unregulated floods on tributaries resulted in a 22% reduction in the 2-year recurrence peak flow between Buffalo Fork and Ditch Creek, because tributary flooding preceded the season of peak dam releases (Table 5).

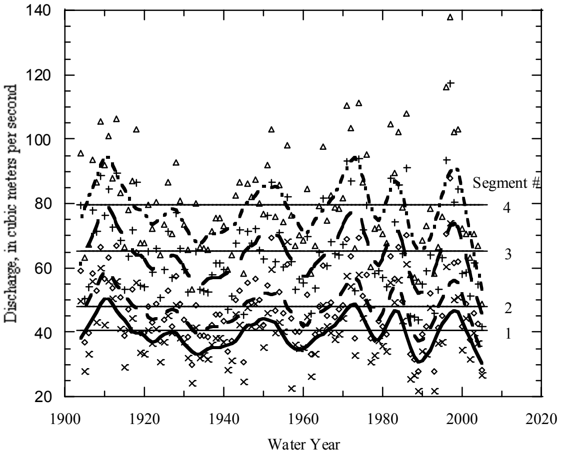

Figure 3. Mean Annual flows for each segment of the Snake River in GTNP. Curved lines are weighted solid horizontal lines are the average discharge over the entire period for each segment.

After 1958, reservoir release rules were changed and lower peak flows were released at approximately the same time that unregulated tributaries were in flood (Fig. 5A). Thus, the magnitude of flood reduction immediately downstream from the dam increased, but the magnitude of flood reduction further downstream was partially offset by tributary inflows. Between 1959 and 2005, the 2-yr recurrence flood was reduced, in relation to the estimated unregulated flood, by 45% immediately downstream from the dam, but by only 36% between Buffalo Fork and Ditch Creek. Thus, the change in operations of JLD that occurred in the late 1950s caused a very different degree of flood reduction immediately downstream from the dam and elsewhere in the study area. For example, the 2-year recurrence flood between the dam and Pacific Creek was reduced 32% from that prior to 1958, but the magnitude of floods downstream from Buffalo Fork only decreased 19%. The duration of flows also changed greatly after 1958 and the characteristics of these changes differed near JLD in relation to further downstream. The duration of base flows of 20 m^3/s increased after 1958 by 38% near the dam and by 52% downstream from Buffalo Fork (Table 6). In contrast, the duration of common floods such as 200 m^3/s decreased by 80% near the dam and by 54% downstream from Buffalo Fork. Thus, the longitudinal pattern of the duration of base flows and common floods differed before and after 1958. Before 1958, the duration of common floods increased 310% from upstream of Pacific Creek to downstream of Buffalo Fork. After 1958, the duration of this flow increased to a much greater degree -- 850% -- due to the change in timing of high dam releases and tributary inflows.

	Segment 1		Segment 2		Segment 3		Segment 4	
Recurrence Interval	Estimated Unregulated	Regulated	Estimated Unregulated	Regulated	Estimated Unregulated	Regulated	Estimated Unregulated	Regulated
1916-1958								
1.25	217	185	263	211	345	282	387	318
2	276	230	334	255	434	340	485	381
5	338	285	409	317	534	419	595	468
10	371	319	449	358	590	472	656	526
1959-2005								
1.25	221	126	264	146	336	215	378	243
2	288	157	349	191	433	276	484	307
5	352	202	426	252	545	361	606	401
10	381	234	460	291	608	418	675	467

Table 5: Magnitude of floods (m^3/s) of four recurrence intervals for the four segments of the Snake River. Estimated unregulated and regulated values are provided for the periods before and after 1958.

Discharge (m^3/s)	Segment 1	Segment 2	Segment 3	Segment 4
1916-1958				
20	121 (days)	129	140	150
50	102	106	112	119
100	66	76	93	99
200	10	19	41	54
1959-2005				
20	167	187	213	344
50	123	132	133	163
100	39	55	71	109
200	2	6		31

Table 6: Flow duration (in number of days) for four flows for each segment before and after 1958

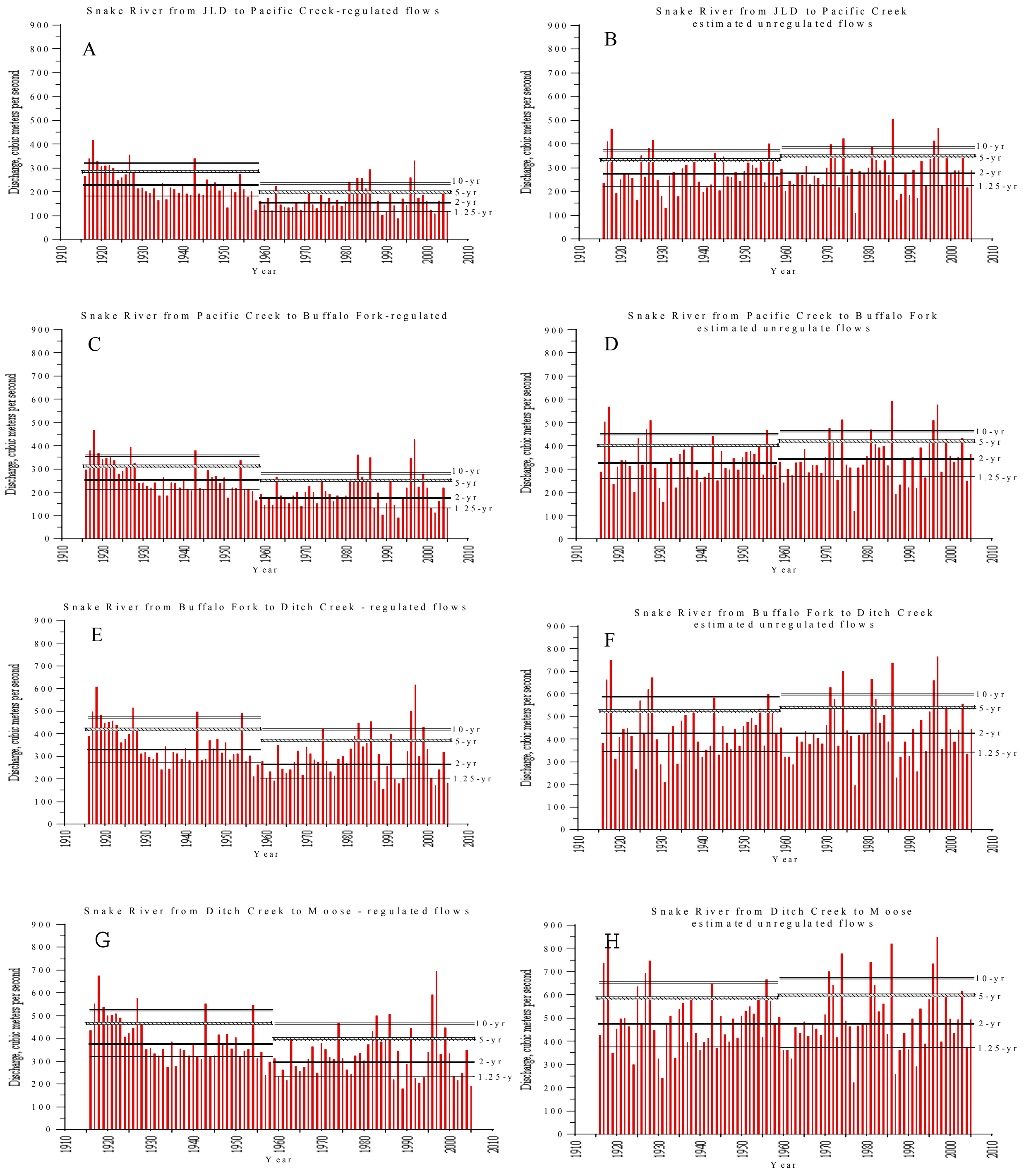

Figure 4: Hydrographs for the Snake River for regulated and estimated unregulated flows for (A,B) Segment 1, (C,D) Segment 2, (E,F) Segment 3 and (G,H) Segment 4. Data based on highest mean daily flow for each year 1916-2005. Magnitudes of floods of 4 recurrence intervals for before and after 1958 are shown.

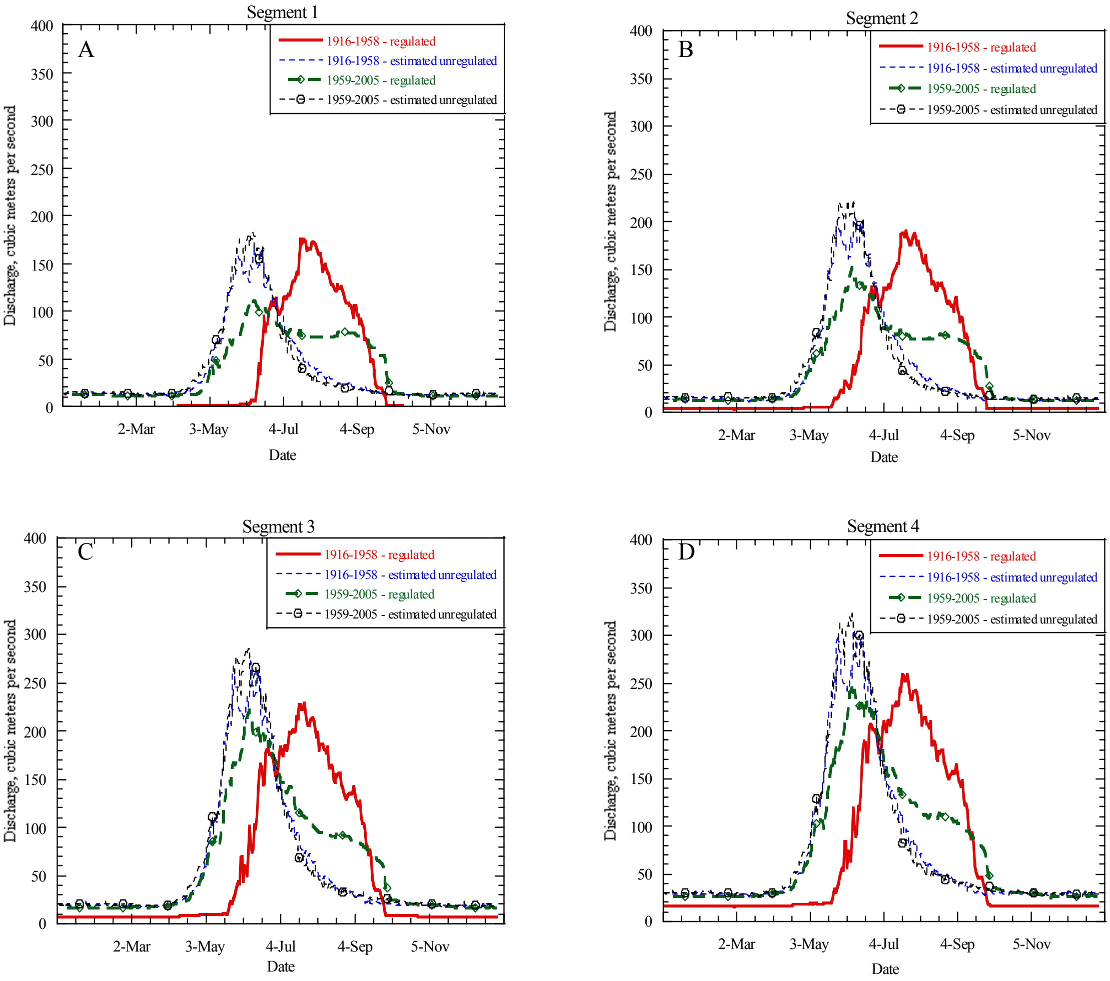

Figure 5: Hydrographs for regulated and estimated unregulated flows before and after 1958 for each segment of the Snake River. Data based on mean daily discharge.

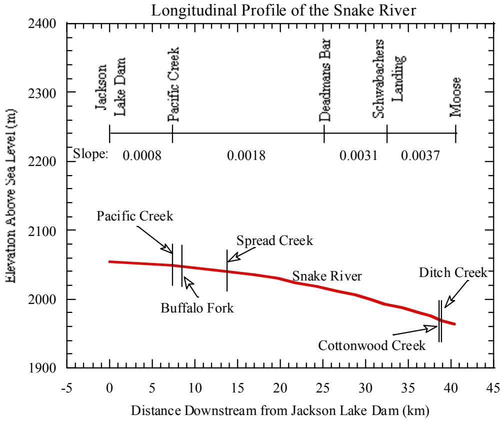

Figure 6: Longitudinal profile of the Snake River from JLD to Moose with tributaries and changes in slope superimposed.

✦ DISCUSSION

The changes to the hydrologic regime of the Snake River in GTNP are relatively small compared to some regulated rivers in the western United States. Since the flow regime change in 1958, the 2-yr flood of the Snake River immediately below JLD decreased 32%. Regulation of Glen Canyon Dam resulted in a 65% decrease of peak flows on the Colorado River (Stevens et al., 1995), that of Flaming Gorge Dam a 57% decrease in the 2-yr flood on the Green River (Grams and Schmidt, 2002), and that of many small diversions a 53% decrease in stream flow on the lower Duchesne River (Gaeuman et al., 2005). Flow contributions of unregulated tributaries caused the magnitude of decreases in flows on the Snake River in

GTNP to reduce to 25% below Pacific Creek and 19% below Buffalo Fork. This means the flow regime change in 1958 reduced flows by only 19% for 35.2 of the 43.4 km of the Snake River in GTNP.

Due to this relatively small change in the flow regime of the Snake River in GTNP, minor long-term impacts to the geomorphology of the Snake River alluvial valley might be expected.

The longitudinal profile of the Snake River from JLD to Moose must be considered in a discussion of downstream trends. The entrance of the tributaries Pacific Creek and Buffalo Fork coincide with a substantial increase in channel gradient from 0.0008 below JLD to 0.0018 below Pacific Creek, 7 km downstream (Figure 6). The gradient continues to increase below Deadmans Bar (0.0031) and Schwabachers Landing (0.0038), 25 and 33 km downstream of JLD respectively. These changes in gradient should result in increased bed mobility, braiding, and channel change with downstream distance from JLD. Because of this, the channel change analysis of individual reaches is important in identifying reaches and periods of time of increased deposition or erosion. Though the channel change and bed transport studies will help determine if the Snake River is capable of transporting sediment delivered by tributaries, a sediment budget for the Snake River and tributaries is necessary for a more complete understanding.

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ALLOMETRIC MODEL DEVELOPMENT IN LODGEPOLE PINE FORESTS OF THE GREATER YELLOWSTONE ECOSYSTEM

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✦ INTRODUCTION

Allometric equations for estimating above- and belowground biomass of lodgepole pine have been developed in Alberta, Canada, southeastern British Columbia, southeastern WY, and in Washington and Oregon (Johnstone 1971; Comeau and Kimmins 1989; Pearson et al. 1984; Gholz et al. 1979, respectively). More recently, allometric equations for young lodgepole pine saplings have also been developed in Yellowstone National Park (YNP) for aboveground biomass by Turner et al. (2004), and for belowground biomass by Litton et al. (2003). However, because of variability in latitude, growing conditions, substrate and climate, existing equations that predict biomass for mature lodgepole pine trees are not appropriate for use in the Greater Yellowstone Ecosystem (GYE), and new allometric equations specific for the GYE are needed. In this study, we will develop new allometric equations for predicting above- and belowground biomass in mature lodgepole pine forests of the GYE.

The specific objective of this study was to develop allometric models for predicting above and belowground biomass of mature lodgepole pine trees in the GYE, and determine how these equations differ with stand density and age.

✦ MATERIALS AND METHODS

STUDY AREA

The study area was within the GYE on the Caribou-Targhee National Forest (CTNF) bordering YNP. The dominant forest type is lodgepole pine forest, which occurs at middle elevations, but Spruce/ Fir (*Picea engelmanii /Abies lasiocarpa*) forests occur at higher elevations and Douglas-fir (*Pseudotsuga menziesii*) forests occur at lower elevations.

Field and Lab Methods

Allometric equations were developed in three lodgepole pine stands on the CTNF that represented two age classes and two density classes. In the young (64 years old) age class, two stands of different densities were examined; one dense (YD) (2,452 trees/ha) and the other sparse (YS) (725 trees ha^{-1}). Because densities of lodgepole pine stands tend to converge as they get older (Kashian et al. 2005), a single sparse (674 trees ha^{-1}) stand was sampled in the older age class (OS) (164 years old).

Although sites differed in density and age, they were located on similar soils. The Koffgo soil series consists of loamy-skeletal, mixed, superactive Vitrandic Cryochrepts. All sites were located at least 50 m from the road to facilitate equipment hauling and to avoid road influences.

All aboveground tree biomass totaling 46 trees was harvested within the three stands, and 24 root systems were excavated to develop allometric equations where easily obtained morphological parameters, such as diameter at breast height, were tested as predictors of above and belowground tree components. Fourteen trees were harvested in the YD stand and 15 trees were harvested in the YS stand; 17 were harvested in the OS stand. For belowground components, 5 root systems were excavated in both the YS and OS stands due to logistical difficulties associated with large root systems, while 14 root systems were harvested in the YD stand.

Prior to harvest, DBH (diameter at breast height, 1.37m) and crown width were recorded. After felling of the tree, total height and height to crown base were measured. Crown base was defined as the point along the bole at the bottom of roughly 90% of the crown mass, and crown length was calculated as:

$$CL = H - HCB$$

where CL = crown length, H = total tree height, and HCB = height to the base of the live crown.

Aboveground Components

Tree Bole

Each bole was harvested and all branches were removed. For each bole, a disc was always taken at DBH and at 90% of crown base. Each bole section was weighed separately using a digital hanging scale (Salter-Brecknell). Discs were dried to a constant weight at 70°C in the lab to determine moisture content, and the dry: wet weight ratio for each disc was applied to determine dry weight of the entire bole section. For each DBH and crown base subsample, the following measurements were taken for determining sapwood area: phloem + bark thickness, total diameter, and heartwood diameter. Sapwood diameter can be determined by subtracting the diameter of phloem + bark and heartwood diameter from total diameter.

Branches

Branches were cut flush with the tree bole and were separated from foliage at 6.4 mm in diameter. Thus, branches consisted of all shoots minus the tree bole that were greater than 6.4 mm in diameter, because biomass smaller than 6.4 mm are likely to be consumed by fire (Despain 1990), allowing for post-fire estimates of branch biomass, independent of fine fuels that were likely to be consumed the fire. A subsample of approximately 4.0 L was taken to determine moisture content for dry weight for each tree, where it was then dried in the lab.

Fine Fuels

The fine fuels component was considered to be all needles and associated twigs less than 6.4 mm in diameter. The fine fuels component was maintained in separate piles of lower, middle, and upper crown sections for each tree, since foliage moisture contents were likely to vary with crown height (Brown 1978). A random subsample approximating the size of approximately 4.0 L volume was taken from each crown section to determine moisture content. The fine fuels subsamples were then weighed to obtain wet weight.

Belowground Components

For each tree, the entire coarse root system (>10mm diameter) was excavated with a backhoe or come-a-long. After excavation, the root system was divided into four size classes: root crown (i.e. the massive structure directly beneath the tree bole), lateral roots >50mm in diameter, lateral roots 25-50mm in diameter, and lateral roots 10-25mm in diameter. Total weight of each root size class was weighed using a digital hanging scale. Subsamples were taken and weighed to determine moisture content for dry weight of each size class.

Statistical Analyses and equation development

All allometric models were developed with SPSS 13.0 (SPSS Inc. 2005). Models for each tree component (Table 1) were developed for the three individual stands, for all sites combined, and were also pooled by density and age.

Model Comparison

Density and Age

To determine whether allometric models differed between stands of varying densities and ages, models pooled by density and age, were compared using the extra sum of squares analysis for nested models (Bates and Watts 1988). In addition, equations for total aboveground biomass and coarse root biomass were used to predict biomass in a different stand from where they were developed. For instance, pooled equations from the two young stands were used to predict above and belowground biomass in the older stand, to determine the degree of error produced from using an inappropriate model.

Non Linear Power Functions ($y = ax^b$, or $y = ax^bx_2^c$)

(Y)	(X)	Site(s)	DBH range (cm)	*n*	*a*	*b*	*c*	R^2	MSE
Total Aboveground Biomass	Volume**	All Sites	5.4 - 33.3	46	0.005	0.793	-	0.95	679.6
	-	Old, Sparse	11.3 - 33.3	17	0.003	0.817	-	0.94	758.4
	-	Young, Dense	5.4 - 15.6	14	0.00004	1.155	-	0.84	109.9
	-	Young, Sparse	11.7 - 25.0	15	0.0004	1.001	-	0.92	445.2
	-	2 Young Stands	5.4 - 25.0	29	0.0001	1.088	-	0.95	289.4
	-	2 Sparse Stands	11.3 - 33.3	32	0.010	0.741	-	0.94	810.0
Total Coarse Root Biomass (>10mm)	Basal Area (cm^2)	All Sites	5.4 - 32.0	24	0.028	1.139	-	0.95	11.8
	-	Old, Sparse	11.3 - 32.0	5	0.188	0.845	-	0.93	36.4
	-	Young, Dense	5.4 - 15.6	14	0.005	1.467	-	0.98	0.3
	-	Young, Sparse	12.7 - 24.3	5	0.002	1.579	-	0.95	8.3
	-	2 Young Stands	5.4 - 24.3	19	0.006	1.406	-	0.97	2.0
	-	2 Sparse Stands	11.3 - 32.0	10	29.939	-0.179	-	0.99	5.8
Root Crown Biomass	Basal Area (cm^2)	All Sites	5.4 - 32.0	24	0.020	1.109	-	0.84	13.6
	-	Old, Sparse	11.3 - 32.0	5	0.224	0.745	-	0.71	65.5
	-	Young, Dense	5.4 - 15.6	14	0.007	1.267	-	0.93	0.2
	-	Young, Sparse	12.7 - 24.3	5	0.007	1.284	-	0.89	5.3
	-	2 Young Stands	5.4 - 24.3	19	0.006	1.304	-	0.95	1.1
	-	2 Sparse Stands	11.3 - 32.0	10	0.050	0.968	-	0.73	33.8
Lateral Root Biomass (>10mm)	Basal Area (cm^2)	All Sites	5.4 - 32.0	24	0.008	1.193	-	0.94	2.1
	-	Old, Sparse	11.3 - 32.0	5	0.010	1.146	-	0.94	4.8
	-	Young, Dense	5.4 - 15.6	14	0.0004	1.738	-	0.91	0.2
	-	Young, Sparse	12.7 - 24.3	5	0.00003	2.153	-	0.94	2.6
	-	2 Young Stands	5.4 - 24.3	19	0.001	1.564	-	0.94	1.0
	-	2 Sparse Stands	11.3 - 32.0	10	0.011	1.147	-	0.89	5.2
Branches	Basal Area (cm^2), Crown Length$_2$ (m)	All Sites	5.4 - 33.3	46	0.022	0.683	1.276	0.69	69.3
	-	Old, Sparse	11.3 - 33.3	17	0.003	1.136	0.850	0.86	21.6
	Basal Area (cm^2)	Young, Dense	5.4 - 15.6	14	0.002	1.548	-	0.91	0.4
	-	Young, Sparse	11.7 - 25.0	15	0.004	1.497	-	0.76	67.9
	Basal Area (cm^2), Crown Length$_2$ (m)	2 Young Stands	5.4 - 25.0	29	0.001	1.855	-0.291	0.88	34.6
	-	2 Sparse Stands	11.3 - 33.3	32	0.042	0.528	1.288	0.54	96.2
Fine Fuels	Basal Area (cm^2), Sapwood Area$_2$ (cm^2)	All Sites	5.4 - 33.3	46	0.418	0.466	0.418	0.68	184.8
	-	Old, Sparse	11.3 - 33.3	17	0.524	0.323	0.403	0.81	58.3
	Basal Area (cm^2)	Young, Dense	5.4 - 15.6	14	0.002	1.695	-	0.96	1.4
	-	Young, Sparse	11.7 - 25.0	15	0.011	1.427	-	0.86	97.1
	-	2 Young Stands	5.4 - 25.0	29	0.007	1.512	-	0.93	48.7
	Sapwood Area (cm^2)	2 Sparse Stands	11.3 - 33.3	32	1.204	0.638	-	0.52	220.9
Needles	Basal Area (cm^2), Sapwood Area$_2$ (cm^2)	All Sites	5.4 - 33.3	46	0.192	0.525	0.317	0.73	67.0
	-	Old, Sparse	11.3 - 33.3	17	0.249	0.323	0.471	0.82	33.0
	Basal Area (cm^2)	Young, Dense	5.4 - 15.6	14	0.002	1.600	-	0.91	1.5
	-	Young, Sparse	11.7 - 25.0	15	0.014	1.312	-	0.78	60.3
	-	2 Young Stands	5.4 - 25.0	29	0.007	1.426	-	0.89	30.7
	Sapwood Area (cm^2)	2 Sparse Stands	11.3 - 33.3	32	0.563	0.701	-	0.61	78.5
Tree Bole	Volume**	Old, Sparse	11.3 - 33.3	17	0.002	0.822	-	0.93	608.5

(Linear Models, $y = ax + b$)

(Y)	(X)	Site(s)	DBH range (cm)	*n*	*a*	*b*	*c*	r^2	SE
Tree Bole	Volume**	All Sites	5.4 - 33.3	46	0.0002	3.420	-	0.96	17.9
	-	Young, Dense	5.4 - 15.6	14	0.0002	-0.327	-	0.79	8.9
	-	Young, Sparse	11.7 - 25.0	15	0.0002	0.055	-	0.95	7.6
	-	2 Young Stands	5.4 - 25.0	29	0.0002	5.482	-	0.93	8.9
	-	2 Sparse Stands	11.3 - 33.3	32	0.0002	1.921	-	0.95	20.8

Table 1. Allometric equations for predicting biomass (Kg) of eight different above and belowground components of *P. contorta* in the Greater Yellowstone Ecosystem. Non-linear power functions are listed first, and linear equations are at the end of the table. MSE is the mean square error for non-linear models, SE is the standard error of the estimate for linear models, *n* is the sample size, and *a*, *b*, and *c* are constants. X is the morphometric predictor variable and Y represents the response variable (biomass (Kg). The subscript $_2$ is for predictors that are associated with the coefficient *c* in non-linear models. ** Volume is the product of basal area in cm^2 and height in meters.

✦ RESULTS

ALLOMETRIC EQUATION DEVELOPMENT

Equation summaries

Forty-eight allometric equations for all measured tree components are shown in Table 1. R^2 values ranged from 0.54 to 0.99, and 37 out of the 48 models had R^2 values > 0.80. For many of the measured tree components, equation strength decreased with increases in tree size, indicating greater variability in the biomass of larger trees. No single independent variable worked best for all allometric equations. Tree volume was the best predictor of both total aboveground biomass and bole biomass, regardless of stand density or age.

The most robust allometric equations were those that predict total aboveground, bole, total coarse root, and lateral root biomass; 23 of 24 of these equations had R^2 values > 0.89. In contrast, the remaining 24 equations, which predict root crown, branch, fine fuel, and needle biomass, were somewhat less robust; 13 of these equations have R^2 values between 0.80 and 0.89, and 9 equations have R^2 values < 0.80.

For many of the tree biomass compartments, including total aboveground biomass, bole biomass, branch biomass, and all root biomass compartments, a single equation that combined morphometry data from all three sites was more robust than equations that aggregated the sites by density or age. However, in general, when aggregated, grouping the sites by tree age produced stronger equations than aggregating by tree density (Table 1).

Equation Comparisons between Stand Densities and Stand Ages

For the 10 equations where statistical comparisons were possible, seven of the 10 equations tested differed significantly ($p < 0.05$) when aggregated by stand density or age. Interestingly, although the equations for root crown and lateral root biomass differed significantly when aggregated by stand age, no significant differences were found in equations aggregated by stand density. In addition, equations for total aboveground biomass were slightly more similar when aggregated by density ($p = 0.037$) than by age ($p < 0.001$).

✦ DISCUSSION

Allometric equation development

Variation in stand density and age affected which of several measured tree morphometric parameters would best predict biomass of lodgepole pine tree components. The product of tree basal area and total height (volume) was the best predictor of total aboveground and bole biomass (Table 1). Notably, a tree's ability to produce stemwood biomass, a major component of tree bole and total aboveground biomass, is strongly influenced by site productivity (Barnes et al. 1980). Therefore, a model including tree height, a variable relating more strongly to site productivity than any other measured parameter (Barnes et al. 1980), can explain a large amount of the variability in bole and total aboveground biomass.

Total coarse root biomass (>10 mm), root crown biomass, and lateral root biomass are best explained by tree basal area (Table 1), where tree diameter and basal area are measured parameters most closely correlating with spacing effects related to tree density (Barnes et al. 1980), suggesting coarse root biomass is at least partly dependent on tree spacing.

Most of the variability in needle and foliage biomass is explained by basal area and sapwood area (Table 1). Sapwood area has been found to be a good predictor of foliage biomass in other studies (Pearson et al. 1984; Comeau and Kimmins 1989), because it is a good measure of a tree's ability to conduct water and nutrients. Needle and foliage biomass in the older stand was best explained either by sapwood area or a combination of sapwood and basal area (Table 1). In contrast, basal area was the single best predictor of foliage biomass in younger stands (Table 1), indicating that foliage biomass in younger forests is better explained by tree spacing rather than by the tree's ability to conduct water and nutrients.

Differences between densities and ages

Allometric models were expected to differ between densities and ages due to differences in biomass allocation patterns. For the most part, this was supported by the data. However, models for tree bole, root crown, and lateral roots did not differ when pooled by density, and models for aboveground biomass were less different when pooled by density than by age. One plausible explanation for this pattern is that stand densities may not have been different enough for some of the models to differ according to stand density or to be less different than for models pooled by age. Although 2,452 trees ha^{-1}

was considered in this study to be a dense stand, "dog-hair" stands of lodgepole pine that are of comparable age can sometimes reach densities higher than 10,000 trees ha^{-1}. Therefore, the relatively small difference in stand densities in this study may contribute to the relative similarity of models pooled by density compared with models pooled by age. Although allometric equations appear to be more similar across densities, application of models significantly different in density from where they were developed should be approached with caution. Furthermore, inappropriate model use can cause significant errors when extrapolating allometric equations to the landscape scale.

✦ ACKNOWLEDGEMENTS

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FIRE AND VEGETATION HISTORY OF THE LAST 2000 YEARS IN JACKSON HOLE, WYOMING

✦

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✦ INTRODUCTION

Fire is an important form of natural disturbance in nearly all terrestrial ecosystems in the western United States, and it serves as a critical link between climate change and ecosystem response (Agee, 1990; Swetnam and Betancourt, 1998). The nature of these linkages depends on the time scale of interest. On short time scales, climate/weather and vegetation characteristics affect the fire conditions of particular years (and decades), as well as the dynamics of post-fire ecological succession. On centennial and millennial time scales, large-scale changes in climate alter regional fire regimes and vegetation composition. The linkages are especially complex in the western U.S., where fire regimes vary across environmental gradients and include frequent surface fires as well as infrequent stand-replacement events.

Fire-history information is obtained from two complementary data sets: tree-ring records and lake-sediment charcoal records. Tree-ring records are spatially precise but temporally limited by the age of living trees and subfossil wood (Arno and Sneck, 1977; Johnson and Gutsell, 1994; Baker and Ehle, 2001). Charcoal records, obtained from the sediments of natural lakes and wetlands, span a much longer time and are associated with pollen records that provide information on the vegetation history of an area (Whitlock and Larsen, 2001). Most charcoal-based fire-history studies have been conducted in middle- and high-elevation forest ecosystems, where natural lakes are abundant. While our understanding of past fire regimes in these relatively mesic ecosystems is improving, we have almost no information on the long-term fire history of low-elevation forest and steppe, despite the fact that these ecosystems are especially sensitive to drought and land-use activities (Swetnam, 2002; McKenzie et al., 2004).

The last 2000 years of environmental history is of particular interest because it encompasses both human-induced and natural environmental change. In Grand Teton National Park (GTNP), displacement of Native Americans and their burning activities, as well as the impacts of Euro-American trappers, miners and homesteaders likely resulted in changes in vegetation and fire regime (Daugherty, 1999). Land management practices, including fire suppression, in the 20th century, have also shaped the composition and structure of forests and possibly steppe communities. Climate variations, such as the Medieval Climate Anomaly (ca. 1100 – 500 cal yr BP; Hughes and Diaz, 1994) and the Little Ice Age (ca. 450 – 50 cal yr BP; Bradley, 1999; Cook et al., 1999), have altered fire regimes and vegetation in GTNP, which in turn would have influenced human activities and impacts. Thus, land use, land management, climate, and fire have helped create the modern low-elevation ecosystems in the Grand Teton National Park, but the interactions among these variables are poorly understood.

Jackson Hole at the foot of the Teton Range is exceptional in the western U.S. in having a number of natural lakes in low-elevation settings suitable for paleoecologic research. To fill in the gap in our understanding of low-elevation ecosystems, we are developing a fire and vegetation history of the last 2000 years at three lake sites located in the dry forest and steppe communities of GTNP. Our sites are Hedrick Pond (lat. 43.73°N, long. 110.59°W, elev. 2048 m), Pothole Lake (lat. 43.78°N, long. 110.62°W, elev. 2033 m) and Swan Lake (lat. 43.89°N, long. 110.63°W, elev. 2072 m) (Fig. 1). Swan Lake is farthest north in the valley and surrounded by lodgepole pine forest. It is separated from Pothole Lake and Hedrick Pond by the Snake River and the southern end of Jackson Lake. Hedrick Pond lies at the ecotone between lodgepole pine and Douglas-fir forest to the south and east and sagebrush steppe to the west. Pothole Lake is located in sagebrush steppe in the middle of the valley; it is separated from Hedrick Pond by the Snake River.

Our objective is to examine the fire history in closely spaced sites to identify spatial and temporal patterns in the fire regime that might be related to human-induced or natural environmental change. Pollen data from lake-sediment cores provide information on vegetation changes, and charcoal records are used to develop a local fire history. Changes in lithology help assess variations in sediment input that might be related to shifts in lake production and watershed inputs. A chronology upon which to build the environmental history comes from radiometric dating of organic and core material. This investigation of Jackson Hole's history is part of a larger research effort to understand the Holocene vegetation, climate, and fire history of Greater Yellowstone Ecosystem (e.g. Whitlock, 1993; Whitlock and Bartlein, 1993; Whitlock et al., 1995; Millspaugh et al., 2004; Whitlock et al., 2006).

✦ METHODS

Sediment cores were collected from the three study lakes (Fig. 1). Cores were taken in the deepest part of the lakes from a floating platform constructed across two inflatable boats. Cores were obtained with a 5-cm-diameter Livingstone piston sampler, which retrieves meter-long cores, and a 7-cm-diameter short corer that recovers the mud-water interface and uppermost sediments. Cores were extruded in the field, wrapped in cellophane and aluminum foil, and transported back to the MSU Paleoecology Lab for study.

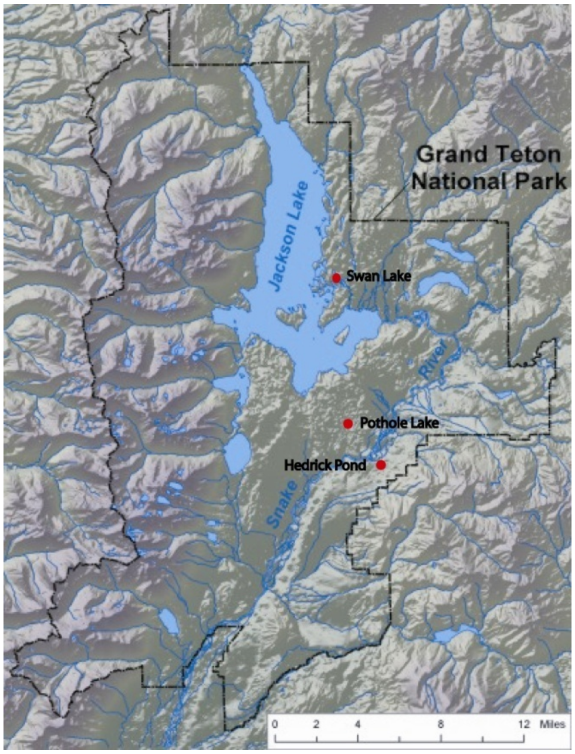

Figure 1: Map of Grand Teton National Park showing location of study sites.

Cores were split longitudinally for lithologic descriptions and subsampling. Changes in sediment color, composition, and lithology were described. One-cm^3 samples were dried at 90°C, and then ashed at 550°C, and 900°C. Weight loss after each heating was used to calculate percentages of dry weight, organic content, and carbonate content, respectively (Dean 1974). Magnetic susceptibility, an indicator of erosion of mineral soil or fire-created magnetite or maghemite (Thompson and Oldfield, 1986), was measured with a Bartington MS2 magnetic susceptibility machine**.** MS units were expressed as cgs x 10^{-6}.

A chronology for each lake was based on a series of ^{210}Pb dates on sediment and AMS ^{14}C dates obtained from terrestrial plant macrofossils. Radiocarbon ages were converted to calendar years, using the CALIB program of Stuiver et al. (2005). Age-depth models were developed for each site and used to describe the sedimentation rates (Fig. 2).

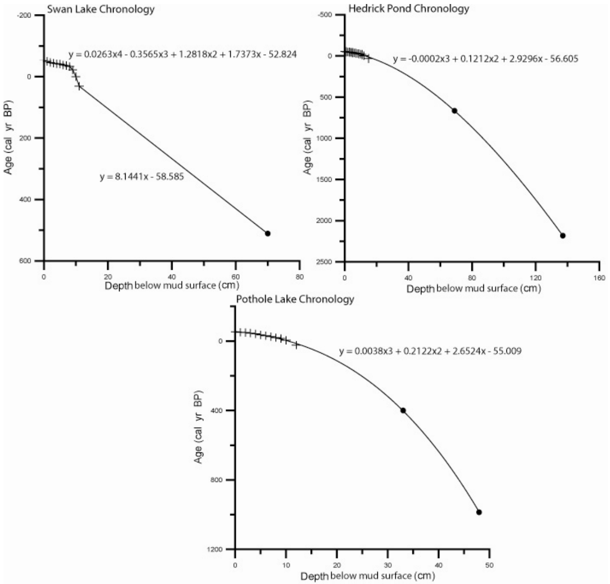

Figure 2: Age versus depth models based on ^{210}Pb (shown as +) and calibrated ^{14}C dates (shown as ●) for Swan Lake, Hedrick Pond and Pothole Lake. The Swan Lake chronology uses two different age models, one based on ^{210}Pb dates and the other based on the last ^{210}Pb date and the ^{14}C date. Other age models incorporate all dates.

Macroscopic charcoal analysis was performed on contiguous 1-cm interval samples to reconstruct the local fire history for each site (e.g. Long et al., 1998). Samples of 3 cm^3 (Hedrick Pond and Swan Lake) and 4 cm^3 (Pothole Lake) were soaked in a 5% solution of sodium metaphosphate and 6% bleach for 24 hours and washed through nested sieves (mesh size 250 and 125 μ). Residues were placed in a gridded Petri dish and identified under a stereoscope at magnifications of 120x and 250x. Charcoal abundance was calculated as charcoal concentration (particles/cm^3), and these data were converted to charcoal accumulation rates (CHAR; particles/cm^2/year) by multiplying charcoal concentration by sedimentation rate (cm/year).

The development of a fire history from the charcoal data followed the approach of Long et al. (1998). Time series of CHAR data were divided into two components. Background CHAR, or the low-frequency slowly varying component, was determined using a locally-weighted (moving) average through the time series. Variations in background CHAR represent changes in regional fire activity, charcoal stored in the watershed, or changes in the biomass of the surrounding area (Long et al., 1998; Whitlock and Larsen, 2001; Marlon et al., in press). For all sites in this study, a window width of 500 years was used to calculate background CHAR levels. This window width has become a standard for Greater Yellowstone area charcoal studies, and it produced a background signal that followed the broad frequency trends in the data (Marlon et al., in press). Peaks, or the high-frequency component, were identified as those levels that exceeded a prescribed threshold ratio of total CHAR to background CHAR. Charcoal peaks were inferred to be fire episodes (one or more fires per sample). A threshold ratio of 1.0, for example, identifies all CHAR values that exceed the background CHAR level as fire episodes. A fire event begins when the threshold ratio is first exceeded and ends when CHAR values drop below the ratio. A threshold ratio of 1.15 was used in this study, because it produced charcoal peaks that corresponded in time with recent fires in the vicinity of each site (Loope, 1974). The ratio did not pick up additional spurious peaks that were not associated with local fire (Figure 3).

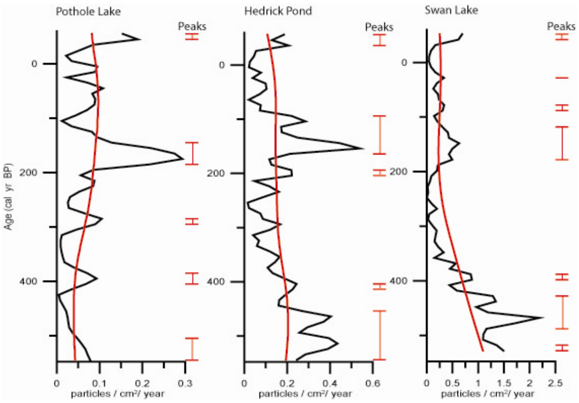

Figure 3: Fire reconstructions for Hedrick Pond, Pothole Lake and Swan Lake for the last 550 cal yr BP. Red line are charcoal accumulation rates (CHAR; particles/cm^2/year); black line is background CHAR calculated using a weighted window width of 500 years. Red bars mark fire episodes and begin when CHAR values exceed background CHAR level by a threshold ratio of 1.15.

Pollen samples were taken at regularly spaced intervals (approximately 30-year intervals) in each core and processed following the methods of Faegri et al. (1989). Pollen slides were counted under a microscope at 400x magnification. Common pollen types identified in the Jackson Hole area include *Pinus contorta* type (diploxylon-type *Pinus*), *Artemisia* spp., and *Picea* spp. Percentage data of terrestrial taxa were tallied based on the sum of all terrestrial taxa. Percentage of aquatic taxa was based on the sum of all taxa. A "spike" of *Lycopodium* spores of known concentration was added to each sample to calculate pollen concentration. Concentration data was multiplied by the sedimentation rate of each sample to calculate pollen accumulation rates (pollen/cm^2/year). Pollen work is ongoing and not presented in this report

✦ PRELIMINARY RESULTS

A 137-cm-long core was obtained from Hedrick Pond. The sediments consisted of homogeneous fine detritus gyttja, and the age-depth model suggested that core spanned the last 2100 cal yr BP. [Note: "cal yr BP" means calendar years before present with "present" set at AD 1950.] A 70-cm-long core from Pothole Lake consisted of an upper unit of fine detritus gyttja that graded downward into silty detritus gyttja (17-50 cm) and dry organic silty clay at the base. The bottom unit at 66 cm depth had a crumbly structure with fine rootlets and appeared to be a soil. Extrapolation from the lowest radiocarbon age at Pothole Lake suggests the existence of a lake environment for the last 2100 cal yr. A core from Swan Lake consists of fine detritus gyttja from 0-13 cm depth that was underlain by gray-brown clay from 13-47 cm depth, and dark brown mud with root fragments from 47-57 cm depth. A radiocarbon age from the mud unit had an age of 550 cal yr BP.

The Swan Lake charcoal record had a sampling resolution of about 9.6 years/cm. Background CHAR levels from 550 to 200 cal yr BP were ~1 particle/cm^2/year, and they decreased to ~ 0.3 particles/cm^2/year in the last 200 cal yr. Peaks were identified at ca. -30, 40, 100, 120-190, 400, 430-490, and 550 cal yr BP, and these are assumed to represent decades of local fire activity.

The resolution of the Hedrick Pond charcoal record is about 17.5 years/cm. Background CHAR was ~0.2 particles/cm^2/year between 2150 and 1500 cal yr BP, and decreased to ~0.13 particles/cm^2/year in the interval between 1500 and 750 cal yr BP. Background charcoal levels increased in the last 750 cal yr BP to ~0.2 particles/cm^2/year. Peaks occurred at ca. -30, 100-180, 200, 400, 560, 950, 1060, 1200, 1430, 1650, 1750, 2000, and 2130 cal yr BP.

At Pothole Lake, the deposition time of each sample was about 27.2 years/cm. The background charcoal was low ~0.04 particles/cm^2/year from 2100 to 1250 cal yr BP, and increased to ~0.1 particles/cm^2/year from 1250 to present. Peaks occurred in ca, -30, 140-190, 300, 400, 560, 700, 950, 1200, 1430, 1650, 1950, and 2130 cal yr BP.

✦ DISCUSSION

The last 550 years

Swan Lake, Hedrick Pond and Pothole Lake have concurrent charcoal peaks that suggest periods of widespread fires in -30 cal yr BP (AD 1980), 140-180 cal yr BP (AD 1810-1770), and 400 cal yr BP (AD 1550) (Fig. 3). Swan Lake also contains charcoal peaks at 40 cal yr BP (AD 1910) and 100 cal yr BP (AD 1850) that were not noted at the other sites. About 175 cal yr BP (AD 1775) and 400 cal yr BP (AD 1550), fires occurred close enough to each of the three sites to be registered in their charcoal records. Tree-rings record large fires in Jackson Hole about 190 cal yr BP (AD 1760), and these are likely the source of charcoal in the study sites (Loope, 1974).

Background levels of CHAR provide information on past levels of burning and the amount of charcoal produced during fire (Long et al., 1998). Swan Lake showed a decrease in background CHAR from ~1 particle/cm^2/year to ~0.3 particles/cm^2/year at about 500 cal yr BP (AD 1400). The period of decreasing background CHAR at Swan Lake coincided with the beginning of cooler/moister conditions during the Little Ice Age. It may be that this shift in fire regime reflects the development of lodgepole pine forest at Swan Lake and a reduction in available fuels compared to the previous period. Conversely, at 500 cal yr BP (AD 1450), Pothole Lake in sagebrush steppe shows a slight increase in background CHAR, which suggests that sagebrush might have been burning more than forests at this time. Background CHAR levels at Hedrick Pond remained fairly constant over the last 550 cal years, implying no appreciable change in biomass over this time.

Trappers and fur-traders arrived in Jackson Hole in the mid-1700s (200 cal yr BP), and miners were present in the valley in the mid-1800s (100 cal yr BP) (Daugherty, 1999). A fire episode recorded at Hedrick Pond, Pothole Lake and Swan Lake at about 175 cal yr BP (AD 1775) corresponds with the arrival of trappers to the valley, and fires at this time may have been human-set. Miners were present in the Pilgrim Creek drainage in the mid-1800s (100 cal yr BP) (Daugherty, 1999) and may have been responsible for the fire registered at nearby Swan Lake at that time. About -30 cal yr BP (AD 1980), fires occurred in Jackson Hole and around the valley margins. Large fires in Yellowstone in 1988 may have contributed some long-distance charcoal to the sites in Jackson Hole along with the charcoal from local fires.

The last 2100 years

Hedrick Pond and Pothole Lake have

charcoal peaks that indicate fire episodes at 560 cal yr BP (AD 1390), 950 cal yr BP (AD 1000), 1180 cal yr BP (AD 770), 1430 cal yr BP (AD 520), 1650 cal yr BP (AD 300), and 2130 cal yr BP (BC 130), as well as those during the last 550 years discussed above (Figure 4). The co-occurrence of charcoal peaks suggests times when one or several fires occurred in Jackson Hole, burning both forest and steppe.

Background levels of charcoal were fairly constant in the Hedrick Pond record with the exception of a slight dip from ~0.2 to ~0.1 particles/cm^2/year between 1500 and 750 cal yr BP (AD 1200). The amount of charcoal produced during fires was reduced at this time. At Pothole Lake, background CHAR rose from ~0.05 to 0.08 particles/cm^2/year at 1300 cal yr BP (AD 650) and fell to ~0.05 particles/cm^2/year at 600 cal yr BP (AD 1350). These changes in background charcoal coincide with the Medieval Climate Anomaly (ca. 1100 – 500 cal yr BP, AD 850 – 1450; Hughes and Diaz, 1994; Cook et al., 1999), when the Greater Yellowstone region experienced drought (Meyer et al., 1995). The rise in background CHAR at Pothole Lake suggests more severe, charcoal-producing events in steppe environments. In contrast, woody fuels at Hedrick Pond may have limited fire severity during this period.

Native Americans have inhabited Jackson Hole for approximately 9000 years before the arrival of Euro-Americans (Connor, 1998), with the oldest archeological records dated by the type of projectile point. Patterns of artifact assemblages throughout the valley suggest that seasonal occupation changed over time, and specifically within the last 2000 cal years. Native Americans used the northern portion of the valley in the late summer and fall between 2000 and 800 cal yr BP (AD 0 – 1150). Between 800 and 200 cal yr BP (AD 1150 – 1750), Native Americans used more sites in southern Jackson Hole during the spring and summer months (Connor, 1998). Although seasonal patterns of occupation changed within the last 2000 years, the charcoal records offer no evidence that these changes were accompanied by heightened burning activities on the part of Native peoples.

✦ CONCLUSION

The results of our study document periods of heightened fire activity during the last two millennia. The widespread fires in the 1980s, which included burning in Jackson Hole, are evidenced in the charcoal records of all three low-elevation sites. Similar fire episodes are recorded throughout the last 2100 years. Most recently, Euro-American activity coincides with fire episodes around 100 cal yr BP (AD 1850) and 175 cal yr BP (AD 1775). These fire periods are also registered in the tree-ring record. Although it is impossible to determine the exact cause of past fires, there is no direct evidence of ecological changes as a result of Native American burning during the last 2100 years. Climate has influenced fire activity significantly over the past 2100 years. For example, the Medieval Climate Anomaly Period shows increased charcoal levels at Pothole Lake in steppe and decreased levels at Hedrick Pond at the forest/steppe ecotone. During the Little Ice Age, background CHAR decreased at Swan Lake in lodgepole pine forest and increased at Pothole Lake. These changes in charcoal levels suggest shifts in fuel conditions as a result of available moisture. During dry periods, steppe areas were more prone to burning and forested areas may have been fuel limited. During wet periods, fires in steppe regions increased with increasing available fuels, and fires in forested areas were suppressed due to increased fuel moisture. Particular fire events coincide with the appearance of Euro-Americans in Jackson Hole and may have been deliberately set. From these initial results, it is clear that climate has predominantly shaped the fire regimes of Grand Teton National Park over the last 2100 years.

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