

UNIVERSITY OF WYOMING

NATIONAL PARK SERVICE RESEARCH CENTER



**35th ANNUAL REPORT
2012**

NATIONAL PARK SERVICE RESEARCH CENTER



35nd ANNUAL REPORT 2012

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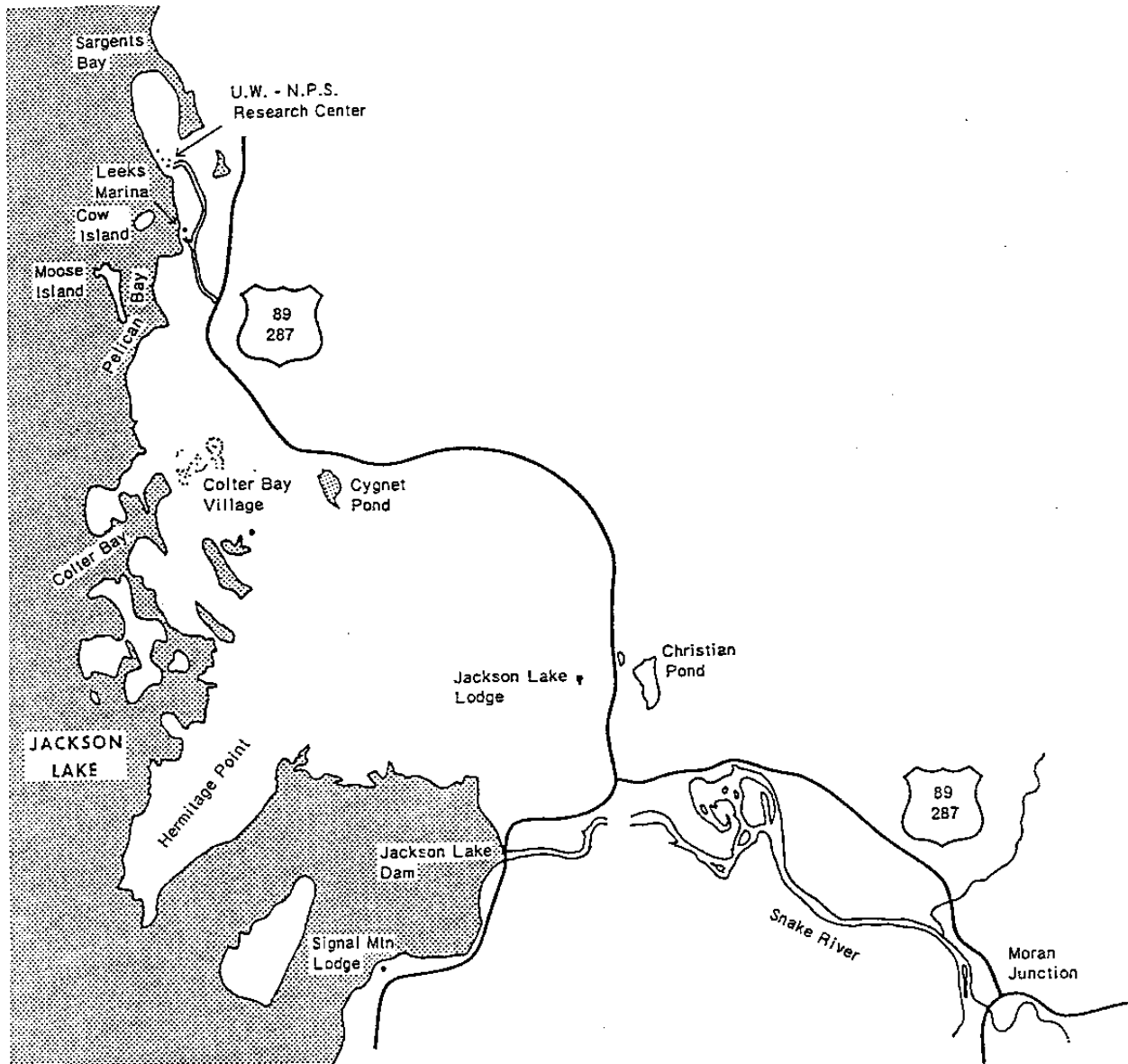
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INTRODUCTION
2012 ANNUAL REPORT



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 permission from the author(s).

FEATURE ARTICLE



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

THOMAS P. HAHN ✦ ELIZABETH M. SCHULTZ ✦ UNIVERSITY OF CALIFORNIA, DAVIS

✦ ABSTRACT

In order to understand the distributions and abundances of animals, many environmental factors must be considered, particularly the availability of food resources. Food resources are especially important to nomadic species survival that moves in response to their spatial and temporal availability. An example of such nomadic species is the red crossbill (*Loxia curvirostra*), which specializes on conifer seeds, a resource that significantly varies both temporally and geographically. Thus, crossbills will move large distances each year to find areas with abundant conifer seeds. While conifer seed impact the distribution, abundance, and reproductive rate of crossbills, it is likely not the only factor driving these patterns. To truly understand what drives the distribution and abundance of crossbills across North America, further study is needed not only on how external environmental factors of food abundance affect these patterns, but how tradeoffs among internal physiological processes such as reproduction and immune function may affect when crossbills migrate or whether or not reproduction occurs. Historically, research to understand how organisms orchestrate their annual cycles with respect to these costly and conflicting physiological processes has focused narrowly on seasonal breeders that constrain reproduction to times of year when thermoregulatory demand is low (i.e., summer), which provide limited opportunities to reveal how physiological costs of different processes may interact with environmental conditions to influence the evolution of investment strategies. In this study, we are examining how the diversity, abundance, and size of cone crop of conifers influence both 1) the quantity and diversity of red crossbills, as well as 2) their seasonal modulation in investment patterns in reproduction and self-maintenance processes such as immune function in Grand Teton National Park, where crossbills can be found breeding in both summer and winter. Preliminary results from this study have

indicated that both conifer diversity and cone crop size affect overall quantity and vocal type diversity of crossbills in Grand Teton National Park, as well as affecting their investment in reproduction and immunity. Overall, results from this study will provide information on how species in general and crossbills specifically, respond to rapidly changing environments, which has become increasingly important in light of the effects of anthropogenic change.

✦ INTRODUCTION

There are many interacting factors that may affect distributions and abundances of animals, including tolerances of physical environmental factors (Brown and Fedmeth 1971), competition (Connell 1983), predation (Hahn and Denny 1989), disease (Hochachka and Dhondt 2000), and the availability of crucial food resources (Brown et al. 1995). In particular, it has been well documented that food resource availability has pronounced effects on the distribution and abundance of those nomadic species that move in direct response to the spatial and temporal availability of food resources (Andersson 1980; Kelsey et al. 2008). One such nomadic species is the red crossbill (*Loxia curvirostra*), which specializes on extracting seeds from conifer cones (Groth 1993). Further, crossbills can be categorized into ten vocal types that are known to specialize on one or two “key” conifers (Groth 1993). Because most conifers are mast seeders and annually produce erratic quantities of cones and seeds (Koenig and Knops 2000), crossbills will move large distances each year to find areas with abundant conifer seeds (Adkisson 1996). While conifer seed impact on the distribution, abundance, and reproductive rate of crossbills ((e.g., during a large cone year, crossbills can have as many as four successful clutches between summer and spring of the following year (Adkisson 1996)), it is not the only factor driving these patterns. For example, even in low cone years, crossbills will still reproduce (Kelsey et al.

2008), but potentially at a cost to survival or self-maintenance processes (Schultz unpublished data). Thus, to truly understand what drives the distribution and abundance of different crossbill types across North America, further study is needed not only on how external environmental factors such as food abundance affect these patterns, but how tradeoffs among internal physiological processes such as reproduction and survival related processes like immune function may affect when crossbills may irruptively migrate or whether or not reproduction occurs.

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



Figure 1. Male Red Crossbill caught in Grand Teton National Park

Study Species: Red crossbills (Figure 1) can be found reliably in Grand Teton National Park every year, although the overall abundance and diversity of vocal types present is highly variable from year to year and is known to be somewhat dependent on the size of the cone crop (Kelsey et al. 2008; Hahn 1998). In this report, we will provide recent data on how the diversity, abundance, and size of cone crop of conifers influence both: 1) the quantity and diversity of red crossbills, as well as 2) their seasonal modulation in investment patterns in reproduction and self-maintenance processes such as immune function.

✦ METHODS

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

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

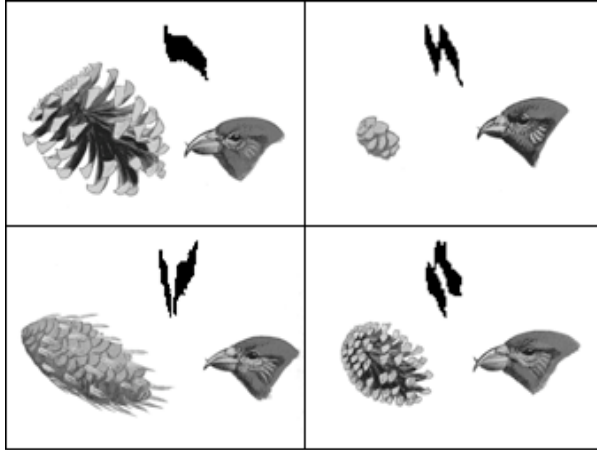


Figure 2. Drawings of the heads, spectrograms of flight calls, and key conifer cones of the four crossbill vocal types studied by Benkman (1993). Crossbills call frequently both while in flight and while perched, reliably call from cages after being captured and when released after banding. All of these call types are readily identifiable by ear.

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

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

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

Capture Methods: We attract crossbills using live caged decoys. Decoys call loudly when they

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

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

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

Measuring Immune Function (survival-enhancing process): Brief Background: Immune function contributes to survival by detecting pathogens and limiting infection, but because maintenance of immunity can be costly (e.g., Schmid-

Hempel and Ebert 2003), many environmental and physiological variables have been hypothesized to cause investment in immunity to vary (Martin et al. 2008; Nelson et al. 2002). Broadly, the immune system can be divided into two main components: innate and adaptive. Innate immune function provides an immediate and non-specific response to a pathogen and can be further categorized into constitutive and induced responses. Adaptive or acquired immunity is activated by the innate response to produce specific antibodies against the pathogen (Martin et al. 2008).

We specifically measure constitutive immunity because it provides a first line of defense against many pathogens and must always be maintained on some level, which create costs that may be important in mediating physiological trade-offs (Martin et al. 2008). To measure constitutive immunity in crossbills, we utilize: 1) complement and natural antibody activity via a hemolysis-hemagglutination assay (Matson et al. 2005), 2) bacterial-cidal assay that measures the capacity of whole blood to limit a bacterial/microbial infection (Millet et al. 2007), 3) LPS induction of the sickness or acute phase response to measure how an individual behaviorally copes and responds physiologically to a short-lived infection, as a measure of induced innate immunity (e.g., Owen-Ashley and Wingfield 2006). To measure the behavioral response, we set up digital video recorders and monitor locomotive (hopping, flights), preening, and feeding/drinking behavior for four hours, three hours post injection. And finally; 4) differential white blood cell counts: a simple, gross measure of innate immunity obtained from a simple blood smear (Campbell 2007).

◆ PRELIMINARY RESULTS

Objective 1: How the diversity, abundance, and size of cone crop of conifers influence the quantity and diversity of red crossbills. As demonstrated by Kelsey et al. (2008), the crossbill types may be specialized for general resource classes (groups of conifer species) rather than single resources. In Grand Teton, type 2s most frequently occur in areas dominated by spruce (both blue and Engelmann) and Douglas-fir, type 3s with Engelmann spruce, type 4s with Douglas-fir, and type 5 lodgepole pine (Kelsey et al. 2008). Additionally, type 2s will selectively forage on Douglas-firs, type 3s will selectively forage on Engelmann spruce in summer, and Douglas-fir in winter, while types 4 and 5 will selectively forage on Douglas-fir to avoid lodgepole pine (Kelsey et al. 2008).

Recent data collected from 2010, 2011, and 2012 (a low, heavy, and low cone abundance year, respectively, Figure 3, 4) further demonstrate that both conifer diversity and cone crop abundance significantly contribute to crossbill type quantity and diversity in Grand Teton National Park (Figure 5). To clarify, cones begin to develop on the trees in early summer (June-July) and are typically harvested by crossbills and other animals up until late spring of the following year (Koenig and Knops 2000). Thus, a heavy cone year like 2011 would last from June/July 2011 through late spring of 2012. Our data suggest that type 5 crossbills are present in years with both low and heavy conifer cone crops, whereas other vocal types (2,3, and 4) are only present in heavy cone years such as 2011 (Figure 5). However, juveniles (hatch year) of vocal types 2, 3, and 4 were numerous in summer of 2012 (a low cone year), and were likely born in winter or spring of 2012 (Figure 6). For results on point count, conifer composition, and cone crop surveys, please see Table 1.

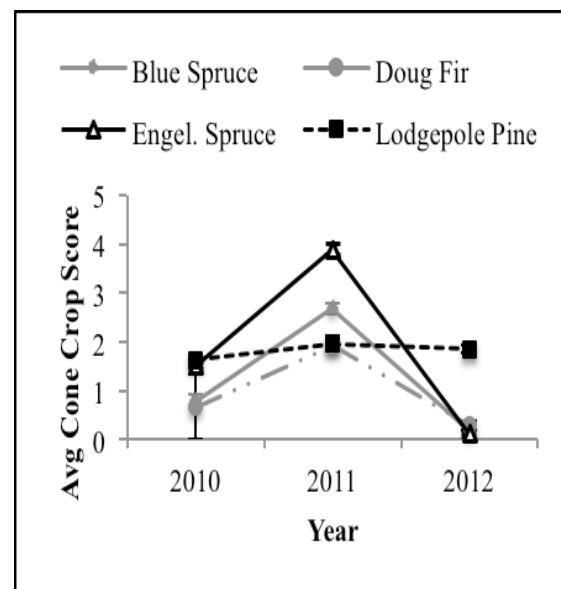


Figure 3. Average cone crop abundance in Grand Teton National Park in 2010, 2011, and 2012. Lodgepole Pine cone abundance appears to be fairly consistent, averaging around 1.5 (out of a max score of 5) every year, whereas the other conifer species fluctuate more dramatically from year to year. 2011 saw the highest cone abundance across all key conifer species, with Engelmann Spruce having the largest crop (average score of 3.9). Bars represent standard error of the mean (SEM).

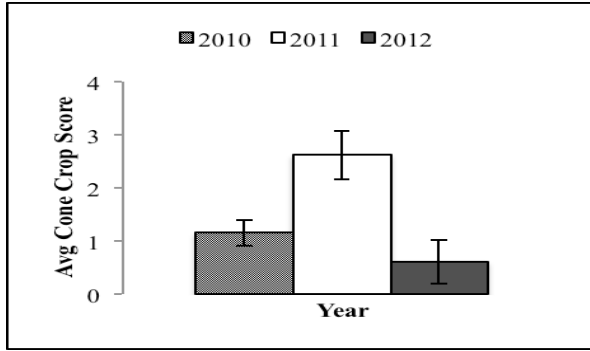


Figure 4. Average cone crop abundance (combining averages of Blue Spruce, Lodgepole Pine, Engelmann Spruce, and Douglas-fir). 2011 saw the overall highest cone abundance, with 2010 and 2012 showing significantly lower overall cone abundances. Bars represent standard error of the mean (SEM).

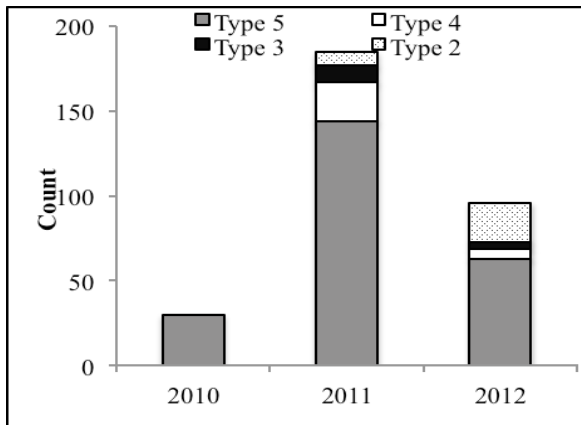


Figure 5. Red crossbill type abundance by year. In 2010 (low cone year), the only crossbill types caught via mist net were type 5. In 2011, types, 2, 3, 4, and 5 were all caught, with type 5 being the most abundant. We caught primarily type 5s in 2012, but did catch young (hatch year) type 2s, 3s, and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

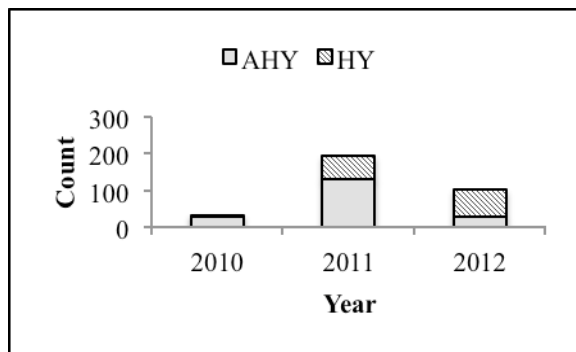


Figure 6. Proportion of adult (After Hatch Year) and juvenile (Hatch Year) red crossbills caught by year. More adults were caught in 2010 and 2011, while more juveniles were caught in 2012 (offspring from winter/spring).

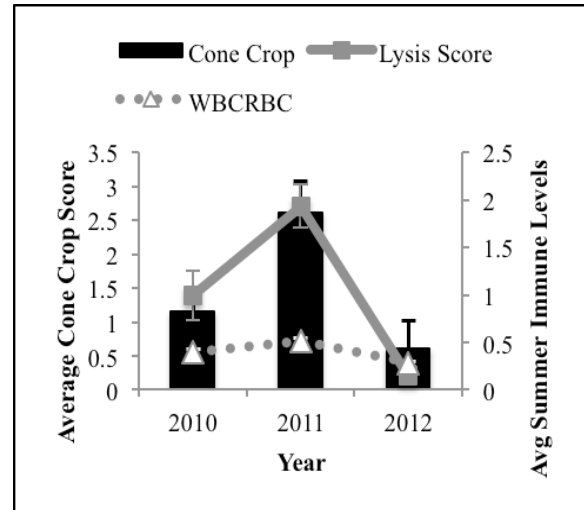


Figure 7. Two immune measures (Lysis Score, i.e., complement levels) and WBC/RBC (overall white blood cell to red blood cell ratio) increase when overall cone crop levels are higher, with the average highest lysis score and white blood cell ratio seen in the heaviest cone year (2011), and lower levels of both components seen in lower cone years (2010 and 2012). Bars represent SEM.

Objective 2: How the diversity, abundance, and size of cone crop of conifers influence the seasonal modulation in investment patterns in reproduction and self-maintenance processes such as immune function in red crossbills: Data from 2010, 2011, and 2012 have demonstrated that years in which the cone crops of key conifers are more abundant, crossbills have higher reproductive potential and immune function (as measured by two different immune assays), which is most likely the result of having more food resources available to invest in multiple competing, energetic processes.

How size of cone crops affects overall crossbill immunity: The hemolysis-hemagglutination assay uses a serial dilution of plasma and rabbit red blood cells to measure activation of the humoral component of constitutive innate immunity by measuring complement levels via lysis ability and natural antibodies via agglutination level: Higher lysis and agglutination scores typically equate to higher levels of immune function (Matson et al. 2005). When comparing seasonal and annual variation of both lysis scores (complement level) and agglutination scores (natural antibody level), average lysis scores exhibit distinct annual (Figure 7) and seasonal (Figure. 8) patterns. Agglutination scores did not exhibit annual or seasonal variation (figure not shown).

Results from microbial-killing assay are not as informative as the other immune measures we've included because we just began conducting this assay during the summer of 2012 and cannot compare it to other years and seasons. However, for this assay, we measured the ability of crossbill whole-blood (not plasma) to eliminate (or "kill") two species of microbe: *Escherichia coli* and *Candida albicans*. *E. coli* killing is primarily mediated by complement proteins, whereas *C. albicans* killing is primarily mediated by white blood cell phagocytosis, thus probing two different mechanisms of immunity with this assay. The overall average of *C. albicans* killing ability was higher than *E. Coli* (Figure. 9).

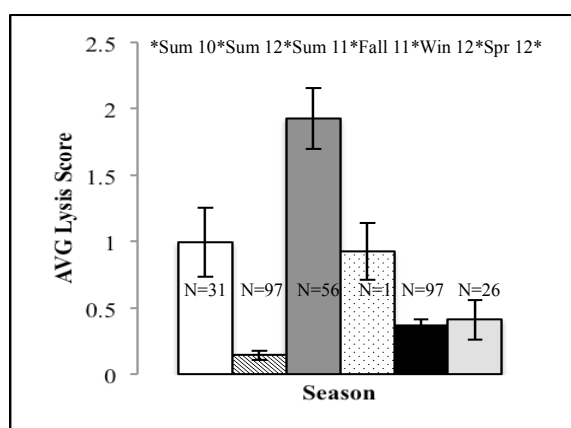


Figure 8. Seasonal pattern of lysis scores (complement level) in red crossbills. Highest lysis scores are seen in the summer, with declining scores during fall, winter, and spring. Lysis scores are also higher in years with heavier cone crops (2011). Bars represent SEM.

	Estimate	S.E.	2.5%	97.5%
Intercept	-1.90	0.79	-3.44	-0.36
Parasite Load	-0.08	0.13	-0.34	0.18
Avg Cone Crop	0.69	0.15	0.39	0.99
Temp	0.01	0.01	-0.02	0.04
BP Score	-0.12	0.08	-0.27	0.03

Table 1. Estimated unit change in lysis score per unit change in each parameter, according to the top-ranked AICc model.

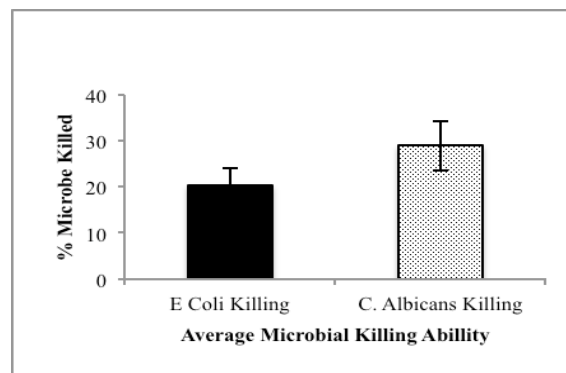


Figure 9. Average microbial killing ability of red crossbills summer of 2012. The killing of both microorganisms is mediated by different mechanisms: *E.coli* killing is mediated by complement proteins, whereas *C. albicans* killing is mediated by white blood cell phagocytosis. Bars represent SEM.

After unsuccessful attempts to accurately measure the LPS induction of sickness or acute phase response in winter of 2012, we decided to defer this assay for future captive studies. From the blood smears and white blood cell differentials we were able to detect distinct annual (Figure 7) and seasonal (Figure 10) variation of average white blood cell levels in red crossbills.

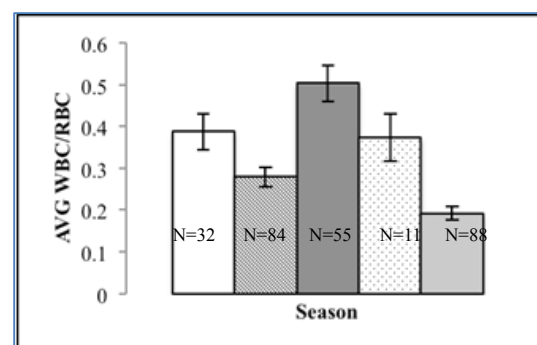


Figure 10. Seasonal pattern of white blood cell/ red blood cell ratios. Highest WBC/RBC ratios are seen in the summer, with declining scores occurring in fall, winter, and spring. WBC/RBC ratios are also higher in years with heavy cone crops (2011). Bars represent SEM.

How size of cone crops affects crossbill investment in reproduction: Overall, crossbills invest more in reproduction (higher reproductive potential as measured by larger cloacal protuberances and presence of spermatozoa in males, and brood patch appearance in females), when cone crop levels are high, regardless of the other environmental conditions (temperature, precipitation levels) (Figure 11). As demonstrated above, in heavy cone years, crossbills are able to maintain high levels of immunity as well as investing significantly in reproduction, suggesting that

with adequate resources, crossbills are able to maintain both physiological processes without exhibiting any tradeoffs.

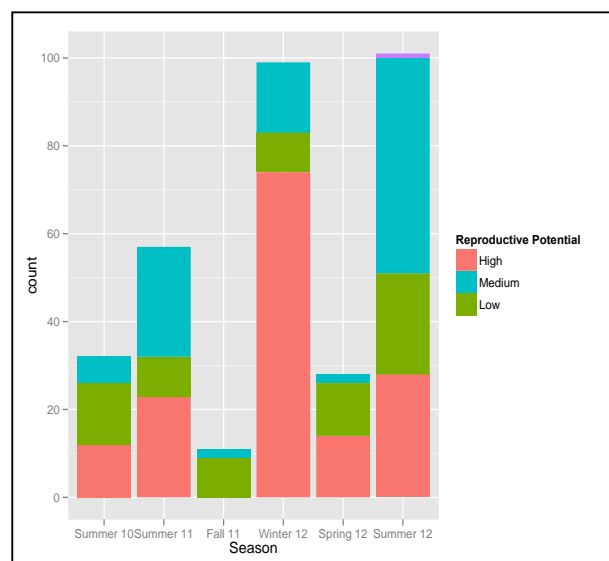


Figure 11: Crossbill reproductive potential (both males and females) across seasons. The largest proportion of crossbills categorized as having high reproductive potential was seen in the winter of 2012 (heavy cone year), and lowest generally seen in the fall and in summers of low cone years (2010, 2012).

Preliminary Statistical Analysis: We used model comparison based on Akaike's Information Criterion for small sample sizes (AICc) and set season as a random intercept to understand the best predictors of the seasonal pattern of two components of immune function (as seen in Figure. 8 and 10): lysis and white blood cell scores. In our models we included the environmental variables of yearly cone crop scores, and high and low temperature, while the physiological variables were cloacal protuberance length, brood patch scores, and parasite load with other variables being age, sex, and vocal type. As an alternative to null hypothesis testing, model selection permits simultaneous evaluation of multiple competing hypotheses based on the observed data. The models within the set are all compared and are assigned a relative weight that allows competing hypotheses to be evaluated quantitatively (Anderson 2008). All data were analyzed with R statistical software (version 2.15.2) using generalized linear mixed models with the lme4 package.

Overall conclusions: Based on our data collected in 2010, 2011, and 2012, we have augmented our 20 year field data set on red crossbills, further

confirming that fluctuations in conifer cone crop size and the overall conifer species diversity affect multiple aspects of red crossbill physiology. Heavy cone years like 2011 that saw large cone crops, specifically on Douglas-firs, Engelmann and Blue Spruces (Lodgepole pine saw relatively static cone crops from year-to-year), positively affected two aspects of immunity (lysis scores and white blood cell counts), as well as increasing reproductive potential in both males and females. Additionally, red crossbills had overall higher immunity and higher reproductive potential during heavy cone years, suggesting that when food resources are plentiful, crossbills are able to sustain both costly physiological processes without tradeoffs. According to our model-selection approach, the highest-ranking model predicting seasonal variation in lysis score included positive effects of cone crop scores (heavier cone crops increased scores) and negative effects of both parasite load and female brood patch score (females with more developed brood patches i.e., higher reproductive potential had lower lysis scores). The highest-ranking model predicting seasonal variation in white blood cell counts included positive effects of temperature and cone crop scores.

Table 2. Estimated unit change in white blood cell scores per unit change in each parameter, according to the top-ranked AICc model.

	Estimate	S.E.	2.5%	97.5%
Intercept	-0.23	0.16	-0.54	0.08
Avg Cone Crop	0.13	0.03	0.06	0.19
Temp	0.01	0	0	0.02

◆ BROADER IMPACTS

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

In addition, the timing and investment in reproduction and survival have been more extensively investigated in seasonally breeding organisms, with most of these studies focusing on captive animals. Thus, we are limited in our ability to answer questions that involve how demanding environmental conditions such as low food availability may affect investment decisions, specifically in regards to reproduction, because seasonally breeding animals typically breed only when environmental conditions are benign. By studying organisms such as crossbills that are able to reproduce in harsh environmental conditions, we will gain more insight into potentially alternative physiological mechanisms that regulate the timing and investment in survival and reproduction. This information can be applied to understanding how organisms effectively allocate resources to competing physiological processes, which is becoming increasingly important in light of recent anthropogenic changes (Wuethrich 2000; Hughes 2000).

◆ ACKNOWLEDGEMENTS

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GRAND TETON NATIONAL PARK



VARIABLE CONDITIONS PRODUCE VARIABLE RESPONSES IN GTNP BREEDING BIRDS



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♦ ABSTRACT

Conditions in the GTNP breeding season can differ dramatically among years, even between adjacent years such as 2011 and 2012. Specifically, 2012 was the warmest and driest spring since the early 1990s, with snow melt-out date (SMOD) on April 17, a few days earlier than the long-term average, and 90% aspen leaf-out also earlier than the mean by nearly a week. In contrast, 2011 was the latest SMOD and aspen leaf-out in some 50 y. Birds settle in breeding habitat with somewhat altered preferences in early, warm and dry years such as 2012 compared to opposite conditions in the 2011. In 2012, many birds typical of lower, more open and less mesic habitats were found breeding in taller, denser and usually wetter habitats, a clear influence of the currently prevailing conditions in the park. A monitoring site of intermediate vegetation height and density, Site #9: RKO Dry Willows, is used to calibrate these habitat shifts.

♦ INTRODUCTION

Late spring and early summer weather conditions can vary dramatically in Grand Teton National Park (GTNP) from one year to another, even in one year to the next. For example, 2012 was the warmest and driest spring since the early 1990s, with a relatively early snow melt-out date (SMOD) on April 17, a few days earlier than the long-term average, and 90% aspen leaf-out make the same (as measured by an accumulated total of 125 growing degree-days –GDD-125) also earlier than the mean by nearly a week. Both GDD125 and SMOD are useful predictors of conditions available for breeding birds in GTNP, and

together with spring temperatures (SPRT: average monthly temperature March-May) and spring precipitation (SPRP: total March-May inclusive) have a reasonably high predictive power for habitat occupancies and species shifts over habitat gradients as well as in-site breeding densities. In some circumstances, long-term census data can show that winter temperatures (those in December-February proceeding the breeding season) have an impact on breeding densities the following spring. In addition, for some longer-lived species, weather effects from seasons and years further back in time can influence habitat occupancy as well as breeding density. This report follows a previous summary account of local influences on breeding bird densities (Cody 2011).

♦ METHODS

Weather data used in this report are those collected from the weather station “Moran 5 N” by Larry Robinson near the Jackson Lake Dam; thanks to Larry for sharing his data and his further observations of birds and weather.

Bird census data from a dozen monitoring sites were collected annually by this author; census protocols for the monitoring program were specified at its initial establishment in the early 1990’s. One of the monitoring sites, Site #9, termed “RKO Dry Willows,” has been censused each year since 1993, 2012 being the 20th year in the sequence. The site is particularly appropriate for examining the effects of variable on-site conditions for breeding birds, as it can vary conspicuously among years e.g. from extremely wet to quite dry; see below for details.

◆ RESULTS

Overall Range of Spring Weather

Events that signal spring or its approach are known to be unpredictable in GTNP; examples of variability that are marked on the calendars of many Jackson Hole residents depicting the date of melt-out of the winter snows, and the dates of leaf-out in the deciduous trees. Elsewhere at northern latitudes, the dates of lilac or cherry tree blooms or the return of cuckoos from southern wintering grounds serve as similar indicators of the advance of the seasons. These indirect measures of the approach of spring are in turn the product of actual spring temperatures and/or precipitation, and in the case of snow melt-out due also to the amount of winter precipitation. A principle component (PC) analysis of these weather variables, indirect and direct, is shown in Figure 1 and illustrates the resultant range of conditions that is experienced in GTNP over a couple of decades.

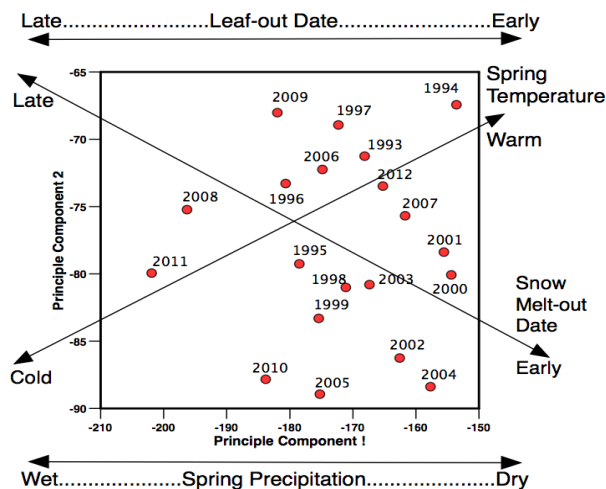


Figure 1. Principle component plot illustrating variability in spring weather conditions in GTNP.

The components are correlated to measured variables of spring precipitation and temperature, leaf-out and snow melt-out dates, as shown by the arrow-headed vectors. Note that adjacent years such as 2009-2010 or 2011-2012 can be quite different in these values. In considering the variation in weather between adjacent (t-1), sub-adjacent (t-2) and older (t-3, t->3) years, it appears that there is no signal among years in SPRT or in GDD125, but there is: a) a weak but notable tendency for SPRP to show contrasts between adjacent years (e.g. alternating high-low-high-low), and b) for SMOD to show similar values over a series of three (but not four) years.

Monitoring Site #9: “RKO Dry Willows”

The RKO monitoring site lies alongside the Snake River, and is marked by a series of parallel swales and crowns, parallel to each other and parallel to the present course of the Snake River, clearly the product of bygone river edge activity and of bank recontouring. The swales are around a meter or so lower than the crowns and ca. 100 m apart. The lower swales can collect and retain water to a depth of several feet and support marshy vegetation bordered by willows. The crowns are topped by low and open vegetation dominated by Great Basin sagebrush (*Artemisia tridentata*), and so represent a semi-desert vegetation in diametric contrast to the swales. In wet springs when the Snake River is running high, its banks directly overflow into this site, and part of the downriver runoff is through the site along the swales. In dry years one can walk through the site dry-shod when the marshy swales are constricted to narrow and muddy ecotones.

Responses of Specific RKO Breeding Birds

In 2012, birds generally more prevalent in drier and lower habitats, were present in higher abundance in the RKO whereas birds generally typically of taller woodland and forest were less prevalent there. Further, two bird species were recorded at the RKO in 2012 for the first time in >20 y of its monitoring: i. Lazuli Bunting *Passerina amoena*, a bird of open scrubby hillsides and a species that is fairly common elsewhere in the park, and ii. Yellow-breasted Chat *Icteria virens*, a species not seen by the author at any time in the park during the preceding 50 y, and a species typical of the drier shrubby habitats fringing the Great Basin Desert (in the West), or a species of early successional scrub vegetation (in the East).

The four most abundant breeding emberizines at this site are Song, Fox, Lincoln’s and White-crowned Sparrow. The years in which these species reach or exceed 1 standard deviation (SD) above their mean densities at the site are illustrated by the highlighted blobs (Figure 2). In 2012 Lincoln’s Sparrow was recorded at the highest densities (5.5 pr., 2.2 SD > mean) since monitoring began in 1993. White-crowned Sparrow was also common in 2012 (3 pr., 0.70 SD > mean), but Song Sparrow and Fox Sparrow were both present at below-average densities (3, 1.13 pr. respectively). The former is most common after relatively cool, wet and late spring seasons, whereas Fox Sparrow reaches its maximum density (2.3 SD > mean) in 2011, which was the ultimate in cool, wet and late spring seasons.

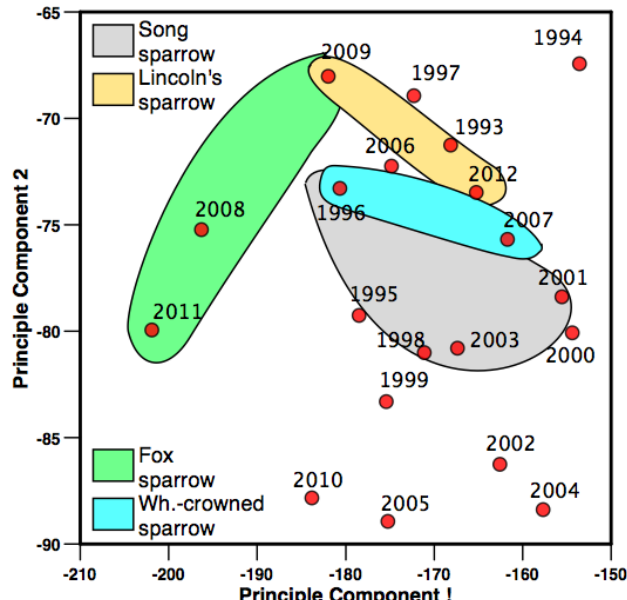


Figure 2. The four commonest breeding emberizine sparrows at the RKO site reach their highest breeding densities in generally quite different years.

Of the RKO breeding birds discussed here, only the Song Sparrow is close to being a resident species; the others engage in short- or long-distance migrations. In view of this distinction, it may not be surprising that only Song Sparrow RKO breeding densities appear to be influenced by preceding winter temperatures. Correlation coefficients with years t-1, t-2 and t-3 winter temperatures are 0.54*, 0.32 and 0.18 respectively (* signifies $p < 0.05$); thus Song Sparrows apparently survive local winters better in warmer than in colder years, and settle in breeding densities in part reflecting that improved survival.

Amongst the less common breeding emberizines at the RKO site are Green-tailed Towhee and Brewer's Sparrow, both typical species of the Great Basin desert sagebrush-dominated regions of the west and southwest (Figure 3). The former nested at this site with greater than a marginal presence only in the two warmest and driest years, 1993 and 1994 (at 3.7 and 1.7 SD > mean). The latter reached its highest ever density in 2012 (3.3 SD > mean), although it was fairly common also in 2001, another early, dry year. Vesper Sparrow, in contrast, is present in cool, wet years; in 1995, which was the second-wettest spring (after 2011) it reached its highest breeding density of 0.5 pr. (2.9 SD > mean).

Two *Empidonax* flycatchers are common breeding birds at the RKO site, although a third species (*E. minimus*) is occasionally present also. As shown

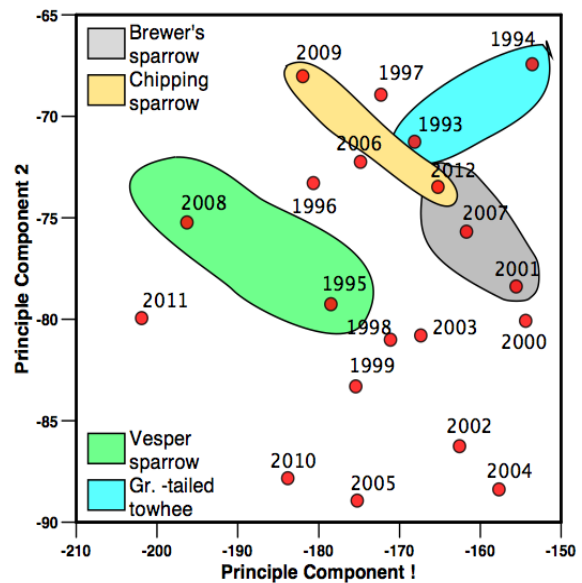


Figure 3. The distributions (over years) in which four less common emberizines reach high breeding densities at the RKO monitoring site.

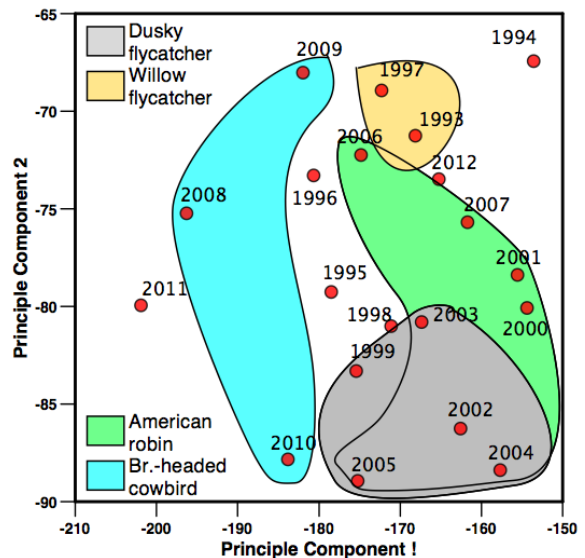


Figure 4. Years in which four common breeding RKO birds, two flycatchers, robin and cowbird, reached their highest breeding densities.

in Figure 4, the two common flycatchers respond to quite different local conditions in terms of breeding densities, with Willow Flycatchers especially common in early, cool and dry years, and Dusky Flycatcher at high densities in warmest, dry years. Over the 20-y census period, Dusky Flycatcher has averaged some 1.8 pr. at the site, Willow Flycatcher somewhat less at 1.1 pr. As Willow Flycatcher is associated with willows and wet sites in general, it would appear contradictory that its RKO densities are not highest in

wet years. In fact, this species is commonest in drier springs that follow wet winters (correlation with WINP: 0.64**; WINP-1: 0.46, WINP-2: 0.22, a response that has carryover effects from previous years' winter precipitation** signifies $p < 0.01$). American Robin is common at practically all second principle components (PCII) values, but only at high first principle component (PCI) values that indicate early and warm spring conditions. The opposite conditions characterize Brown-headed Cowbird densities, highest at low PCI values, for reasons not readily apparent to this author.

Four species of paruline warblers breed at the RKO monitoring site, one commonly, one routinely but at low density, and two others occasionally. Yellow Warbler is present at much higher densities (20-y ave. 9.9 pr) than Common Yellowthroat (ave. 3.4 pr), while Wilson's Warbler averages just 1/3 pr y^{-1} and MacGillivray's Warbler only 1/10 pr y^{-1} . The distributions over years of high density are shown in Figure 5 for Yellow Warbler and Common Yellowthroat, in which it appears that neither species benefits or responds to the more extreme weather conditions, but each species is commoner in relatively average years. Warbling vireo is casual at this site (present in 4/20 years), and the three years of its higher densities (which include 2012) coincide with those of the earliest onset and the warmest of springs. Gray Catbird has a similar incidence at Site #9 as Warbling Vireo, but catbirds reached high density (of 3.8 SD > mean) in just a single year, 2009. As 2009 does not show up as a distinct year in any of the variables we have discussed—SPRT, SPRP, SMOD, GDD¹²⁵—it is likely that catbird density is regulated by off-site rather than on-site factors.

Carryover Effects of Climate Variation

Some instances have been mentioned above in which RKO breeding bird densities appear to reflect weather conditions from previous years, rather than or as well as conditions in the current breeding year. In a number of cases there are statistically significant effects of weather variables on density from one or two years preceding the year of the density measurements. These are reported in Table 1; values at the $p < 0.01$ level are shown in boldface.

The values in the table confirm, in general, relationships already highlighted above; others make sense with the advantage of hindsight. For example, many more species are responsive to conditions the previous year than those in the present year. This implies that, rather than current conditions at the

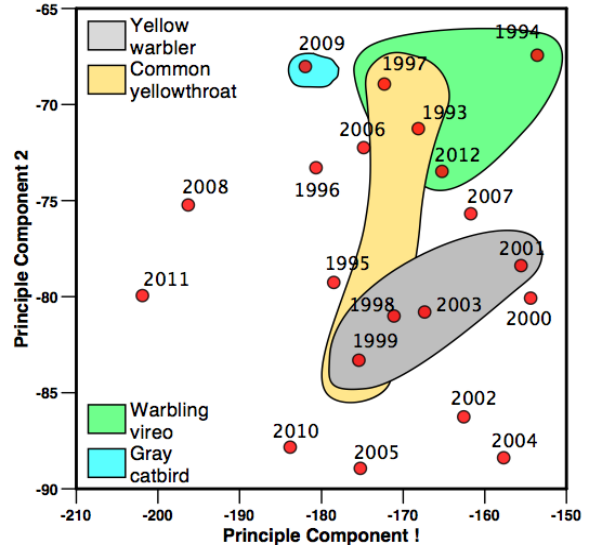


Figure 5. Years in which four additional RKO breeding species, two of them regular breeders (the warblers) and two not, reached high densities of over 1 SD > mean density.

Table 1. Years in which four additional RKO breeding species, two of them regular breeders (the warblers) and two not, reached high densities of over 1 SD > mean density.

Species/variable	PCI	PCII	SPRT	SPRP	SMOD	GDD ¹²⁵				
PCI			0.44	-0.61		-0.74				
PCII			0.50			-0.67				
Song Sparrow										
Fox Sparrow	-0.52			0.44	0.61					
Brewer's Sparrow				-0.44						
Bl.-headed Grosbeak		-0.46								
Dusky Flycatcher	0.46				-0.55					
Gray Catbird		0.44			0.47					
Warbling Vireo			0.53			-0.51				
Br.-headed Cowbird				-0.44						
			SPRT	SPRP	SMOD	GDD ¹²⁵	SPRT	SPRP	SMOD	GDD ¹²⁵
			-1	-1	-1	-1	-2	-2	-2	-2
Fox Sparrow					0.45					
Lincoln's Sparrow					0.59					
Chipping Sparrow				0.46	0.67	0.53				
Savannah Sparrow				0.65		-0.50				
Gr.-tailed Towhee				0.70		-0.62				
Lazuli Bunting				0.50	0.47					
Dusky Flycatcher				-0.48					-0.49	
American Robin							-0.59		0.57	0.54
Gray Catbird				0.57						
Common Yellowthroat					-0.52			0.50		
MacGillivray's Warbler				0.48		0.47	-0.49			
Br.-headed Cowbird				-0.62						

RKO site, some breeding densities are attributable to successful reproduction in the previous year. In the case of American Robin, the largest are likely the longest-lived of those species listed, and it is conditions two years prior to the present that best predict the present robin breeding densities. Additionally in the case of Common Yellowthroat, whose territories are centered on the wet, marshy areas on the site, it is precipitation two years previously that best determines present breeding densities. These results in turn make most sense in that there is a reasonably high degree of philopatry in the GTNP breeding birds.

✦ **LITERATURE CITED**

- Cody ML. 2011. Influence of Spring Weather Conditions on Breeding Bird Densities in GTNP. In: Harlow HJ, Harlow MA editors. UW NPS Research Station Annual Report. 34:33-38.

SEASONAL AND ALTITUDINAL VARIATION IN FATTY ACID COMPOSITION OF NATIVE BEES

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✦ ABSTRACT

Fatty acids (Fas), the most important energy resources in insects, may change in structure and thus function with changing temperature, a hypothesis termed ‘homeoviscous adaptation’. We investigated whether the proportional composition of the most common fatty acids changes with seasonal (June to August) and altitudinal (2060 – 3290 m) variation in environmental temperature among four species of native bees. We identified the composition and proportion of each fatty acid using gas chromatography coupled with a flame ionization detector (GC-FID). Based on preliminary data, the most common fatty acids found in bees were palmitic acid (C 16:0), stearic acid (C 18:0), oleic acid (C 18:1), linoleic acid (C 18:2) and linolenic acid (C 18:3), with other fatty acids including myristic acid (C 14:0) and palmitoleic acid (C 16:1) also present in small amounts. We are currently 23reticulat GC data for larger bees and establishing protocols for fatty acid composition analysis of small tissue samples. Based on the seasonal and altitudinal variation in ambient temperature, we expect to see variation in fatty acid proportions in bees from different months at both sites.

✦ INTRODUCTION

Environmental temperature has profound effects on organisms and, in particular on ectotherms, which cannot regulate body temperature independent of environmental chamber. Changes in the temperature of their surroundings (and therefore body temperature) can thus strongly affect the physiology and survival of these organisms (Hazel and Williams 1990). Among various other effects, these thermal disturbances, by altering lipid properties, affect the performance of

lipid related enzymes and proteins (Van Dooremalen, et al. 2011), and therefore can impact membrane structure and function (reviewed by Hazel 1995). These effects on lipids are particularly important because of the critical role lipids play as key energy storage molecules (fats), and as fundamental components of cell membranes (phospholipids and sterols).

Many ectotherms, including insects, store energy primarily as fat to sustain themselves during an annual quiescent phase (diapause, Hahn and Denlinger 2011) and the quantity as well as quality of fat stored strongly affects subsequent survival and fitness (e.g., Arrese and Soulages 2010). Aside from their importance in energy homeostasis, fatty acids (Fas) – the components of lipids – are necessary for insect growth and morphogenesis, synthesis of pheromones, hormones, sex attractants, phospholipids and waxes, reproduction, and maintenance of colony hygiene. Further, lipids are the dominant components in cell membranes (Hazel and Williams 1990), which act as physical barriers between intra- and extra-cellular compartments, and govern molecular transport, ATP-generation, cell signaling, and neural activity—the biochemical underpinnings of organism physiology. Therefore, in addition to the importance of fats for storage, they are critical for cell membrane function.

Changes in temperature can alter the function of fats, both as energy storage molecules and as key components of cell membranes. Whereas reduced temperatures compromise the mobilization of energy from stored fat and reduce the fluidity of phospholipid membranes (reviewed by Hochachka and Somero 2002), increased temperatures can lead to complete disruption of membranes through unintended breakages and fusions of lipids (Mariani et al. 1990;

Hochachka and Somero, 2002). Such changes in fluidity can significantly alter cell membrane function with important physiological consequences. However, insects may take advantage of diversity in lipid types to regulate membrane properties and maintain membrane function in the face of changing temperatures (Hazel 1995), a hypothesis termed “homeoviscous adaptation” (Sinensky 1974).

The homeoviscous adaptation (HVA) hypothesis deals with the physical state of the membrane: its fluidity or lack thereof (Sinensky 1974). It posits that membranes function optimally only within a limited range of fluidity, that is the rate of movement of lipids in the lipid bilayer. HVA is therefore necessary to maintain fluidity and hence to preserve membrane integrity in low temperature conditions (Joanisse and Storey 1996).

Aside from its role in proper membrane function, membrane fluidity is also important in lipid metabolism as lipids can be metabolized only when they are fluid (Irving, et al. 1957).

Membrane fluidity depends primarily on the ratio of unsaturated to saturated fatty acyl chains in phospholipids (Ohtsu, et al. 1998). Fluidity is increased by increasing the degree of unsaturation. Whereas saturated fatty acids (SFAs, lack double bonds) yield more net energy but are less fluid at low temperatures, unsaturated (UFAs), in particular polyunsaturated fatty acids (PUFAs, 2 or more double bonds), stay liquid and therefore are more easily mobilized at lower temperatures but are more costly to produce and have a lower net energy yield. These considerations suggest that organisms in warm environments should favor SFAs (for their high net energy production) and organisms in cold environments should favor UFAs (to maintain lipid fluidity for both energy mobilization and membrane function; Linder 2000).

Although the ability to regulate FA composition to maintain membrane function in changing environmental temperatures should be particularly important for ectotherms, the HVA hypothesis has rarely been tested in terrestrial insects (Hahn and Denlinger 2011; but see Bennett, et al. 1997). The limited data available on insects and even more limited data available on seasonal and altitudinal variation in FA composition in insects make it unclear if the HVA hypothesis holds in these situations.

To address this limitation we are testing the ‘HVA hypothesis’ in native bees, which are small, largely ectothermic insects abundant throughout the

growing season and across altitude. We collected bees monthly from June to August, 2012 from two altitudes in Grand Teton National Park (GTNP). We are currently determining fatty acid composition of these samples by GC analysis. These data will provide, to our knowledge, the first test of seasonal and altitudinal variation in fatty acid composition in bees.

✦ METHODS

Study area

We collected bees from two sites along Death Canyon trail in GTNP (Figure 1): a low elevation site near Phelps Lake (2060 m asl; N 43°30.220', W 110°48.327'), and a high elevation site near Static Peak (3280 m asl; N 43° 40.799', W 110° 49.096'). Both sampling sites were open meadows with abundant flowers supporting a diverse bee community.

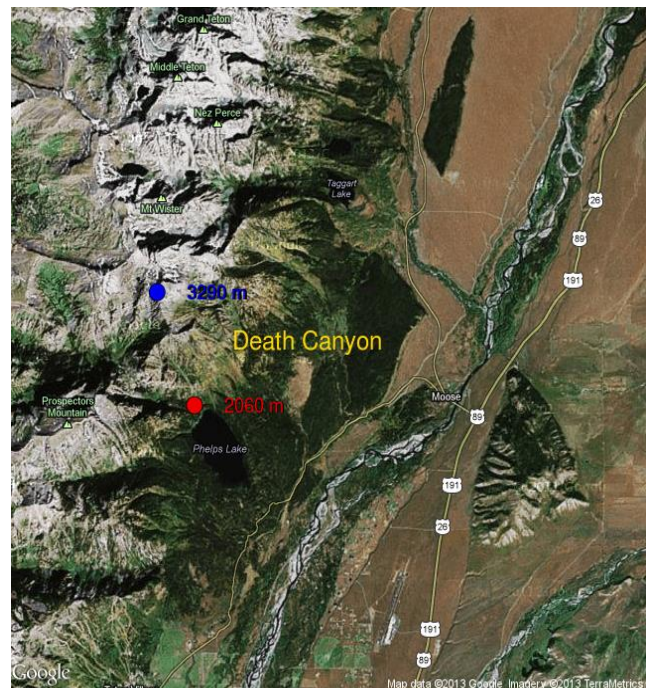


Figure 1. Bee collection sites within Grand Teton National Park. Point colors indicate low (red) and high (blue) elevation sites.

Bee collection and identification

We collected bees by visual netting monthly from June to August at the low elevation site and in July and August at the high elevation site. We collected up to 10 individuals of each of the most common genera – *Andrena*, *Bombus*, *Hylaeus*, *Lasioglossum*, *Megachile* and *Osmia*. Bees were euthanized in cyanide within 30 s of capture and subsequently transported to the laboratory on ice. Within 24 h of capture, bee body mass was measured to 0.001g (Acculab PP2060D) in the field and then re-measured to 0.0001g (analytical balance, Acculab ALC-210.4, NY, USA) within eight days after returning to the lab. Bees were identified to genus and sub-genus (Michener et al.1994; Koch et al. 2012), and then stored at -20 °C until used for analyses. Study was completed under permit GRTE-2012-SCI-0036 (Study #: GRTE-00219).

Characterizing the thermal environment

We measured bee body temperature and environmental temperature throughout the season at both sites to determine temperature variability and calibrate expectations for changes in lipid physiology. We measured shaded air temperature 12 cm above the ground (roughly at flower height) every field day using a custom-made T-type thermocouple (4 mm long, 1 mm diameter) attached to a thermocouple reader (Omega HH23, TC-Omega, USA/Canada). The thermocouple was calibrated to a NIST-traceable thermocouple in a laboratory water bath (0 to 45 °C).

Air temperature is not always a good predictor of animal body temperature because of micro-climatic variation in the determinants of heat balance (see Bakken 1992). We therefore measured bee body temperatures and “operative temperatures” (body temperatures when there is no metabolic heat production) for bees spanning the range of body sizes (from smallest to largest: *Osmia*, *Colletes*, *Andrena*, *Megachile* and *Bombus*). To minimize the effect of passive cooling, we inserted the thermocouple needle into the center of the bee thorax and read the body temperature within an average of 45 s of capture (range: 20-70 s). After subsequently euthanizing the bee in cyanide, we mounted it on a thermocouple and measured operative temperatures (shaded and unshaded at 12 cm above the ground; Figure 2).

Fatty acid composition analysis

We randomly selected a maximum of 10 individuals of each of the larger bee genera (*Osmia*,



Figure 2. Operative temperatures were measured by inserting a fine thermocouple probe into a freshly killed bee.

Andrena, *Megachile* and *Bombus*) for fatty acid composition analysis. When fewer than 10 individuals of a genus were available, we included all individuals in the analysis. Because we were interested in internal lipid composition of the bees, we used a small paint brush, forceps and a laboratory air stream to remove any pollen attached to the bee cuticle, pile, or scopa. We then lyophilized the bee for 48 hrs (Freezone 4.5, Labconco, Kansas city, USA), measured its dry weight and then homogenized it in 6 ml methanol solution using tissuemizer (Tissuemizer, Tekmar, Cincinnati OH). The homogenization was carried out in a 16 ml test tube containing 1 mg of internal standard (C 13:0; see Box 1). The fatty acids were then derivatized into fatty acid methyl esters (FAME) using methanolic KOH and prepared for GC analysis as described by Murrieta, et al (2003). We separated FAME using a Hewlett-Packard 6890N, equipped with flame ionization detector and a 60 m X 0.25 mm fused silica capillary column (0.25 μ m film thickness). Oven temperature was maintained at 75 °C for 1 min and then increased to 170 °C at the rate of 6.5 °C/min. The oven temperature was held at 170 °C for 27 min, then increased to 215 °C at 10 °C/min and held for 30 min. Finally, the temperature was raised to 230 °C at 40 °C/min and held for 3 min. Hydrogen from purified air was used as the carrier gas with a split ratio of 50:1 and a split flow of 35.5 ml/min. We will identify fatty acids by comparing retention times with fatty acid methyl ester (FAME) standards.

◆ RESULTS AND DISCUSSION

We collected a total of 80 bees from 10 genera at the high elevation site (3290 m) and 169 individuals from 19 genera at the low elevation site (2060 m; Table 1).

Hylaeus and *Osmia* were common

throughout the season at both high and low elevations. *Lasioglossum* was common at 3290 m, but rare at 2060 m. We might have missed the peak season for *Lasioglossum* at 2060 m leading to sampling of fewer individuals of the genus. Though seasonally variable, *Heriades* and *Megachile* were common at 2060 m but less so at 3290 m. Seasonal and altitudinal variation in genus abundance limited the number of genera that could be included in altitudinal (Table 2) and seasonal (Figure 4) comparisons of lipid physiology.

Seasonal and altitudinal variation in temperature

As expected, air temperature was higher throughout the season at the low elevation site (2060 m) compared to the high elevation site (3290 m; Figure 5). We therefore expect strong differences in fat physiology across elevation. Similarly, although

the seasonal trend in air temperature was different across the sites, ambient temperature varied widely across the season. We thus expect to see differences in lipid physiology across the season at each site (see specific predictions below).

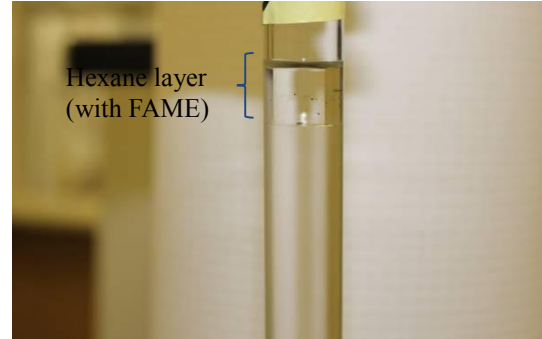


Figure 3. Separation of FAME from bee tissue.

Table 1. Total bees collected from two GTNP sites throughout the season

Box 1. Preparation of sample tubes with internal standard (IS)

Wash 16 ml clean glass tubes with hexane to remove any organic solvent/lipid and dry the tubes

Weigh each tube with caps on

Add 1 ml of 1mg/ml of IS (C 13:0) in chloroform

Reweigh the tubes with respective caps on

Unscrew the caps and leave the tubes in hood to evaporate the chloroform (it takes ~ 28 – 36 hrs).

Store the tubes with caps on, at -20 °C until used.

Genus	June		July		August	
	2060 m	3290 m	2060 m	3290 m	2060 m	3290 m
<i>Andrena</i>	10		7	2	1	2
<i>Epeolus</i>						1
<i>Halictus</i>	4		1			
<i>Hoplitis</i>			6	3	1	3
<i>Hylaeus</i>			4	4	9	11
<i>Lasioglossum</i>	11		3	5	1	13
<i>Megachile</i>			5	2	15	2
<i>Osmia</i>	10		11	13	6	9
<i>Ashmeadiella</i>			3		1	
<i>Colletes</i>				1	2	1
<i>Heriades</i>			3		10	
<i>Sphecodes</i>					1	
<i>Bombus</i>	10		7	6	13	2
<i>Anthophora</i>			3		3	
<i>Ceratina</i>			2			
<i>Chelostoma</i>			1			
<i>Dufourea</i>			1			
<i>Perdita</i>			2			
<i>Protosmia</i>			1			
<i>Stelis</i>			1			

Seasonal and altitudinal variation in total water content

So far, total water content has been measured for three bee genera: *Andrena*, *Megachile* and *Osmia*. We will be measuring the same for other genera in future. For *Andrena*, *Megachile* and *Osmia*, the total water content decreased from June/July to August.

Table 2. Sample sizes of bee genera with sufficient sampling at the two sites (2060 m and 3290 m) to allow for analysis of altitudinal variation in FA composition.

Genus	Month	2060 m	3290 m
<i>Bombus</i>	July	7	6
<i>Hylaeus</i>	July	4	4
	August	9	11
<i>Osmia</i>	July	11	13
	August	6	9

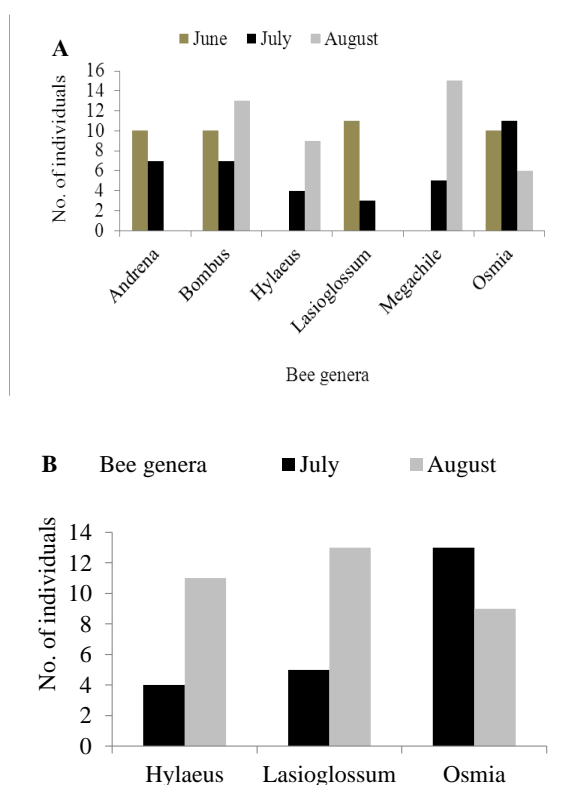


Figure 4. Bees with sufficient sampling across the season to allow for analysis of seasonal variation in FA composition at 2060 m (June to August) (A) and 3290 m (July and August) (A).

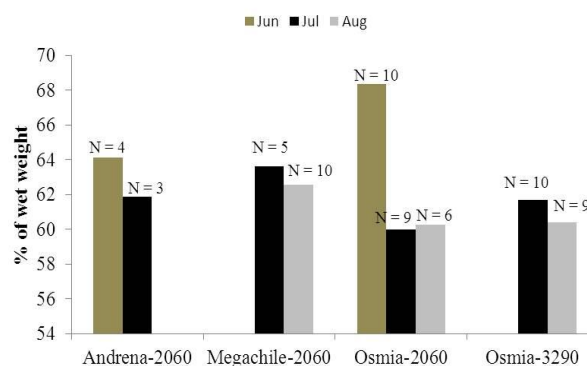


Figure 5. Seasonal variation in total body water content of *Andrena*, *Megachile* and *Osmia* at low elevations site and *Osmia* at high elevation site.

Seasonal and altitudinal variation in temperatures

As expected, air temperature was higher throughout the season at the low elevation site (2060 m; Figure 6) compared to the high elevation site (3290 m, Figure 6). We therefore expect strong differences in fat physiology across elevation. Similarly, although the seasonal trend in air temperature was different across the sites, ambient temperature varied widely across the season. We thus expect to see differences in lipid physiology across the season at each site (see specific predictions below)

Preliminary GC data

Preliminary analyses suggest that the most common fatty acids found in native bees are palmitic acid (C 16:0), stearic acid (C 18:0), oleic acid (C 18:1), linoleic acid (C 18:2) and linolenic acid (C 18:3). In standard fatty acid nomenclature, the value to the left of the colon refers to the number of carbons in a FA and the value to the right of the colon refers to the number of unsaturated bonds in the FA. We therefore included these five FAs in the FAME standard (Figure 7). As we didn't detect the presence of tridecylic acid (C13:0) in bees, we used this fatty acid as our internal standard. Many other fatty acids including myristic acid (C 14:0) and palmitoleic acid (C 16:1) are also present at low levels in bees.

By comparing the retention times of fatty acids from bee samples with the chromatogram for the FAME standards (Figure 7), we were able to identify fatty acids in *Bombus impatiens* (Figure 8). We will use this approach to identify FA profiles in the remaining samples.

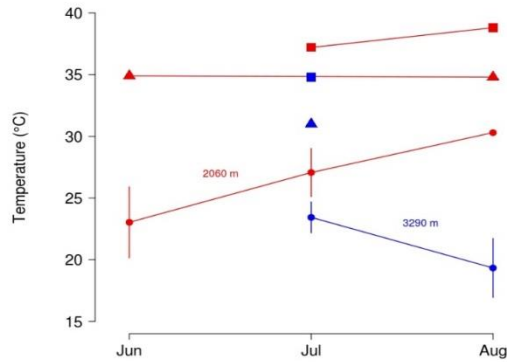


Figure 6. Seasonal variation in ambient temperature at 2060 m (red circles and line) and at 3290 m (blue circles and line). Triangles and squares are body temperature of *Bombus* and *Megachile*, respectively, at low (red) and high (blue) elevations.

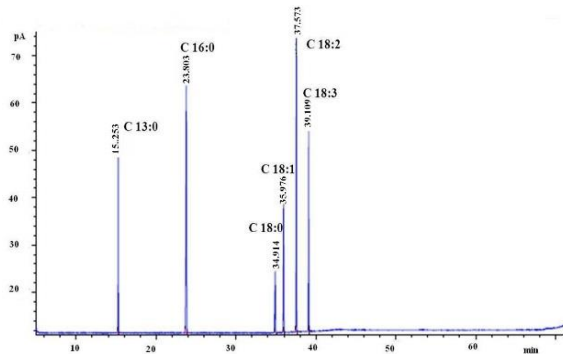
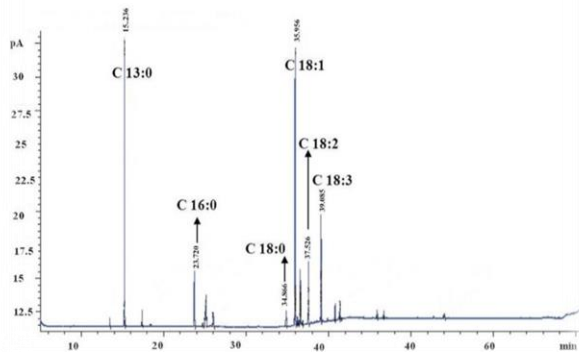


Figure 7. GC-FID chromatogram showing six standard FAMES. The rotated number above each peak gives the retention time in minutes and the text denotes the type of fatty acid represented by the peak.

Figure 8. GC-FID chromatogram showing fatty acids



present in a bumblebee (*B. impatiens*). We identified the fatty acids by comparing the retention time with the standards. Labels as in Figure 7.

PROJECT PROGRESS AND PLAND FOR COMPLETION

The summer field work yielded excellent seasonal and altitudinal sampling of a diverse group of native bees (Table 1). In the lab, we have validated the derivatization approach for native bees, including optimizing the FAME preparation technique, and generating standard peaks for determination of fatty acid profiles (Figure 7). We are now in the process of analyzing GC data to determine the fatty acid composition of each bee by comparison with FAME standards and plan to complete data analysis by May 2013. Additionally, we have collected pollen from bee scopa and if possible for such small samples, will determine FA composition of these samples for comparison with results for bees. These data will allow us to test several predictions:

Prediction 1: Endothermic bumblebees will have lower and invariant PUFA: SFA ratios.

Bumblebees maintain a constant body temperature even when ambient temperature varies widely (Figure 6). They can regulate high body temperatures independent of environmental temperature both during foraging trips and while in the hive (Heinrich 1974). Because bumblebees maintain high body temperatures independent of season and altitude, we predict they will have low PUFA: SFA ratios relative to other bees and that PUFA: SFA ratios won't vary with season or altitude in bumblebees.

Prediction 2: PUFA: SFA ratios will be higher for the bees collected in early spring and late fall.

The cool temperatures of early spring and late fall (Figure 6) may require higher PUFA: SFA ratios. Further, bees emerging from diapause are likely to still have diapause fatty acid signatures and those preparing for diapause are likely to begin accumulating PUFA's in their fat bodies (Hahn and Denlinger 2011).

Prediction 3: High altitude bees will have higher PUFA: SFA ratios.

Lower temperatures at higher elevations (Figure 6) will likely require higher PUFA: SFA ratios to maintain membrane function. We predict that, within-species, bees collected from higher altitudes will have higher PUFA: SFA ratios. Our collections will allow us to compare FA composition across altitude for 3 genera in July, and 2 genera in August (Table 2).

Prediction 4: Shifts in PUFA: SFA ratios will be driven by endogenous lipid physiology not by diet.

Diet can strongly influence fatty acid composition in body tissues and even propensity for entering diapause (Ruf and Arnold 2008). However, tissue fatty acid composition can change even when diet is the same (Khani et al. 2007). Bees acquire dietary lipids only from the pollen they eat. Pollen can contain from 1-18% lipid by mass (Roulston and Cane 2000), but pollen lipid content has not been found to change systematically with any measured environmental or ecological factor (Roulston et al., 2000). We therefore predict little seasonal or altitudinal variation in pollen lipid content or quality (PUFA: SFA), such that changes in bee PUFA: SFA ratios are driven by endogenous shifts in lipid physiology.

◆ ACKNOWLEDGEMENTS

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CLIMATE CHANGE IN THE ALPINE ZONE: A CONTINUOUS, MULTI-PROXY RECORD OF HOLOCENE GLACIER ACTIVITY AND ENVIRONMENTAL CHANGE AT GRAND TETON NATIONAL PARK



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✦ ABSTRACT

Alpine environments are particularly sensitive to climate fluctuations and recent changes to their hydrological and ecological components have been documented in mountain ranges around the world. Paleoclimate reconstructions from these regions can improve our understanding of alpine climate change by placing recent observed changes in a long-term context and by improving our ability to accurately predict and model future changes. This research is designed to use lake sediments to reconstruct the glacier history and paleohydrology of the Teton Mountain ecosystem to provide a framework for characterizing the impacts of climate change occurring in Grand Teton National Park. Multiple physical and geochemical parameters contained in sediments from lakes strategically positioned along elevation transects will be used to develop the first continuous records of: 1) alpine glacier fluctuations, including the timing and character of deglaciation, and 2) coupled fire, vegetation and hydroclimate histories spanning the elevation gradient of the Tetons. This work is critical for assessing and managing the ecological impacts of future climate change in this unique ecosystem and for improving our understanding of how changes here are connected to the broader climate system.

✦ INTRODUCTION

The impacts of modern climate change on natural environments pose serious challenges for the National Park Service resource conservation efforts. Among the most vulnerable of National Park lands are the abiotic (e.g. hydrologic, glacial) and ecologic components of mountain ecosystems, where evidence for climate change impacts are numerous and include disappearing alpine glaciers, mountain pine beetle infestations, and reduced biodiversity. Mountain regions have been identified as particularly sensitive to climate changes (Fischlin, 2007), and it is likely that the observed impacts of current and future changes will be proportionally more apparent at higher elevations (e.g. Beniston et al., 1997). For these reasons, National Parks that contain alpine environments are ideal sites for research dedicated to the assessment of climate change impacts and their context within the range of natural variability. This work is designed to reconstruct the timing and magnitude of alpine climate variability at Grand Teton National Park (GRTE), and to assess the glacier and environmental responses to such variations.

The Tetons occupy a strategic position with respect to the climate dynamics of the western U.S. and GRTE contains a relatively pristine and intact ecosystem. However, despite the importance and sensitivity of this geographical region, few climate records exist. The majority of paleoclimate research efforts in the Teton Range have focused on the deglacial history of the area (Licciardi and Pierce,

2008; Pierce et al., 2011) or on the dynamics of small extant alpine glaciers (Fryxell, 1935; Edmunds et al., 2011; Reynolds, 2011). Here, we will use lake sediments from basins positioned along three elevation transects to produce complementary, high-resolution records of Holocene glacier activity and environmental change. The combined records will be studied to evaluate glacial and vegetative responses to global (and local) climate forcing mechanisms operating since regional deglaciation, with particular attention paid to the behavior of climate indicator proxies during the past 200 years. Once constrained, variability in the proxy records will be used to evaluate the evolution of Holocene climate since deglaciation of the Teton Range.

◆ STUDY AREA

Grand Teton National Park is one of the most visited National Parks in the country, attracting more than 2 million people every year (www.nps.gov). At the heart of the ~485 mi² park stands the Teton

Mountain Range, a rectangular (~40 miles long by ~10 miles wide) fault-block mountain range flanked on both sides by broad, low-lying basins (Love et al., 2003). The unique tectonic setting and glacial history of GRTE has created a series of glacially carved, U-shaped valleys situated on the eastern flank of the range (Figure 1A). Many of the valleys contain a chain of lakes composed of multiple small basins, positioned in high elevation glacial cirques, which drain into a large, moraine-dammed piedmont lake at the valley mouth (Figure 1B). Lake basins at GRTE formed following regional deglaciation ~15,000 years ago (Licciardi and Pierce, 2008). Sediment fill in each lake marks the timing of glacier retreat from individual basins (lake inception) and contains a continuous and datable record of subsequent upstream glacier activity and environmental conditions in the catchment. This study focuses on three valleys: Avalanche Canyon, Glacier Gulch, and Cascade Canyon (Figure 1). Each valley spans >3,000 vertical feet of elevation and transects multiple vegetation environments from high alpine tundra down to mixed conifer forests at the valley floor.

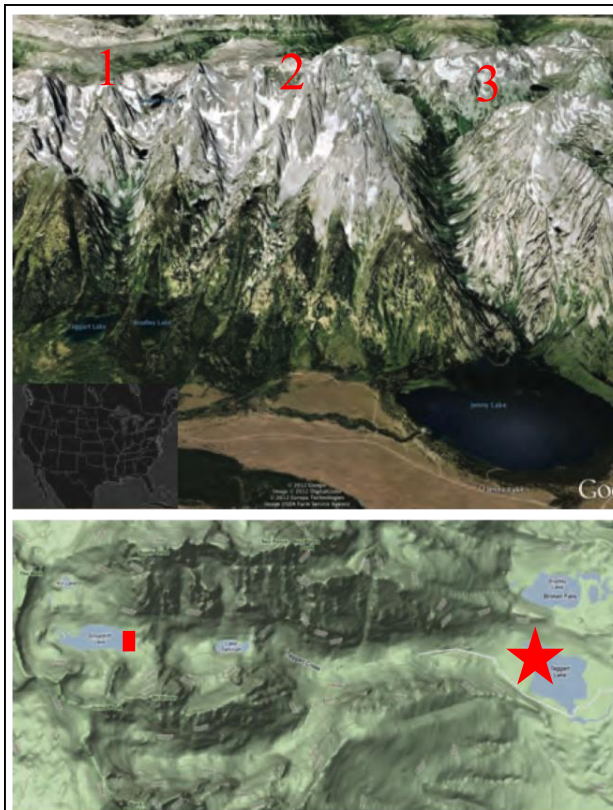


Figure 1. Location of field site at GRTE. (A) Oblique aerial view of the eastern flank of the Teton Range. The three valleys (and respective lakes) included in this study are numerically labeled in red. From south to north: 1) Avalanche Canyon (Taggart Lake, Lake Taminah, Snowdrift Lake), 2) Glacier Gulch (swampy meadow, Delta Lake), 3) Cascade Canyon (Jenny Lake, Lake Solitude, Mica Lake). Inset map highlights location of field site within U.S. (B) Aerial view of Avalanche Canyon showing typical chain of alpine lakes targeted for this project. Note multiple small, high elevation lakes that are positioned in glacially scoured cirque basins. These lakes drain down valley into Taggart Lake (red star). The large terminal moraine complex visible on the right side of the frame impounds Taggart Lake and marks the greatest extent of the valley glacier during the most recent (Pinedale) glaciation.

Avalanche and Cascade Canyons no longer contain glacier ice and sediment cores taken from lakes in these valleys will be used to develop

complementary deglacial chronologies and paleohydrologic records. Glacier Gulch is a steeply dipping canyon that emanates from the clearly observable cirque below the north face of the Grand Teton. At the head of this canyon lies the Teton Glacier, one of the few existing glaciers in the Teton Range and a significant icon of GRTE. Recent glaciological studies have shown that Teton Glacier is sensitive to climate change and has fluctuated in area and volume in response to 20th century climate variability (Edmunds et al., 2011; Reynolds, 2011). The terminal moraine at the base of Glacier Gulch surrounds a swampy meadow (bog) that represents the position of an ancient lake. It is likely this feature was once analogous to the piedmont lakes (i.e. Taggart Lake, Jenny Lake) included in this study. However, the basin has since been infilled with sediment produced by the activity of Teton Glacier. Sediment cores retrieved from Glacier Gulch will provide a continuous record of Teton Glacier activity and address lingering questions regarding its Holocene history (such as whether or not it completely disappeared during the early Holocene and what was the timing of its reformation and behavior during Neoglaciation).

◆ METHODS

Field Program

Fieldwork was initiated in July 2012 and included reconnaissance of potential field sites, bathymetric mapping, seismic surveys, and lake coring. This work was made possible through a 2012 UW-NPS research grant. Summer field operations were based out of the UW-NPS Research Center, which provided fast and convenient access. Bathymetric mapping of the two piedmont lakes, Taggart and Bradley, was accomplished using a portable GPS based “fishfinder” device strapped to a hard-shell sea kayak that was generously lent to us by Dr. Hank Harlow and the UW-NPS research center. Depth soundings were recorded along a grid paddled on each lake surface and bathymetric maps were created by interpolation of the point datasets. Two subsequent summer field excursions to GRTE took place in August and October 2012, respectively. The purpose of these trips was to evaluate the access to high elevation lake sites and assess potential hazards related to approaching these sites in winter conditions with coring equipment and a team of field assistants.

Seismic surveys were conducted on Jenny and Taggart lakes using an EdgeTech sub-bottom profiler (CHIRP) to map the spatial distribution of

sediment and to identify optimal coring locations. Seismic reflection data was collected along transects performed in a gridded manner covering the lake surface area and each transect was obtained in conjunction with a differential GPS device to record spatial coordinates. Sediment cores were retrieved from Taggart, Bradley, and Jenny Lakes during three coring campaigns between January and May 2013. All cores were retrieved from a stable ice platform on the lake surface using a percussion coring system (Nesje, 1992). In addition, a short surface core was taken from each lake to capture the sediment water interface and undisturbed upper sediments.

Geochronology

Establishing an accurate and reliable geochronology is a critical step in the development of useful paleoclimate records. Age control of the sediment cores will be obtained through a combination of radioisotope analysis and tephrochronology. Surface sediments and those deposited within the past ca. 100 years will be dated using short-lived isotopes (¹³⁷Cs and ²¹⁰Pb) while older sediments will be dated using radiocarbon on terrestrial macrofossils. The radiometric-derived chronologies will be augmented by the presence of volcanic ash (tephra) deposits from known volcanic eruptions. Multiple Holocene tephra layers have been noted in nearby lake records (Whitlock, 1993; Spaulding et al., 2011) and have been discovered in extruded cores taken in this study (see results section below). Geochemical identification of all tephra layers will be achieved through electron probe microanalysis. The tephrostratigraphy at GRTE will improve the geochronology of this study by providing chronostratigraphic marker horizons and additional absolute age constraints.

Analytical Program

We will use radiocarbon to date basal sediments from the piedmont lakes and bog to time the initial recession of glacier ice from respective terminal moraines and use basal ages from high-elevation lakes to provide a succession of constraints on glacier size and rate of recession. Sediment physical characteristics (accumulation rate, magnetic susceptibility (MS), density, grain size) are primarily influenced by the contribution of glacially eroded material (Dahl, et al., 2003) and will be analyzed to track upstream glacier behavior throughout phases of retreat in neighboring valleys. Whole-core density and MS measurements will be taken in 0.5 to 1.0 cm intervals using a gamma-ray attenuation porosity evaluator (GRAPE) logging system. Core segments will then be split, and core halves photographed using

a CoreScan flatbed scanner. Grain size analyses will be conducted at 1 to 20 cm resolution using a Malvern Long Bed Mastersizer and sediment accumulation rates will be determined from the individual chronologies established for each basin.

Charcoal accumulation and pollen assemblages preserved in lake sediments reflect biomass burning and vegetation type, respectively, and can be efficiently measured (Whitlock, 1993; Power et al., 2008; Power et al., 2011). Hydrologic and ecologic changes reflect variations in regional atmospheric circulation and are recorded by bulk biogeochemical properties (e.g. TOC, BSi, C:N, $\delta^{13}\text{C}$) and in the hydrogen isotope ratios (D/H) of lipids (e.g. *n*-alkanes) and other molecular biomarkers from aquatic and terrestrial organic matter that are preserved in lake sediments (Meyers and Teranes, 2001; Huang et al., 2002; Sachse et al., 2004; Tierney et al., 2010). We will measure these hydrologic indicators in addition to charcoal and pollen taxa along each valley transect to develop coupled hydrology, fire, and vegetation histories at various elevations.

Sedimentary organic matter (OM) proxies are commonly used indicators of environmental change and reflect changes in the productivity of lakes and their surrounding catchments (Meyers and Teranes, 2001). Climate changes are reflected in OM content through water temperature and lake-ice duration, or through changes in water column nutrient cycling and sediment delivery processes. Traditionally, total organic carbon (TOC) is used as a measure of within-lake primary productivity (Meyers and Teranes, 2001). However, in glacier occupied watersheds, TOC can be influenced by the influx of glacially derived clastic material (e.g. Larsen et al., 2011). Biogenic Silica (BSi) is an amorphous form of silica that is biogenically precipitated in the water column by a variety of aquatic organisms. In lake sediments, it primarily encompasses diatom frustules (Conley and Schelske, 2002) and like TOC, can be a reliable measure of primary productivity. Both TOC and BSi have been shown to correlate strongly with Holocene climatic changes, notably summer temperature (Battarbee et al., 2002; McKay et al., 2008). Lake sediment OM is derived from both terrestrial and aquatic sources. The abundance ratio of C:N and $\delta^{13}\text{C}$ will be used to evaluate changes in the source and production of vegetation growing in and around lakes. A major advantage of these proxies, relative to TOC and BSi, is that they are relatively independent of sedimentation rate. All bulk biogeochemical indicators will be sampled for at 1 to 5 cm resolution.

◆ PRELIMINARY RESULTS

Seismic Surveys

Preliminary results from the seismic surveys indicate large variations in the distribution and thickness of sediment related to the complex lake floor morphologies and dynamic history of lake sedimentation. The seismostratigraphy of Taggart Lake is faintly resolved and acoustically opaque, suggesting a high sand or clay content. Isolated pockets of laminated sediment packages are evident in deeper regions and near the base of a prominent ridge feature. These areas will be targeted in the coring program. The sediment in Jenny Lake has a stratified appearance and contains multiple strong seismic reflectors (Figure 2). Approximate sediment thickness ranges from <0.5 m to >5.0m. Multiple acoustically transparent ridges are visible in the seismic profile and are draped with sediment. These ridges are interpreted as recessional moraines built by the Cascade Canyon glacier during deglaciation ca. 14,000 years ago. Multiple strong seismic reflectors can be traced across the basin. The strongest reflectors are present in the bottom part of the sediment fill and are interpreted as dense, glaciolacustrine deposits. A few distinct reflectors, which are evident in the central sub-basin are absent in more distal sub-basins. The seismostratigraphic pattern will be used in conjunction with lake cores to unravel the character of deglaciation of Jenny Lake.

Sediment Cores

Cores were collected from multiple sites within each lake basin and range in length from 40 cm to 287 cm. A total of eight, seven, and four cores were retrieved from Jenny, Taggart, and Bradley Lakes, respectively. At least one core from each lake contains light grey clay-rich basal sediments. These sediments are interpreted as deglacial deposits and confirm complete recovery of the Holocene sediment package. The depth to this clay layer in Jenny Lake corresponds to a distinct acoustic reflector seen in the seismic profiles at roughly 250 cm depth. Efforts to establish a secure geochronology for the lake sediments are currently underway. Two tephra layers were observed in an extruded core and sampled in the field for geochemical analysis. These layers were found at depths of ~100 and ~150 dm in a core taken

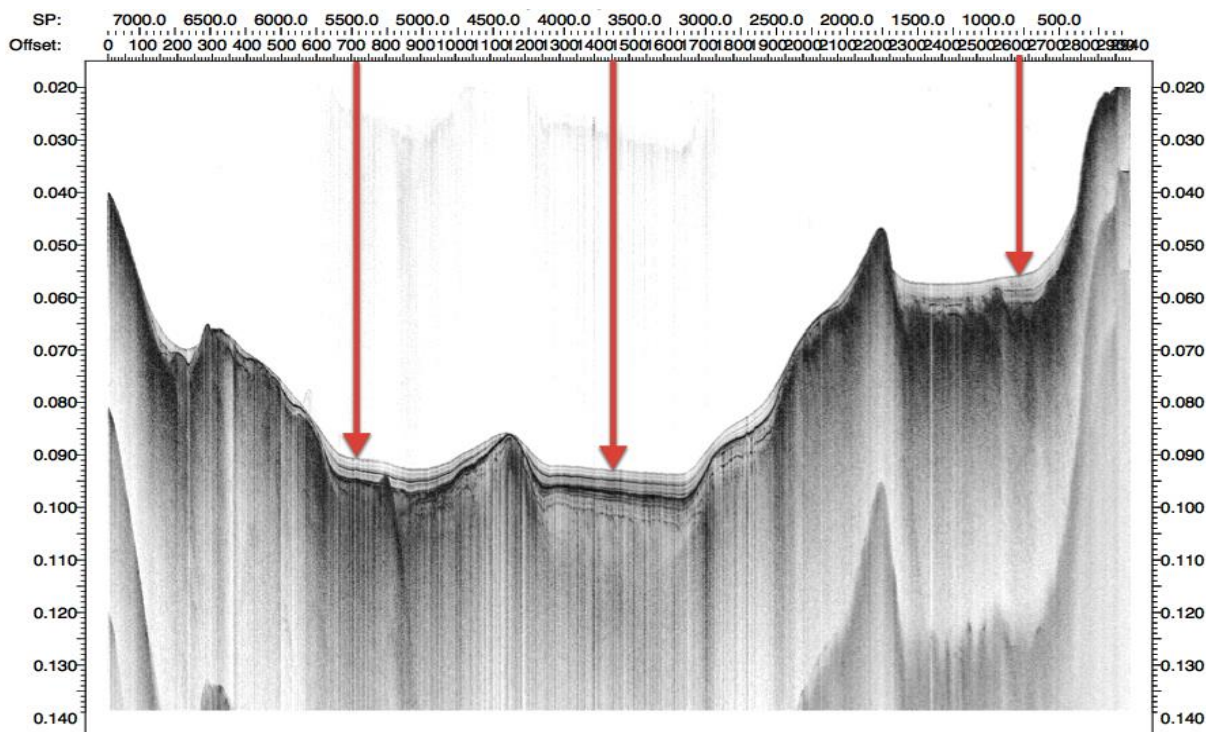


Figure 2. Seismic profile across Jenny Lake showing regular undisturbed lacustrine sediment fill interrupted by multiple recessional moraine ridges. This transect was performed in October 2012 using a CHIRP sub-bottom profiler. Lake core sites are shown (red arrows).

from Jenny Lake, and tentatively identified as the Mazama (~7.6 ka) and Glacier Peak (~13.6 ka) ash layers in accordance with nearby lake records (Whitlock, 1993). Both tephra samples have been sent to the University of Alberta for electron probe microanalyses and geochemical identifications are pending.

Anticipated Results and Discussion

The expected outcomes from this study will contribute to the understanding of past climate dynamics that have occurred in alpine environments of the western U.S. by providing a complete record of glacial fluctuations and complementary hydroclimate changes at GRTE, including the elevation effects of ecosystem responses to these changes. The implications for determining future changes to the Teton Mountain ecosystem resulting from natural and human-induced effects on the climate system are significant. In particular, empirical data and results from this work may improve the accuracy of predicting vegetation shifts, hydrologic (e.g. soil moisture, winter snowpack, lake water quality) changes, and ecosystem health. For example, we predict that intervals of higher-than-present summer

temperatures in the past, such as those documented in the early Holocene, would have reduced moisture availability, induced changes in vegetation, increased burning frequency, and caused earlier snowmelt. If documented, such changes will likely serve as analogues for the future. The continuous deglacial chronology established through this effort will define early Holocene climate variability in the Tetons. Furthermore, results from this work will contribute to our understanding of the climatic and non-climatic forcing mechanisms behind alpine glacier fluctuations and will both complement and reduce the uncertainties of existing moraine dating methods (e.g. refine local ^{10}Be production rates).

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TIME OF ECLOSION AND MATING SUCCESS OF MALE SAGEBRUSH CRICKETS

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✦ ABSTRACT

Few studies have measured multivariate sexual selection acting on the sexual signals of male insects in wild populations. Sagebrush crickets are ideally suited to such investigations because mating imposes an unambiguous phenotypic marker on males arising from nuptial feeding by females. However, an important assumption underlying such studies is that males collected as virgins and those collected as non-virgins had equal opportunities to mate, an assumption that may be violated if males eclose (i.e. emerge following pupation) at different times of the breeding season. If mated males are those in the population that eclosed earlier and hence had a longer period to obtain matings than males in the virgin group, then differences in the songs of virgin and mated males could simply be an artifact of age-related changes in male morphology as opposed to a causal factor underlying variation in male mating success. Accordingly, we conducted a mark-recapture study to determine if there is an association between first appearance in the population and the likelihood of mating in free-living males. We captured all of the virgin males calling in the study population and marked them uniquely with a numbered tag. Subsequently, we tracked the mating success of 98

male subjects through the mid-point of the breeding season. There was no significant effect of date of capture (a proxy for time of eclosion) on time to mating. We conclude, therefore, that any differences in the songs of virgin and mated males stems from their effect on male mating success and not from any age-related effects.

✦ INTRODUCTION

The sagebrush cricket, *Cyphoderris strepitans* (Orthoptera: Haglidae), is one of only three extant species of hump-winged grigs in North America, relatively obscure ensiferans that are restricted to mountainous areas of western North America (Morris and Gwynne 1978; Kumala et al. 2005). *C. strepitans* occurs in high-elevation sagebrush meadows nestled within coniferous forests in Wyoming and Colorado. In Grand Teton National Park, where the majority of field studies of *C. strepitans* have been conducted (Sakaluk and Ivy 1999; Sakaluk et al. 2004; Leman et al. 2009), sexual activity commences in mid-May. Each night of the breeding season, males emerge from the ground cover to secure a calling perch in sagebrush or lodgepole pine, where they sing to attract sexually receptive

females (Snedden and Sakaluk 1992; Snedden and Irazuzta 1994). Copulation is initiated when a female climbs onto the dorsum of the male, and ends with the transfer of a spermatophore to the female. During copulation, the female feeds on the male's fleshy hind wings and ingests hemolymph seeping from the wounds she inflicts (Morris 1979; Eggert and Sakaluk 1994). The wing-feeding behavior of females provides us with a powerful tool for documenting male mating success because the mating status of males can easily be determined by examining their hind wings for the melanized scars resulting from mating.

Over the past two years, we have used wing-wounding as a bivariate measure of male fitness (intact wings = virgin, wounded = mated) in studies designed to measure sexual selection in free-living crickets. Specifically, we have attempted to identify the morphological and acoustical traits that are the targets of sexual selection by collecting an equal number of virgin and non-virgin males at the midpoint of the breeding season, recording their songs, and preserving them for subsequent morphological analysis. Preliminary analyses have revealed stabilizing selection on male carrier frequency and strong directional selection for longer pulse durations and hence, greater energy expenditure (Ower et al., in review).

The selection analyses described above assume that males in the virgin and mated groups had equal opportunities to mate, an assumption that may be violated if males eclosed at different times of the breeding season. If mated males are those in the population that eclosed earlier and hence had a longer period to obtain matings than males in the virgin group, then differences in the songs of virgin and mated males could simply be an artifact of age-related changes in male morphology as opposed to a causal factor underlying variation in male mating success. Accordingly, we conducted a mark-recapture study in 2012 to determine if there is an association between first appearance in the population and the likelihood of mating in free-living males.

◆ METHODS

At the beginning of the breeding season, we established a study plot in Grand Teton National Park near the border with Bridger-Teton National Forest (43°54'40.56"N, 110°28'20.24"W). This population was chosen because no males had mated at our first population census. On four of the first five days of the study, we attempted to capture all of the virgin males calling in the study area and any mated males that had

been previously marked. Each male was marked with a numbered tag secured to his pronotum with cyanoacrylic glue. Fluorescent paint was also applied around the pronotum and to the femora to facilitate the recapture of marked individuals with portable fluorescent lanterns. Seven days after the population was first censused, the population attained a ratio of approximately 1:1 virgin to mated males, at which time the study was terminated. We recorded data on the date of initial capture and mating success for 98 males initially marked as virgins. We used failure-time analysis to examine the effect of a male's capture date on his time to mating (Allison 1995), specifically, a Cox regression as implemented by PROC PHREG in SAS (version 9.2, SAS Institute Inc. 2010). The EXACT option was specified in the model statement to handle ties, instances in which different males had the same time to mating. This option was employed because it assumes that mating times are, in reality, continuous and ordered, assumptions that are almost certainly met by our data.

◆ RESULTS

Our analysis revealed no significant effect of date of capture on time to mating (Wald $\chi^2 = 0.32$, $P = 0.57$). We also compared virgin ($N = 55$) and mated males ($N = 43$) with respect to their date of capture. Mated males were first captured significantly earlier than virgin males (Student's t test with equal variances, $t_{96} = 2.07$, $P = 0.042$), but the difference in the time of their initial appearance in the population was less than half a day ($(0.49 \pm 0.24$ days (mean \pm SE)).

◆ DISCUSSION

Few studies have measured multivariate sexual selection acting on the sexual signals of male insects (Brooks et al. 2005; Bentsen et al. 2006; Gershman et al. 2012), and almost none in wild populations (Punzalan et al. 2010). The dearth of studies in wild populations is almost certainly a consequence of the difficulty in measuring male mating success under natural conditions. Although this difficulty can be circumvented by broadcast of experimentally manipulated male sexual signals to females in natural populations (Bentsen et al. 2006) or by intensive long-term video recordings (Rodríguez-Muñoz et al. 2010), such studies are the exception rather than the rule. Sagebrush crickets, *Cyphoderris strepitans* (Orthoptera: Haglidae), offer an excellent model system with which to pursue measurements of

multivariate selection in wild populations because mating imposes an unambiguous phenotypic marker on males that results from an unusual form of nuptial feeding by females (Morris 1979; Eggert and Sakaluk 1994).

An earlier study, in which males were experimentally muted and returned to their natural population, revealed that song is essential to male mating success (Snedden and Sakaluk 1992). More recent work has quantified sexual selection operating on male song by recording songs of virgin and mated males captured from wild populations (Ower et al., in review). This work has revealed a complex pattern of multivariate nonlinear selection characterized primarily by strong stabilizing and disruptive selection on male song traits. However, an important assumption underlying these studies is that males collected as virgins and those collected as non-virgins had equal opportunities to mate, an assumption that may be violated if males eclose at different times of the breeding season. The present study shows no significant effect of date of capture (a proxy for time of eclosion) on time to mating. We conclude, therefore, that any differences in the songs of virgin and mated males stems from their effect on male mating success and not from any age-related effects.

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FENCES, CONSERVATION, AND TOURISM: A HISTORY OF THE JACKSON HOLE WILDLIFE PARK

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On a pleasant July day in 1948, a small crowd congregated in rows upon rustic logs on the edge of a broad meadow in Jackson Hole, Wyoming. Beyond the meadow to the west, they spied glimpses of the Snake River through aspen, fir, and pine trees. On the horizon, Mt. Moran loomed, framed by a vast expanse of azure sky. The crowd's eyes however were not fixed upon the distant view, but on the small makeshift podium placed at the foot of the benches, and on the seven dignitaries who were scheduled to speak that day (Figure 1). They had come to dedicate the Jackson Hole Wildlife Park (JHWP). Conceived in 1945, the Park would provide controlled habitat for a host of primarily big game animals from the region, affording tourists the opportunity for education and close-up viewing of native mammals.

Laurance Rockefeller was the most anticipated speaker. He was the grandson of John D. Rockefeller, America's preeminent oil tycoon, and son of John D. Rockefeller Jr., (Figure 2) who had purchased the lands on which the JHWP now sat. Laurance oversaw the administration of those lands. In expounding on the Park's purpose, Laurance argued that tourism and conservation were linked, stating that visitors would "see wildlife..., learn to identify the various animals and birds, to appreciate them, to understand the problems involved in their protection, the need for preserving forests, safeguarding watersheds, saving the wilderness – in effect, the people will see what they are asked to conserve." In addition, Rockefeller argued out that the Wildlife Park

would promote equality and the local economy through affording greater access to wildlife for all visitors, while also bringing in tourist dollars. In short, Laurance presented a JHWP which offered universal benefits for nature – human and non-human.¹



Figure 1. Laurance Rockefeller speaks at the opening ceremony. Reprinted, by permission, from Grand Teton National Park: Jackson Hole Wildlife Park, Historic Records Collection”

Though Rockefeller's speech presented an uncomplicated picture of Wildlife Park benefits, events which preceded its establishment demonstrated that tourism, conservation, and economics were far more complex and contested than Laurance revealed. In 1927, John D. Rockefeller Jr. formed the Snake River Land Company, and used it to secretly buy cattle ranches in Jackson Hole, hoping to eventually turn those lands over to the federal government for the establishment of a national park. The land which

¹ Quotes taken from Laurance S. Rockefeller, "Remarks Made at the Opening Ceremonies of the Jackson Hole Wildlife Park, Monday July 19, 1948," in Grand Teton National Park: Jackson Hole Wildlife Park, Historic Records Collection (Hereafter referred to as Wildlife Park Collection), Box 5, Series 13, Folder 1; The literature which connects tourism and conservation in American History is

deep. For an argument which largely praises that connection see Robert Righter, *Crucible for Conservation: The Creation of Grand Teton National Park* (Boulder: Colorado Associated University Press, 1982). For a more critical appraisal, see Richard West Sellars, *Preserving Nature in the National Parks* (New Haven: Yale University Press, 1997).

would become the JHWP was purchased as a part of this scheme.

Rockefeller did not act alone however. His philanthropy had its origins in the minds of several local conservationists, including dude rancher Struthers Burt and Yellowstone Park Director Horace Albright both of whom hoped to preserve Jackson Hole for wildlife and tourism. To ensure that speculation would not drive up the costs of the land, Rockefeller employed Kenneth Chorley, a confidant who would eventually direct most of Rockefeller's conservation efforts, to gain executive approval for the withdrawal of nearly all of the remaining lands in Jackson Hole which had been open for settlement. Land use was further restricted when on February 26, 1929 the 96,000 acre Grand Teton National Park was created, setting aside the Teton Peaks and several alpine lakes at their base from development. The net effect for locals of so much land withdrawal was a loss of agency, as population growth in the region from this point on would be almost entirely confined to the town of Jackson, at the southern end of the valley, and to lands nearby which were already owned by cattle and dude ranchers. By 1930, when Rockefeller's plans for Jackson Hole were revealed, local opposition to the NPS – to Albright and Rockefeller in particular - and distrust of non-locals had intensified.²

Though conflicted ideas regarding the value and management of Jackson Hole did not die out during the 1930s, it was the presidential proclamation of Jackson Hole National Monument (JHNM) on March 5, 1943 that stoked the greatest controversy during the first half of the twentieth century. The Monument encompassed almost all lands in Jackson Hole - including future Wildlife Park lands - aside from the town of Jackson and the nearby Elk Refuge, and was managed by the federal government. Local ranchers howled out of fear that they would lose grazing rights and that their land would be devalued. Teton County and the state of Wyoming cried foul owing to the potential loss of tax base from the withdrawn lands, and from the perception that states' rights were being trampled by the federal takeover of lands which had previously been administered by the

² Righter, 43-65; Horace M. Albright, Director of National Park Service to Wilford Neilson, Editor, *Jackson Hole Courier*, Washington, D.C., 5 April 1933, in *Mr. John D. Rockefeller Jr.'s Proposed Gift of Land for the National Park System in Wyoming*, unpublished typescript obtained from the University of Wyoming at Laramie, 1-41.

³ Conclusions are drawn from issues of the *Jackson's Hole Courier*, March –June, 1943, with more dense analysis of these articles occurring later in this paper. The arguments for the Wyoming congressional delegation

state. Wyoming's congressional delegation unanimously denounced the JHNM, twice attempting and failing to abolish it.³

The Monument also became a cause célèbre for conservationists. Dude ranchers such as Struthers Burt and Charles Cornell Moore, as well as former NPS Director Horace Albright, regarded the JHNM as a fulfillment of their plan for Jackson Hole as hatched twenty years earlier. Meanwhile, writers for a diverse array of progressive publications promoted nationwide embrace of the JHNM, believing that it would protect the area from commercial exploitation, provide a vast natural playground for tourists, and promote the preservation of the landscape and its wildlife.⁴ Thus, in October, 1945, when the Jackson Hole Game Park (the original name for the JHWP) was launched, the use of its lands was still contested, and those responsible for the Park's creation continued to draw both ire and praise.



Figure 2. John D. Rockefeller Jr. and his wife Abby at Jenny Lake, 1931. Reprinted, by permission, from Grand Teton National Park: Jackson Hole Wildlife Park, Historic Records Collection”

Support and opposition to the new Park unveiled a somewhat new cast of characters and an evolving set of issues. Laurance Rockefeller, Horace Albright, and Struthers Burt were joined in their backing by Wyoming governor Lester Hunt, and the state's Fish and Game, and Highway Commissions.

are primarily drawn from Congress, House, Committee on Public Lands, “To Abolish the Jackson Hole National Monument, Wyo.: Hearings before the Subcommittee on Public Lands of the Committee on Public Lands,” 80th Cong., 1st Session, 14-18 April, 1947, H.R. 1330.

⁴ Examples of these publications include Bernard DeVoto, “The West Against Itself,” *Harper's Magazine*, January 1947, 1-13, and Struthers Burt, “The Jackson Hole Plan,” *Outdoor America*, November – December, 1944.

Together, they embodied a cautiously optimistic new coalition of local and state tourism boosters. In 1943, when the Jackson Hole National Monument was created, both governor Hunt and the Wyoming Department of Fish and Game (WDFG) strenuously opposed, arguing that it would reduce tax revenues, hurt the cattle industry, and limit hunting opportunities for locals. Though they still resented federal authority and the National Park Service (NPS) in particular, locals and Wyoming state officials had rapidly come to embrace the growing hordes of visitors who poured into Jackson Hole to ski, visit the Monument, and gawk at wildlife. It turned out that wildlife had much greater economic value for viewing than hunting. Moreover, outsiders such as Rockefeller and Albright may not have become overnight celebrities, but projects such as the Game Park could potentially be molded to suit new aims.⁵

Fairfield Osborn was another figure who played a prominent role in the founding and molding of the new Park. As president of the New York Zoological Society, Osborn was primarily interested in the fauna of the JHWP. He argued that the Wildlife Park re-created a natural environment that contributed to public education, stating that if nature was threatened, it should be brought to the people. Thus, the Wildlife Park and its attached research station were desirable since they allowed the public to get a glimpse *en masse* of animals which few would encounter in their natural habitat. Further, Osborn paid special attention to obscuring any fencing from the public, even arguing that the large mammals would scarcely be aware of their confinement. Osborn believed that the success of conservation required mass education, and the Wildlife Park would be a tool for this enlightenment.⁶

Ironically, the most principled opposition to the Wildlife Park came from friend and fellow

⁵ My conclusions come primarily from analyses of the *Jackson's Hole Courier* from 1943-1947. See especially "Governor Lester C. Hunt States Views on Proposed Jackson Hole Game Park," 31 January 1946, 1.

⁶ An excellent summary of Osborn's philosophy for the Wildlife Park is provided in "When Nature is the Zoo: Vision and Power in the Art and Science of Natural History" *Osiris* 11 (1996): 117-143. On Osborn's advocacy of the role of humans in nature, see Fairfield Osborn, *Our Plundered Planet* (Boston: Little, Brown and Company, 1948), 194-201; On the role of a fence in the Wildlife Park, see Fairfield Osborn to Carl Jorgenson, 22 January 1949, Charles Cornell Moore Collection, Conservation

conservationist, Olaus Murie. A wildlife biologist, former director of the Jackson Hole Elk Refuge, and soon to be president of the Wilderness Society, Murie also sat on the board of the Jackson Hole Preserve, Inc., which managed and directed the use of Rockefeller lands in Jackson Hole. In November, 1945, Murie resigned his position in protest, calling the Wildlife Park a 'roadside zoo.' In a 1946 article for *National Parks Magazine*, Murie opined that fenced wildlife could set a precedent for similar attractions in national parks. Though the Wildlife Park was placed on Rockefeller lands, John D. Rockefeller Jr. had always intended that they be used in an expanded Grand Teton National Park, an eventuality that might force the NPS to accept the JHWP within its borders. Additionally, Murie argued that the Wildlife Park was representative of a general trend toward laziness in the American approach to the outdoors. Calling it "recreation on a platter," he argued that the JHWP would enable thousands of tourists to observe magnificent animals while hardly exiting their vehicle. Further, he posited that this would cheapen the experience of encountering animals in the wild since wildlife could be observed behind concealed fences by simply driving into the valley. For Murie, the Wildlife Park commercialized the wonder of nature and packaged it for a mass audience. In the process, the authenticity of a direct encounter with wildlife was lost.⁷

The issues involved in the creation of the Jackson Hole Game Park help to illuminate many of the larger conservation issues of the period. The proliferation of national parks and other public lands, the development of the automobile, and an increase in leisure time during the first half of the twentieth century enabled more Americans to visit places such as Jackson Hole. Conservationists, most of whom were extra-local and did not rely on the land directly for their livelihood, generally viewed tourists as

Collection, Denver Public Library (Hereafter referred to as Moore Collection), Box 1, File Folder 114.

⁷ Olaus Murie to Struthers Burt, 5 December 1945, Olaus Murie Collection, Conservation Collection, Denver Public Library (Hereafter referred to as Murie Collection), Box 2, File Folder 43; Olaus Murie, "Fenced Wildlife for Jackson Hole," *National Parks Magazine*, January-March 1946, 8-11; Gregg Mitman, *Reel Nature: America's Romance with Wildlife on Film* (Cambridge: Harvard University Press, 1999), 89; On the Wilderness Society's opposition to roadside nature, see Paul Sutter, *Driven Wild: How the Fight Against Automobiles Launched the Modern Wilderness Movement* (Seattle: University of Washington Press, 2002), 23-53.

natural allies in protecting the land and its flora and fauna. Broadly speaking, Laurance Rockefeller, Struthers Burt, Horace Albright, and Fairfield Osborn fell into that camp. However, Olaus Murie represented a growing number of conservationists who, in the 1940s, questioned such an anthropocentric approach. He argued that easy human access to nature only served to fragment critical habitat, endangering the very resources conservationists sought to protect. In many ways, this debate over what constituted effective conservation would be central to the saga of the Wildlife Park from 1945-1953.

In the two-and-one-half years between the approval of the Park in 1945, and its opening in 1948, the Wildlife Park Trustees, which included Rockefeller, Osborn, representatives of WDFG, and a few interested Jackson Hole locals, busied themselves developing its infrastructure, and shoring up public support. As part of this preparation, they enlisted a group of visiting college students in 1947 to survey seventy-five locals on their knowledge of the Wildlife Park, their support for its mission, and their feelings about those who directed its operations. A brief overview of survey results revealed that all but one of the respondents was familiar with the JHWP and that the vast majority supported it. Responses to multiple queries on tourism showed that, depending on the question, anywhere from 77%-100% of those surveyed supported visitors to Jackson Hole. Moreover, a consistently sizable majority supported conservation, the display of big game animals for the public, and the use of fences to corral them within the confines of the Wildlife Park. The survey made clear however that many locals still distrusted the federal government, as a far larger percentage responded that the state of Wyoming was more capable of managing the JHWP than the federal government.⁸

Additional moves broadened the scope of the Park, and garnered increased support. One of the first moves was to change the original moniker “Jackson Hole Game Park,” to “Jackson Hole Wildlife Park.”(Figure 3). Though casual observers could not miss the fact that the park prioritized big game animals, it was also clear that the term “game” implied hunting, an activity that repelled some tourists and suggested that the representative species of the Park existed primarily as sport and as food. In seeking to

⁸ CR Carpenter and Hollis Farnum, “Information Schedule on Jackson Hole Region: A Project: The Jackson Hole Summer Research Program”, Unpublished Typescript in Wildlife Park Collection, Box 4, Series 6, Folder 1.

attract a broad array of tourists, Wildlife Park trustees sought a different kind of consumption. In 1947, trustees made a more substantive change, when it decided to include a research station as part of the Wildlife Park. Eventually this station would provide opportunities for biologists to carry out studies of area wildlife and their habitat. Though the inclusion of the research station was promoted by trustees such as Osborn, it was clear that it contained political motivations as well. Several conservation organizations withheld their endorsement of the Wildlife Park until 1947. Some of them, most notably the Izaak Walton League and the American Society of Mammalogists, offered the Park their support once they learned that research would be included in its mission. It turned out that, for some conservationists, the unsavory and artificial aspects of enclosed wildlife were trumped by opportunities for scientific research.⁹

In preparation for opening in 1948, several practical matters needed to be addressed before tourists could visit the Wildlife Park. Of the 1,500 acres in the park, 400 of them were to be fenced for permanently enclosing large mammals. James Simon, director of the JHWP in 1947 reported approximate “stocking” numbers: 20 antelope, 20 buffalo, 10 elk, 6 moose calves, 10 mule deer, and 10 white-tailed deer. Buffalo were to be acquired from Yellowstone National Park, moose calves as well as elk were to be captured by Simon and his staff, and the remainder of the animals were to be procured from WDFG. The cost of labor, capture, and transport of this massive haul of fauna was just over \$3,000. Of course, these mammals were unaware that their mobility was now limited by contract. Consequently, fences and cattleguards were constructed to secure the arrangement. The initial enclosure for the 400 acres required five miles of fencing that would be eight feet high. In addition, cattleguards were to be placed across major roads coursing through the park. The combined material costs of the cattleguards and fencing came to over \$27,000. This infrastructure would prove to be a source of ongoing tension – addressed later in this article – as Wildlife Park managers and trustees sought to keep animals inside park boundaries while obscuring all evidence of their confinement. Concealing artifice through human engineering was essential if tourists were to have authentic experiences with nature.¹⁰

⁹ Mitman, “When Nature was a Zoo”; On the name change, see Harold Fabian to Vanderbilt Webb, Wildlife Park Collection, Box 1, Series 1, Folder 1.

¹⁰ “Cost in Delivering and Capturing of Game Animals for Wildlife Park”, undated, Wildlife Park Collection, Box 1, Series 1, Folder 1; Richard Winger

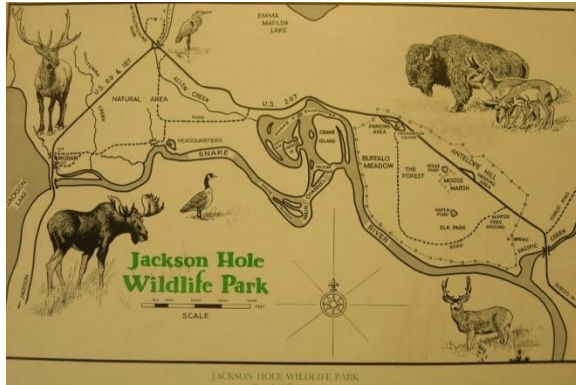


Figure 3. Map of Jackson Hole Wildlife Park, available for visitors in 1948. Reprinted, by permission, from Grand Teton National Park: Jackson Hole Wildlife Park, Historic Records Collection.

Though there is little quantifiable evidence as to whether these tourists had an authentic encounter with nature, some visitor figures from 1947-1951 are available. At the end of 1951, one year before the JHWP closed, 275,000 people had visited, with the totals progressively increasing after 1947.¹¹

In addition to viewing wildlife (Figure 4), educational literature was available for browsing and purchase. Among the individual pamphlets available were those on moose, elk, deer, coyotes, buffalo, and other animals. Visitors could also purchase a set of slides on Yellowstone for \$1.95, or a booklet titled, "Exploring our National Parks and Monuments." They could even buy a "Jackson Hole Wildlife Park" collectible handkerchief should their visit inspire an emotional response, or if they simply sought souvenirs. Those who desired a more comprehensive overview of wildlife within the greater Jackson Hole ecosystem could purchase Fairfield Osborn's "Jackson Hole Wildlife Park" brochure. In addition to helping the curious traveler understand the wildlife within the enclosure, it also provided brief vignettes on the region's fish, birds, flora, and smaller mammals. The same visitor could also peruse a more in-depth pamphlet on the elk of the region, the research

to Laurance Rockefeller, 10 July 1946, Wildlife Park Collection, Box 1, Series 2, Folder 5; Mitman, "When Nature was a Zoo."

¹¹ "Minutes of a Special Meeting of the Members and Board of Trustees of Jackson Hole Wildlife Park", 25 August 1951, in Wildlife Park Collection, Box 3, Series 2, folder 3.

¹² Unsigned to HF Schieman, 10 June 1953, James Simon to HF Schieman, 12 February 1953, HF Schieman to James Simon, 10 June 1953, above letters

of which was provided by the foremost expert on the species in North America, Olaus Murie. Ironically, the average tourist reading this pamphlet (and having arrived by car) would be unaware of Murie's critique of roadside wildlife viewing. That same individual would not likely be conscious of how Murie and Osborn clashed over the role of tourism in conservation. Nonetheless, concerns over how humans encountered wildlife remained a source of tension amongst those who managed the Wildlife Park.¹²



Figure 4. Tourists visit the Wildlife Park. Reprinted, by permission, from Grand Teton National Park: Jackson Hole Wildlife Park, Historic Records Collection.

Lists of animals brought into the Wildlife Park revealed that no big game predators were included. By the early 1920s, wolves in the region had been hunted almost to extinction. Coyotes maintained an active presence in the area, but their right to exist was contested since they preyed on the same animals desired by both tourists and hunters.¹³ For the employees of WDFG who managed the day-to-day operations of the Park, coyotes were alternately perceived of as nuisances to be kept out of the enclosed portion of the park, or vermin to be shot. In fact, records from 1947-1952 provide convincing evidence that deterring coyotes from entering the enclosure

in Wildlife Park Collection, Box 3, Series 3, Folder 15; Fairfield Osborn, *Jackson Hole Wildlife Park, and The American Elk, or Wapiti*, in AHC, University of Wyoming, "UW-National Park Research Center Records", Box 1.

¹³ For a brief history of human perceptions of wolves and coyotes in the United States and attempts to eradicate them, see Donald Worster, *Nature's Economy: A History of Ecological Ideas* (New York: Cambridge Press, 1977).

occupied large chunks of their time. Snow drifts piled up at the base of Park fences enabling coyotes to leap into the enclosure. On more than one occasion, coyotes killed resident deer. It was far more common however for these predators to be shot by WDFG.¹⁴

The same snow drifts that enabled coyotes to prey on deer also allowed wildlife to escape the enclosure. Soon after assuming management duties, park director James Simon gave up all pretense of keeping moose and elk within the enclosure. The long legs of moose and the athleticism of elk, combined with deep and encrusted snow demonstrated just how permeable were JHWP borders.¹⁵

Elk presented issues which were both specific to the JHWP and representative of broader complexities within Jackson Hole. The elk herd in Jackson Hole was one of the largest in the world. Prior to homesteading in the late nineteenth- and early twentieth-century, the herd migrated south to lower elevations for the winter. However, increased human population and property fences blocked migration patterns. Consequently, an Elk Refuge was established in Jackson Hole in 1912 which served primarily to provide winter feed in the harsh Jackson Hole climate. That extra feed enabled the region to both maintain an artificially high carrying capacity of elk, and provide more abundant elk without challenging the property rights of local landowners.¹⁶

In some ways then the Wildlife Park supported the mission of WDFG. By feeding elk in the winter, the JHWP provided additional winter habitat for elk in the region. Though a small number of those elk remained protected in the enclosure throughout the year, the majority of elk came to the JHWP in the cold months and remained only for the available feed. During fall hunting season, they could often be found in the nearby Teton National Forest where they might become a trophy for a local sportsman, or for a visitor who had been enticed by the big game opportunities in Jackson Hole. Of course, both brands of sportsmen paid for Fish and Game-issued hunting permits. In addition, visiting hunters

would especially benefit local and state economies in their pursuits. Moreover, WDFG officials presumed that some of those who gawked at elk in the JHWP in the summer might be enticed to pay large sums of money to shoot at them in the fall. This was the perspective held by Lester Bagley and Carl Jorgenson, WDFG officials, and vote-wielding trustees of the JHWP. It was a position shared by Wyoming governors Lester Hunt and Frank Barrett, both of whom were non-voting trustees of the JHWP.¹⁷

Such views often placed Bagley and Jorgenson in conflict with the other trustees. One issue that demonstrated this conflict was the Jackson Hole National Monument (JHNM). Wyoming Department of Fish and Game, Governor Hunt, and many Jackson Hole locals opposed the JHNM since its inception in 1943 because it prohibited hunting within its boundaries.¹⁸ This put them at odds with JHWP President Laurance Rockefeller whose family fortune made both the Monument and the Wildlife Park possible. Trustees Harold Fabian and Kenneth Chorley had worked as Rockefeller's representatives since the 1930s. They could be counted on to side with Laurance. Finally, fellow trustee Fairfield Osborn worked closely with Rockefeller to conceive of the JHWP in 1945, and thus held similar views on its purpose. Taken as a whole, this group sought to bring tourists into the Park, but gave only lukewarm support to hunting, and was far more willing to trust the National Park Service than either locals or the WDFG.

Between 1947 and 1952, these philosophical rifts were revealed on several occasions. As a sponsor of the JHWP, the state of Wyoming offered an annual appropriation that hovered around \$5,000. Hoping to have greater control in day-to-day management operations, they argued that half of their allotment should be used to pay the salary of JHWP director James Simon. The majority of the trustees refused this concession, believing that it would limit some of their autonomy in JHWP operations. In 1951, Senator Lester Hunt (former Wyoming governor) complained of the "lack of wild animals on public display," and

¹⁴ "Feeding Reports, 1948-1949", AHC, University of Wyoming, "UW-National Park Research Center Records", Box 1, "Department of Fish and Game".

¹⁵ James Simon to Members of the Jackson Hole Wildlife Park Board of Directors and Advisory Board Members, 15 April 1952, in Wildlife Park Collection, Box 5, Series 11, Folder 1.

¹⁶ For an excellent general history of Jackson Hole which includes chapters on elk, conservation, and tourism see John Daugherty, *A Place Called Jackson Hole: The Historic Resource Study of Grand Teton National Park* (Moose, WY: National Park Service, 1999).

¹⁷ Richard Winger to Laurance Rockefeller, 10 July 1946, in Wildlife Park Collection, Box 1, Series 2, Folder 1.

¹⁸ The prohibition on hunting could be rescinded once annually when the NPS, in collaboration with WDFG determined if the elk numbers had exceeded carrying capacity. If so, they would issue temporary hunting permits. This was the subject of annual controversy since the WDFG generally supported an annual hunt on the Monument, while the NPS often disagreed and was loathe to issue permits.

that “Fairfield Osborn was more interested in the research work than he was in the exhibition of animals.” He thought that the original mission of the JHWP (apparently to display large game animals to a desirous public) was not being prosecuted. WDFG and other officials of the state also clashed with the JHWP over cattleguards, fences, and the roads that ran through the Wildlife Park. Consequently, it came as no great surprise when the state of Wyoming pulled its funding for the JHWP in 1952, the last full year of the Wildlife Park’s existence.¹⁹

Perhaps the most significant reason why the state of Wyoming dropped its support was related to an event only indirectly connected to the JHWP. On December 16, 1949, finally confident that their lands would become part of a national park, Laurance and John D. Rockefeller Jr. transferred over 32,000 acres of land to the federal government, including those acres comprising the Wildlife Park. The following September, Congress added the Jackson Hole National Monument and the original Grand Teton National Park to those acres to form an expanded national park.²⁰ Though the JHWP continued to operate under a renewable ten-year lease signed by the NPS and Wildlife Park trustees in 1950, it was becoming clear that management of the Wildlife Park would require close cooperation with the National Park Service. Given the long history of animosity between the state of Wyoming and the NPS, there was little chance for successful collaboration.

On August 23, 1952, the JHWP trustees listened intently as Fairfield Osborn read a letter penned by Laurance Rockefeller which requested that the trustees effectively end their oversight of the Wildlife Park and transfer its operations to Grand Teton National Park. For Rockefeller, this was not a defeat, but a long-awaited triumph. In 1927, when his father had begun purchasing land in Jackson Hole, his goal was to eventually turn that land over to the federal government for the creation of a national park, a park that would include the lands on which the JHWP sat.

¹⁹ For examples of these philosophical rifts, see Wyoming Fish and Game Commission to Fairfield Osborn (undated), in Wildlife Park Collection, Box 1, Series 2, Folder 2, James Simon to Fairfield Osborn, 23 January 1949, Wildlife Park Collection, Box 4, and Kenneth Chorley to Harold Fabian, 17 July 1951, in Wildlife Park Collection, Box 4, Series 4, Folder 1.

²⁰ Daugherty, 320-327; Righter, 126-141.

²¹ Comments from Laurance Rockefeller in “Minutes of a Special Meeting of the members, Board of Trustees, and Advisory Board of Jackson Hole Wildlife Park” 23 August 1952, in Wildlife Park Collection, Box 5, Series 14, Folder 2.

Among voting trustees, there was little discussion and no hint of disagreement with Rockefeller’s stated wishes.²¹

Amongst those present at that meeting, there were only two dissenting voices: Struthers Burt and Charles Cornell Moore. Both men had at one time been dude ranchers in the area. In fact Burt played a prominent role in attracting the Rockefellers to Jackson Hole in the 1920s. Though both Burt and Moore hoped to see Jackson Hole preserved from development, they did not wish to see its management passed completely out of local hands. In a letter to Rockefeller, Moore reminded Laurance that federal control had been a “thorn in the side of those who would conserve Jackson Hole.” He also argued that turning over the Wildlife Park to the NPS “just makes another Park which in all probability will be under the charge of a ranger with no particular interest.” For Rockefeller, that NPS ranger represented the triumph of conservation in Jackson Hole. For Burt and Moore, Park Service control of the Wildlife Park signified that Jackson Hole locals no longer possessed a voice in the conservation of the lands on which they lived.²²

Burt and Moore’s fears that NPS control of the Wildlife Park would lead to its demise were well-founded. On July 1, 1953 the Park Service discontinued the JHWP, tore down its fences, and released the animals which remained (Figure 5). Their decision was largely due to its policy of not confining or feeding wildlife within the boundaries of a national park.²³ However, the research component of the JHWP carried on. Initially, the Jackson Hole Research Station was to be administered by the New York Zoological Society. This made logical sense because Fairfield Osborn was its president, and the Society possessed the financial resources and scientific expertise to support ongoing research in Grand Teton. Eventually, the New York Zoological Society discontinued its affiliation with the Research Station, and management of its programs and facilities became a joint project of the University of Wyoming and the

²² Comments from Laurance Rockefeller; Charles Cornell Moore to Laurance Rockefeller, 12 September 1952, in Wildlife Park Collection, Box 5, Series 14, Box 2.

²³ That policy was instituted in 1942. For more on this, see Marguerite Shaffer, “Performing Bears and Packaged Wilderness: Reframing the History of National Parks,” in *Cities and Nature in the American West* (Reno: University of Nevada Press, 2010), and Sellars, *Preserving Nature in the National Parks*.

²⁴ Kenneth Diem, “The Research Station’s Place in History,” 1978, unpublished typescript in Diem collection at American Heritage Center.

National Park Service. In an ironic twist which would have been appreciated by both Burt and Moore, the Research Station was moved in 1978 to the location of a private residence, the AMK, on the shores of Jackson Lake. It resides there today.²⁴

Today, tourists entering Grand Teton from the east pass through the site of the former Wildlife Park. One of the roadside pullouts occupies the site where formerly there was a viewing platform and information on large game animals to be found in the Park. That platform and all other human constructions have been removed. A traveler will also pass within full view of the gentle hillside where Laurance Rockefeller delivered his invocation speech in 1948. Yet there is no evidence of the platform on which he spoke, or the benches cut into the terraced hillside where an expectant audience listened. One can even drive into the former Wildlife Park all the way to the banks of the Snake River at Oxbow Bend where a sign commemorates a historical wagon trail that passed through there in the nineteenth century. Yet the placard makes no mention that the same spot where travelers once forded the river was also a site managed for viewing large ungulates. It should then come as no surprise that there remains no visual evidence of animal enclosures or winter feeding operations.

This seems unfortunate and perhaps even a bit disingenuous. Grand Teton is a park where the human past is emphasized. Tourists can visit the sites of former cattle ranches and dude ranches (some of which are being restored). There are sites which commemorate movies filmed within park boundaries. Grand Teton even contains entire neighborhoods of non-NPS employees within its boundaries. And, one of the crown jewels of the park is the Rockefeller Preserve, the brainchild of Laurance Rockefeller, where both natural and constructed evidence of his philanthropy abounds. Yet none of the interpretive displays hint at his role in the Wildlife Park. As the history of the Jackson Hole Wildlife Park demonstrates, tourism, conservation, science,

education, and the viewing of wildlife have not always operated in harmony. Nonetheless, managing the tension between them remains central to the daily operation of national parks. It is no less true today than on that fateful day in 1948 when Laurance Rockefeller opened the Wildlife Park.



Figure 5. View of the meadow where the Wildlife Park once existed. Photo was taken from the spot where visitors sat in 1948 to hear Laurance Rockefeller speak at the opening ceremony. Photo by author

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GRAND TETON NATIONAL PARK FOCUSED VISITOR SURVEY



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♦ ABSTRACT

In the summer of 2010 research was conducted in Grand Teton National Park to ascertain trip characteristics of GRTE visitors, examine pertinent socio-demographic visitor characteristics, develop an understanding of how visitor socio-demographics affect trip characteristics and outcomes, and determine how these characteristics and demographics affect interest in and experiences with the Indian Arts Museum. Researchers spent seven weeks in the park and followed the onsite data gathering with an at home follow-up for visitors.

♦ INTRODUCTION

During spring, 2010, the researchers contracted with the Grand Teton Association (GTA) to conduct a visitors' study in the Moose and Colter Bay areas of Grand Teton National Park (GRTE) during the summer, 2010 season. Research objectives were identified and the methodology designed in cooperation with GTA and GRTE. The research called for an on-site survey at Moose and Colter Bay as well as an at-home survey for visitors to complete after their trip to the Park. The results of the at home and on site surveys have been combined where possible. Otherwise, results are organized by the location of the data collection (Colter Bay, Moose, and at home), which will allow the reader to focus on visitors in the specific areas of interest. Furthermore, reporting of the results has the aim of addressing the research objectives, which will assist the park managers and

others to answer questions regarding visitors' experiences in GRTE.

♦ RESEARCH OBJECTIVES

1. To examine pertinent socio-demographic visitor characteristics.
2. To ascertain trip characteristics of GRTE visitors:
 - Purpose for trip, including destination determination.
 - Trip length and time for trip.
 - Trip expectations.
 - Trip activities and events.
 - Trip services expected and utilized.
 - Pre-trip planning and information sources.
 - Pre-existing knowledge of and expectations about the area and potential experience.
 - Expectations and utilization of specific sites including the Colter Bay Visitor Center and the Indian Arts Museum Vernon Collection.
 - Expectations, anticipated results and preferences concerning relocation of specifically identified facilities.
3. To develop an understanding of how visitor socio-demographics affect trip characteristics and outcomes.

◆ METHODS

During spring, 2010 the research team contracted with the Grand Teton Association to provide a social survey of Grant Teton National Park visitors during the summer, 2010 season. Survey instruments were developed in cooperation with National Park Service (NPS) employees; instruments were designed to elicit information to answer research questions and to meet the research objectives of the project.

The study design included three separate survey instruments and one interview instrument: 1) On-site interview/survey at Colter Bay and Moose, 2) At-home survey, and 3) the Indian Arts Museum Interview. The At-home Survey was self-administered by visitors after returning home through Survey Monkey, an Internet-based survey program.

First, to obtain information and addresses for the at home survey, visitors were stopped at a location across from the General Store at Colter Bay, asked a small set of questions about their trip and were asked to participate in an at-home survey after they returned home. This brief interview and solicitation took about 3 minutes to complete. The goal was to collect a minimum of 1,500 participants for the at-home survey. This goal was met.

Second, research assistants conducted the On-site Interview at Colter Bay and Moose by soliciting voluntary personal interviews of visitors at two locations: 1) across from the General Store at Colter Bay and 2) outside Moose Visitor Center. Respondents were approached about participating as they were exiting the parking lot at Colter Bay and exiting the visitor center at Moose. Respondents at both locations were asked parallel questions. The interview took about eight minutes to complete. Researchers had established a goal of a minimum of 300 interviews with about two-thirds coming from Colter Bay, where the Indian Arts Museum is located, and one-third from the Moose area. These proportions were maintained and reflected in the data.

Third, a brief Museum Interview of four-questions was administered to willing visitors immediately upon their exit from the Visitor Center Colter Bay. These questions were open-ended with the objective of providing additional, detailed information, especially about their experience at the Visitor Center and Indian Arts Museum.

In addition to the on-site surveys and interviews, a traffic counter was used at the exit to

Colter Bay near the General Store to track approximate traffic totals during the on-site survey period.

Fourth, the At-home Survey was administered during fall, 2010. All respondents with legitimate email addresses were sent an invitation to participate in the self-administered survey through Survey Monkey. Researchers sent the initial invitation and then sent three follow-up reminders to participate over a four-week period. The survey consisted of over 40 questions which duplicated most of those asked on-site as well as additional questions regarding recreational experiences. The goal to obtain a 50 percent response rate was met.

Survey Solicitation

During June, July, and August, two research assistants participated in research activities at Colter Bay and Moose. Researchers spent two-thirds of their time at Colter Bay and one-third of their time at Moose. This time was allocated based on research objectives.

The interviewers were stationed across from the General Store on the exit lane of the drive. One large road sign stating the presence of a traffic survey was posted at the intersection across from the restaurant. Another sign was posted on the road immediately before the survey area. As vehicles stopped for the traffic stop, a researcher approached the stopped vehicle. A brief script was read, informing the driver of the survey and asking the driver to participate in the survey. If the driver agreed to participate in the At-Home Survey, the driver completed the contact information form that included their name, mailing address, and email address. Then, the driver was asked three brief questions. The driver then departed the traffic stop area. Because of traffic congestion concerns identified by park officials, the research assistants stopped no more than three vehicles at one time. Thus, if three vehicles were stopped, other approaching vehicle or vehicles were waived past the traffic stop. Individuals who had participated already in a prior stop were also waived past. Tour buses were excluded from the study as were NPS and business vehicles.

Individuals were free to refuse to participate in the research project. About four percent of the total traffic count as measured by the traffic counters refused to participate in the study.

◆ RESULTS

Key Points:

Overall, the results of the three different surveys are similar. Based on previous studies and experience, the demographic characteristics contain no surprises. The respondents were well educated, about half were traveling with children. About half were repeat visitors to GRTE. Half were between 40 and 60 years of age. About 20% were day visitors and 80% were planning to stay overnight in the park.

- In the Museum, the bead and wardrobe exhibits were listed as the most important, ranking higher than all of the other exhibits combined. The moccasin exhibit was the next most important.
- Of the Colter Bay respondents (N=163), 38% of those visiting the museum said they were less likely to visit the museum if moved to Moose, while 53% indicated they were not sure or that it would make no difference in their likelihood of visiting the Museum. Of the Moose respondents (N=56), 82% said they would be likely to visit the museum if it was located at Moose and about half of the respondents had visited the museum. Of the At-Home Survey respondents (N=540), 26% said they were less likely to visit at Moose while 12% said they were more likely to visit and 72% said they were not sure.
- The participants in this study indicate that wildlife and nature are primary interests. Regardless of the location of the Museum, a natural history relationship established with the cultural objects displayed may significantly increase visitation.

Selected Results of Interest:

- Of the services and facilities used at Colter Bay, the General Store was ranked first in the degree to which respondents liked services and facilities at Colter Bay. The showers and Visitor Center came in second with 28% of respondents identifying these facilities.
- Of the recreational activities used at the Colter Bay, the museum ranked 10th.
- 39% said they were aware of the Indian Arts Museum before the trip began; being aware of the Museum before the trip began did not increase the likelihood that they visited the Museum.

- The typical respondent indicated being in the Museum between 30 minutes and one hour while about a third of respondents said they were in the Museum for one hour or longer
- Fifty-one percent of the At-Home Survey indicated they visited the Museum. Women were slightly more likely than men to visit the Museum. Individuals in their 40s or older were significantly more likely to visit the Museum than those in their 20s and 30s. Education was not significantly related to visiting though those with a high school education or less were the most likely (59%) to visit. Those who went to the Museum had a slightly lower party size and lower number of family members than those who did not visit the museum. Those visiting the park for the first time were slightly more likely to visit the Museum, as were those staying longer in the park and those entering through the East entrance.
- Visitors to the Museum placed a higher importance than those that did not visit on these five activities out of nineteen: non-motorized boating, museum, visitor center, horseback riding, and ranger programs.
- Almost 80% of those attending at least one ranger program at Colter Bay visited the Museum while only 44% of those not attending a ranger program visited the Museum.
- About 83% of Colter Bay visitors visited the Colter Bay Visitor Center.
- Services used at Colter Bay indicated the most important was restrooms at 76%, followed closely by 71% using the information counter, and 55% using the bookstore.

Traffic Counts

Upon exiting the survey area, vehicles passed through an infrared traffic counter. Results of the traffic counts are in Table 1 below. In eight 6-hour sampling periods, over 7,000 traffic counts were recorded, yielding about 930 vehicles per time period or about 155 vehicles per hour.

Tour Buses

Between June 29 and August 4 of the data collection time period, the research assistants

identified by name and counted the number of tour buses leaving the Colter Bay area on thirteen days of the sampling time framework. Results show that 32 tour buses were counted, an average of 2.5 per day (Table 2). Over a 90-day summer period, the number of buses was estimated to be 225. Assuming an average of 40 visitors per bus, one could estimate that well over 9,000 bus visitors went through the Colter Bay area each summer. Due to time constraints for the tours, the buses were not stopped at the Colter Bay traffic stop nor were any individuals travelling on buses interviewed.

Table 1. Traffic counts during sampling period.

Date	Count	Time Period
7/8/2010	934	9:00 am -3:00 pm
7/12/2010	878	9:00 am -3:00 pm
7/28/2010	964	9:00 am -3:00 pm
7/29/2010	947	1:00 pm – 7:00 pm
7/30/2010	933	9:00 am -3:00 pm
8/1/2010	921	1:00 pm – 7:00 pm
8/4/2010	953	9:00 am -3:00 pm
8/6/2010	922	1:00 pm – 7:00 pm
Total	7,452	
Mean	931.5	

Survey Results Characteristics of Colter Bay Visitors

The characteristics of the respondents (Table 3) are based upon 871 completed surveys either at home or in the Colter Bay parking area. The characteristics should be representative of the generalized visitor to Colter Bay with the exception of the gender data. A larger than expected proportion of the respondents was male. This is due to the preponderance of males in the interviews conducted on-site at Colter Bay. Because the interviewers approached the driver's side of the vehicle, males were interviewed disproportionately as compared to females. However, the remainder of the data should be representative of the generalized visitor.

The visitors were predominantly white with only 15% indicating a race other than Caucasian. As expected the visitors were well educated with 80% having completed a Bachelor or Graduate degree. Only 4% had a high school or less education. Approximately 70% of the parties surveyed had children present with a mean of 2.6 children in those parties having children present in the Park. For all groups surveyed, the mean group size was 3.4 members. However, the median was 2.0 indicating that

half of the respondents had no more than 2 people in their group.

Approximately 56% of the respondents had made one or more previous trips to GRTE with 44% being on their first trip to the park. The median number of previous trips was one, indicating that about half of the visitors had only one previous trip to the Park. The mean was 4.6 previous trips suggesting that many were experienced visitors with numerous trips to the area. The results seem to indicate three types of visitors related to experience. About 45% are first time visitors while about 30 percent are on their second trip to the area and about 25% have made several previous trips to the park.

Table 2. Tour buses at Colter Bay.

Number	Date	Name
1	6/29/2010	Green Tortoise
2	7/2/2010	West Valley Charter
3		Holiday Motor Coach
4	7/5/2010	Lamoille Valley Bus
5	7/8/2010	Lewis Stage
6	7/9/2010	Lake Shore Motor Coach
7		Yellowstone Tours (old yellow bus)
8	7/12/2010	Arrow Stage Line
9		Lamoille Valley Bus
10, 11		OC&W Coachways (2 buses)
12	7/13/2010	Lewis Stage
13	7/15/2010	Lake Shore Motor Coach
14		Lewis Stage
15		Lin Lines
16	7/25/2010	Arrow Stage Line
17		Lamoille Valley Bus
18		Le Bus
19		Yellowstone Tours (new silver bus)
20	7/28/2010	MTR Western
21		Capital
22		Holiday Motor Coach
23	7/30/2010	Lake Shore Motor Coach
24		Yellowstone Tours (old yellow bus)
25	8/1/2010	Holiday Motor Coach
26		Utah Trailways
27	8/4/2010	Smith Coachways
28, 29		Holiday Motor Coach (2 buses)
30		Lake Shore Motor Coach
31		Yellowstone (old yellow bus)
32		Fabulous Coach Lines

Table 3. Demographic characteristics of respondents based upon the combined data from on-site and at home surveys.

Trip Characteristics

Characteristic	Percent	Mean	Median	Minimum	Maximum
Gender					
Male	62				
Female	38				
Race					
Non-White	15				
White	85				
Education					
High School or Less	4				
Some College	16				
Bachelor Degree	34				
Graduate Degree	46				
Children	70	2.6		0	7
Age 0-12	69	1.7		0	4
Age 13-18	70	1.5		0	4
Age		48.7	49.0	18	82
Party Size		3.4	2.0	1	30
Previous Trips to GRTE		4.6	1.0	0	100

The generalized characteristics of survey participants' trip to GRTE and Colter Bay are described in Table 4. The characteristics are based upon the merged data from on-site interviews at Colter Bay and the at home surveys. Over 75% of the visitors were planning to stay overnight in the Park with the median length of stay being four days and the mean was 4.9 days. Those spending one or more nights in the Park were asked what type of lodging they were using. The plurality of respondents (41%) were either staying in a tent or camping. Significantly, another 23% indicated that they were in some type of RV or camper trailer. A total of 30% were staying in a cabin, cottage, or hotel in the Park. Approximately 70% of the visitors indicated that a location other than GRTE was their most important trip destination. However, among those who had made previous trips to the park 57% indicated that GRTE was their primary destination. There is a statistically significant relationship between the number of trips and whether GRTE was the primary destination.

Table 4. Generalized Characteristics of respondents based upon the combined data from on-site and at home surveys.

Characteristic	Percent	Mean	Median	Minimum	Maximum
First Trip to GRTE					
No	56				
Yes	44				
Trip Type					
Overnight	76				
Day Only	24				
Days in the Park		4.9	4.0	1	43
GRTE Most Important Trip Destination					
No	70				
Yes	30				
Entrance into Park					
North	41				
East	14				
South	45				
Exit from the Park					
North	38				
East	11				
South	50				
Visited Colter Bay on Trip					
No	7				
Yes	93				
Visited Colter Bay Visitor Center					
No	24				
Yes	76				
First Trip to Colter Bay					
No	34				
Yes	66				
Previous Visits to Colter Bay	34	8.9	3.0	0	100

Over 90% of the respondents had visited Colter Bay on this trip to the Tetons. For 66% it was their first trip to the Colter Bay area. Of the 90% who stopped at Colter Bay, 76% went to the Visitor Center. Most who did not visit the Visitor Center during this trip were individuals who had made previous trips to Colter Bay. Approximately 45% of those staying at Colter Bay indicated it was the most important destination on this trip.

Recreational Activity at Colter Bay

Respondents were provided a list of 19 recreational activities available to them in the Colter Bay area. Using a five-point scale with 1 being not important to 5 being very important, they were asked to indicate the importance of the activities on their trip. Results show the items in descending mean order; the activities at the top, therefore, are more important than

others below (Table 5). The top five recreational activities all have means greater than 4 out of 5 on the scale: Observing Wildlife, Observing Nature, Walking, Photography, and Day Hiking. Ranking eight through ten respectively are the Visitor Center, Ranger Program, and the Museum. Observing Wildlife and Observing Nature have relatively small standard deviation values suggesting great amount of consistency of responses; high importance values were consistently given by the respondents. The fact that the Museum, Visitor Center and Ranger Program were ranked close together indicates they were often chosen as a set and ranked similarly. This conclusion is supported by the factor analysis that follows. The high ranking of Observing Wildlife and Observing Nature is consistent with the factor analysis findings also. They seem to be the very most important activities for visitors to Colter Bay.

Table 5. Importance of Recreational Activities

Recreational Activities	N	Mean	Std. Deviation
Observing Wildlife	497	4.74	.582
Observing Nature	504	4.73	.627
Walking	479	4.27	1.060
Photography	466	4.26	1.044
Hiking Day Only	433	4.26	1.132
Camping	419	3.83	1.519
Picnicking	408	3.61	1.286
Visitor Center	468	3.55	1.196
Ranger Program	391	3.22	1.359
Museum	446	2.98	1.285
Cabins	365	2.82	1.568
Non-Motorized Boating	378	2.68	1.487
Fishing	380	2.61	1.559
Swimming	380	2.57	1.398
Hiking in Backcountry	367	2.50	1.520
Bicycling	374	2.50	1.395
Horseback Riding	369	2.45	1.433
Motorized Boating	378	2.25	1.457
Jogging	365	1.97	1.356

Recreational Activity Importance-Factor Analysis

Principal components analysis was used to factor analyze the importance of the 19 recreational activities. Combined, the five factors explained 60.2% variance. The first factor, *Recreational Activity*, had four water-related activities with Bicycling. Factor two, *Interpretive Services*, had three variables loading: Visitor Center, Museum, and Ranger Program. Of note here, the importance rating of all three of these produced significant positive relationships with visiting the Museum. The third

factor *Nature Study* had two variables, Observing Wildlife and Observing Nature. The fourth factor is the *Hiking* factor, which included: Day Hiking, Walking, and Hiking in the Backcountry. And, the fifth factor was the Importance of Cabins at Colter Bay.

Table 6. Rotated Component Matrix Recreational Activity Importance.

	Component				
	1	2	3	4	5
Importance of Motorized Boating	.704				
Importance of Swimming	.690				
Importance of Bicycling	.678				
Importance of Fishing	.667				
Importance of Non-Motorized Boating	.664				
Importance of Jogging		.823			
Importance of Visitor Center					
Importance of Museum		.777			
Importance of Ranger Program		.732			
Importance of Picnicking					
Importance of Observing Wildlife			.872		
Importance of Observing Nature			.859		
Importance of Photography					
Importance of Hiking Day Only				.822	
Importance of Walking				.651	
Importance of Hiking in Backcountry				.606	
Importance of Cabin					.756
Importance of Camping					
Importance of Horseback Riding					

This factor analysis suggests that 4 important market segments visit Colter Bay. There is a water/active recreation group for which the Marina is a very important service of the area. There is a segment that is interested in interpretive services that form the core user group of the Museum. There is a group that is interested in hiking or walking the trails in the area and finally there is a group who are primarily interested in seeing wildlife in its natural environment. Each of these segments may utilize numerous facilities and services in Colter Bay, but they are most concerned about the facilities included in their grouping. The median and mean number of services utilized on the trip by each respondent were both 4.

Over 90% of the visitors to Colter Bay used 7 or fewer services while in the area.

Services at Colter Bay

Respondents were asked what services or facilities they liked best at Colter Bay. Results for respondents’ first answer are below in Table 7 in descending order of frequencies. Eleven unique answers were provided. The general store was identified by a plurality of respondents (21%) while the Visitor Center was given by about one in six respondents (16%). The Indian Arts Museum ranked 6th out of the 11 answers (10%).

Factor analysis of services at Colter Bay was conducted to determine if patterns existed in the data on services used while at Colter Bay. A principal components analysis was performed on 12 services, yielding an explained variance of 51.4%. Three factors emerged with eight values of 1 or greater. The results show that four services hung together for factor 1 which we named the *Visitor Services* factor: visitor center, restrooms, general store, and Museum (Table 7). This outcome makes sense considering that the visitor center, restrooms, and Museum are all located in the same building.

Table 7. Services or facilities liked best.

Service	Frequency	Valid Percent	Cumulative Percent
General store	40	21.1	21.1
Visitor Center	31	16.3	37.4
Showers	30	15.8	53.2
Campsite	24	12.6	65.8
Restaurant	22	11.6	77.4
Indian Arts Museum	19	10.0	87.4
Marina	17	8.9	96.3
Lake	3	1.6	97.9
Trails	3	1.6	99.5
Amphitheatre	1	.5	100.0
Total	190	100.0	

General Store is nearby and provides many of the same services found at the Visitor Center. Factor 2: *Overnight Services*, has only two variables occurring together—lodging and laundry. Factor 3: *Developed Recreation*, the weakest factor, has only two services hanging together—the corral and marina (Table 8).

Table 8. Rotated Component Matrix of services.

	Component		
	1	2	3
Visitor Center	.772		
Restrooms	.749		
General Store	.531		
Indian Arts Museum	.501		
Trails			
Ranger Program			
Picnic Facility			
Laundry		.977	
Lodging		.977	
Marina			.706
Corral			.670
Restaurant			

Colter Bay Visitor Center Services

Respondents were asked which of seven services they used at Colter Bay during their trip; they were to check one or more services. A total of 543 respondents said they used one or more of the services for a total of 1,476 Colter Bay services used (mean = 2.7 services per respondent). Frequency of use in descending order is shown below:

Services used at Colter Bay

- Restroom 76.4%
- Information Counter 70.9%
- Bookstore 55.1%
- Museum 36.5%
- Ranger Program 20.8%
- Permit Office 9.8%
- Water Station 2.4%

First visitors were more likely than repeat visitors to use the information counter, the restroom, and the water station while repeat visitors were more likely than first-time visitors to use: the permit office, the bookstore, the museum, and ranger program. Among those who were first-time visitors, 33% went to the museum, but among the repeat visitors, 40% went to the museum (Table 9).

Less important reasons for choosing to stay at Colter Bay were the museum, boating opportunities, traditions and fishing. Another reason volunteered frequently by the survey participants was the area’s proximity to Yellowstone National Park. Many indicated that the Colter Bay area was the most

centrally located area to visit both Yellowstone and Grand Teton.

Table 9. Colter Bay services by first trip to Colter Bay.

		First Trip		Total	
		No	Yes		
Services Used	Information Counter	Count	119	258	377
		%	71.7%	73.7%	
	Restroom	Count	126	280	406
		%	75.9%	80.0%	
	Permit Office	Count	24	28	52
		%	14.5%	8.0%	
	Water Station	Count	3	9	12
		%	1.8%	2.6%	
	Bookstore	Count	100	191	291
		%	60.2%	54.6%	
Museum	Count	67	115	182	
	%	40.4%	32.9%		
Ranger Program	Count	44	68	112	
	%	26.5%	19.4%		
Total	Count	166	350	516	

Table 10. Visitors' selection for Reason for Choosing [to

Reasons for Choosing Colter Bay	N	Mean	Std. Deviation
Experiencing Nature	481	1.94	.246
Wildlife Viewing	481	1.91	.280
Experiencing Wilderness	470	1.90	.303
Rustic Nature	466	1.86	.347
For the Lake	482	1.85	.361
Peace and Quiet	469	1.83	.378
Marked Trails	453	1.79	.404
Accessible	496	1.75	.432
Family Friendly	465	1.71	.454
Not As Crowded	460	1.70	.457
Campgrounds	462	1.62	.486
Museum	450	1.39	.488
Boating	443	1.37	.485
Family Tradition	459	1.29	.454
Fishing	434	1.28	.451

visit] Colter Bay on this Trip to GTNP.

Respondents were asked to indicate which factors they thought were important in their decision to visit Colter Bay (Table 10). Not important was coded as 1 and important was coded as 2. The results confirm the findings of the recreational preferences of the Colter Bay visitors. Experiencing undisturbed nature and viewing wildlife were the most important

reasons for visiting the Colter Bay area, with over 90% of respondent rating them as an important reason. Less important reasons for choosing to stay at Colter Bay were the museum, boating opportunities, traditions and fishing. Another reason volunteered frequently by the survey participants was the area's proximity to Yellowstone National Park. Many indicated that the Colter Bay area was the most centrally located area to visit both Yellowstone and Grand Teton.

Table 11. Aware of Indian Arts Museum prior to trip.

	Frequency	Valid Percent	Cumulative Percent
Valid	586	72	72
	226	28	100
	812	100	

Indian Arts Museum Results

A key component of the research project related to the Indian Arts Museum in the Colter Bay Visitor Center. First, respondents were asked if they were aware of the Museum before their trip began. Only 28% indicated that they were aware of the Museum (Table 11). However, some 80% of respondents who had planned to visit the Museum did in fact visit the Museum.

Researchers wanted to know if there was a relationship between whether it was the respondents' first trip or a repeat trip to the Park and respondents' awareness of the Museum. Among those who were on their first trip to the Park, only 20% knew about the Museum while 56% of the repeat visitors knew about the Museum, a difference of about 35%. This suggests that a large number of respondents only learn about the Museum once in the Park. Once visitors actually arrive at Colter Bay approximately 50% of the actually visit the museum (Table 12).

Table 12. Percent of visitors to Colter Bay who visited the Indian Arts Museum.

	Frequency	Valid Percent	Cumulative Percent
Valid	No	276	49.2
	Yes	285	50.8
	Total	561	100.0

For those respondents who visited the Museum during this trip, respondents were then asked if they would visit the Museum again 76 indicated they would visit it again (Table 13).

Table 13. Would visit Indian Arts Museum again.

	Frequency	Valid Percent	Cumulative Percent
Valid No	93	23.8	23.8
Yes	298	76.2	100.0
Total	391	100.0	

Respondents were asked that if the Indian Arts Museum at Colter Bay were discontinued or moved, what exhibit topics they would prefer to see in the Museum (Table 14). Almost two-thirds (65.7%) of the respondents indicated that the exhibits should stay the same. Only 16% had no interest in new exhibits while 19% were preferred new exhibits.

Using crosstabulation and Chi-Square, personal factors (gender, race, age, education) showed no statistically significant relationship to the Indian Arts Museum exhibit preferences. In households with younger children (age 0 through age 12), there was a weak, statistically significant relationship ($X^2 = 15.673$, $df = 2$, $p = .000$; $V = .19$) (Table 15). Respondents with children (23%) were twice as likely to be interested in new exhibits as those without younger children (10%).

Furthermore, respondents were asked if the Indian Arts Museum was located at the Moose Visitor Center whether they would be less likely or more likely to have visited the Museum while on their trip (Table 16). About 26% indicated that they would have been less likely to have visited the Museum at Moose while only 12% said that they would have been more likely. The majority of (62%) respondents were not sure about the likelihood of visiting the Museum in Moose.

Lastly, researchers wanted to know if visiting the Museum while on their trip would affect respondents' opinions about visiting the Museum if it was moved to Moose (Table 17). Those who visited the Museum (36%) were almost three times more likely to indicate that they would be less likely (14%) to go to the Museum if the Museum were at Moose ($X^2 = 36.411$, $df = 2$, $p = .000$, $V = .26$).

Time Spent in the Indian Arts Museum

For those visiting the Museum on this trip, researchers asked how long visitors spent in the Museum (Table 18). Answers ranged from less than 15 minutes to more than 2 hours. Some 13% (1 in 7) indicated that they were in the Museum for less than 15 minutes. The median length of stay was 30 minutes to 60 minutes with 79% of respondents indicating that they spent about 1 hour or less in the Museum. Twenty percent indicated that they were in the Museum 1 to 2 hours while only 1% said they were in the Museum for more than 2 hours (Table 18).

Table 14. Opinion on Indian Arts Museum exhibits.

	Frequency	Valid Percent	Cumulative Percent
Valid Exhibits Should Stay the Same	283	65.7	65.7
Not Interested in New Exhibits	67	15.5	81.2
Interested in New Exhibits	81	18.8	100.0
Total	431	100.0	

Table 15. Opinion of Museum exhibits by Children in household age 0 to 12.

		Children age 0 to 12 in Household		Total
		No Children age 0 to 12	Children age 0 to 12 in Household	
Opinion on Indian Arts Museum Exhibits	Exhibits Should Stay the Same	Count 98	Count 185	Count 283
		% 67.1%	% 64.9%	% 65.7%
	Not Interested in New Exhibits	Count 33	Count 34	Count 67
	% 22.6%	% 11.9%	% 15.5%	
	Count 15	Count 66	Count 81	
	% 10.3%	% 23.2%	% 18.8%	
Total	Count 146	Count 285	Count 431	
	% 100.0%	% 100.0%	% 100.0%	

Table 16. Likelihood of visiting Museum if at Moose.

		Frequency	Valid Percent	Cumulative Percent
Valid	Less Likely	203	30.1	30.1
	More Likely	80	12.0	42.1
	Not Sure	392	57.9	100.0
	Total	675	100.0	

Table 17. Likelihood of visiting Museum if at Moose by Visit Museum on trip.

			Visit Museum		Total
			No	Yes	
Likelihood of Visiting Museum if at Moose	Less Likely	Count	35	101	136
		%	14.3%	36.2%	26.0%
	More Likely	Count	40	21	61
	%	16.3%	7.5%	11.6%	
	Not Sure	Count	170	157	327
	%	69.4%	56.3%	62.4%	
Total		Count	245	279	524
		%	100.0%	100.0%	100.0%

Table 18. Length of Time Spent in the Indian Arts Museum by Visitors.

		Frequency	Valid Percent	Cumulative Percent
Valid	Less than 15 minutes	54	13.0	13.0
	15 to 30 minutes	107	25.8	38.8
	30 minutes to 1 hour	166	40.0	78.8
	1 to 2 hours	83	1.2	98.8
	More than two hours	5	100.0	100.0
	Total	415		

A part of the Museum is the special events and programs at the Museum. These could serve to increase learning, enjoyment, and the likelihood that a respondent would visit the Museum. Respondents were asked to indicate if they were at the Museum when there was a special event or program at the Museum (Table 19). About a quarter (27%) said that this was true. As a follow-up question, they were asked if they visited the Museum because of the special event or program. Only two individuals indicated that this was true.

Table 19. Special event or program at Indian Arts Museum during visit.

		Frequency	Valid Percent	Cumulative Percent
Valid	No	75	73.5	73.5
	Yes	27	26.5	100.0
	Total	102	100.0	
Total		250		

Guest Artist at Museum

Respondents were asked if they visited the Guest Artist area in the Museum during their visit to the Museum (Table 20). Only a third noted that they did visit the guest area and only about 10% said that they purchased one or more items at the guest artist area (Table 21).

Table 20. Visited guest artist at the Museum.

		Frequency	Valid Percent	Cumulative Percent
Valid	No	376	67.0	67.0
	Yes	185	33.0	100.0
	Total	561	100.0	

Table 21. Made a purchase at the guest artist area.

		Frequency	Valid Percent	Cumulative Percent
Valid	No	509	90.2	90.2
	Yes	55	9.8	100.0
	Total	564	100.0	

A resounding 76% indicated that they would visit it again (Table 22).

Table 22. Would visit Indian Arts Museum again.

		Frequency	Valid Percent	Cumulative Percent
Valid	No	83	23.8	
	Yes	201	76.2	100
	Total	107	100	

Indian Arts Museum Interviews

During the summer, 2010, two researchers were stationed at the Colter Bay Visitor's Center (Indian Arts Museum). They interviewed selected individuals as they were exiting the Museum one-half

day weekly. The following represents a summary of responses to the open-ended questions.

First, respondents were asked what they hoped to learn in the Museum. Answers were categorized into 6 categories listed below in descending order of frequency. The plurality of responses was centered on learning about Indian culture. Several respondents simply indicated that they had no specific expectations. A few said that they wanted to see how Indians made art and objects.

- Indian culture
- No expectations
- Others
- How they made art and objects
- What was there
- Meet Indians

Respondents were asked about which exhibit they liked most. Responses were categorized and are listed by category in descending order of mention. Bead work was identified by more respondents as the exhibit they most liked more than any other exhibit. Moccasins and weaponry were the second and third most identified, followed by the guest artist and clothing.

1. Bead work
2. Moccasins
3. Weaponry/warfare
4. Guest artist
5. Clothing

Last, respondents were asked which part of the Museum was most important for people to see. Answers were grouped into six unique categories. By far the “whole thing” was the most common response.

1. Whole thing
2. History
3. How they lived
4. Art work
5. Teepee
6. Artists

Moose Results

During one of every three days, the research assistants spent time at the Moose Visitor Center area interviewing individuals outside of the Center. Respondents were asked questions during the interview, which took about 10 minutes to complete, that paralleled the ones being asked at Colter Bay. Data were collected on 133 individuals. Demographic characteristics were not significantly different from those collected in the at home survey and in the Colter Bay interviews.

Trip characteristics were different in several ways for visitors interviewed at Moose. The visitors at the Moose visitor center were more likely to have entered from the south through Jackson and their median length of stay was three days, while at Colter Bay it was 4 days. They were also less likely to be staying overnight in the park. Only 56% were planning to utilize lodging in the park as compared to 80% in the Colter Bay interviews. Just over half indicated Grand Teton was their most important destination, while at Colter Bay only 30% believed GRTE was their most important destination on this trip. While only 43% said it was their first trip to GRTE, 65% said it was their first stop at Moose.

Moose Museum Questions

Respondents were asked if the Indian Arts Museum had been at Moose, would they have visited the Museum (Table 23). Over 82% indicated that they would have visited the Museum if it was located at Moose as compared to only approximately 50% who actually visited at Colter Bay. As a follow-up question, respondents were asked if they had visited the Indian Arts Museum during this trip (Table 24). Fifty-percent noted that they had visited the Museum while 45% said that they had not. An additional 7 individuals indicated that they were planning to go to the Museum, but had not yet done so on the trip. Moreover, some 70% said that they had visited the Colter Bay Visitor Center in which the Museum is located (Table 25). This suggests that 20% of the respondents went into the Colter Bay Visitor Center, but did not go into the Museum while in the Visitor Center.

Table 23. Would have visited Museum if located at Moose.

		Frequency	Valid Percent	Cumulative Percent
Valid	No	10	17.9	17.9
	Yes	46	82.1	100.0
	Total	56	100.0	

Table 24. Visited Indian Arts Museum.

		Frequency	Valid Percent	Cumulative Percent
Valid	No	22	44.9	44.9
	Yes	27	55.1	100.0
	Total	49	100.0	

Table 25. Visited Colter Bay Visitor Center.

	Frequency	Valid Percent	Cumulative Percent
Valid No	16	30.2	30.2
Yes	37	69.8	100.0
Total	53	100.0	

Summary and Conclusions

- The results of the three surveys are similar. The demographic characteristics contain no surprises. The respondents were well educated, about half were traveling with children. About half were repeat visitors to GRTE. Half were between 40 and 60 years of age. About 20% were day visitors and 80% were planning to stay overnight in the park.
- About 83% of Colter Bay visitors visited the Visitor Center while only about 16% did not.
- Services used at Colter Bay Visitor Center indicated the most important was restrooms (76%) followed closely by information counter (71%) and bookstore (55%). The museum was indicated in 36% of cases and ranger programs in 21 % of cases. The visitor center was very important to the visitors to Colter Bay. They indicated they used a mean of 2.7 of the services offered. The median time spent in the museum was 30-60 minutes with only 12% staying less than 15 minutes.
- Of all the recreational activities available at Colter Bay the Museum ranked 10th in importance value to the visitors. Observing wildlife was first with observing nature a close second. The Museum's mean rating of 2.9 is halfway between the scale values of 1 to 5 with 1 being very unimportant and 5 being very important; thus the mean suggests that the Museum's importance level is, on average, neither important nor unimportant to these visitors.
- While a great many visitors go to the Indian Arts Museum, going to the Museum ranks 10th among the activities listed. The top five ranked activities all have to do with outdoor activities, such as wildlife and nature observation. Of those having children, there was a desire to have new exhibits. Thus, we recommend that NPS strongly consider rotating Indian Arts exhibits, and increasing exhibitry concerning natural history of the Colter Bay area. The Museum was ranked 6th out of 11 activities and moreover if the Museum were moved, total visitation to Colter Bay would not be impacted. Only 40 percent of the respondents who visited Colter Bay went to the Museum. The average person was interviewed about two-thirds through in their planned number of days to stay in the park. This means that going to the Museum was low on priority. Also, there was only a slight increase in Museum visitation among those who were in the Park for one day.
- A high percentage (80%) of the visitors to Moose indicated they would visit Indian arts exhibitry if it were in the Moose Visitor Center. This indicates a potentially higher rate of visitation than currently exists at Colter Bay.
- By far the most popular exhibit was the bead work. If only part of the exhibits are utilized, the most important to bring back are the bead work, moccasins, and war implements. If the exhibits are revised, an improved teepee exhibit may satisfy the general interest in Indian culture and teepees.
- Based on comments and observation, the Museum benefits greatly from being in a Visitor Center. If the Museum were separated, it is the researchers' opinion there would be much less visitation to the Museum.
- Consider rearranging the exhibits with the bead work on the first floor with a teepee visible from the top floor which may serve to draw people downstairs.

GREATER YELLOWSTONE AREA



THE INTERACTIONS OF CLIMATE AND BIOTIC FACTORS ON LIFE HISTORY CHARACTERISTICS AND VITAL RATES OF YELLOWSTONE CUTTHROAT TROUT IN SPREAD CREEK, WY

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✦ ABSTRACT

Habitat degradation and introduction of non-native salmonids have caused substantial declines in abundance and distribution of Yellowstone cutthroat trout. Additionally, global climate change is expected to exacerbate current threats through changes to thermal regimes, hydrology, stream productivity, and distributions of non-native species. Understanding how factors such as climate and local stressors (e.g., non-native species) interact to affect Yellowstone cutthroat trout is critical for developing management strategies to enhance future persistence. However, research investigating relationships among these factors and life history characteristics and vital rates of Yellowstone cutthroat trout is lacking. To address this need, we examined the influences of temperature, streamflow, food availability, and presence of brook trout on life history characteristics of Yellowstone cutthroat trout in Spread Creek, Wyoming. We used passive integrated transponder (PIT) tags and a combination of stationary and mobile PIT tag antennae within a capture-recapture framework to monitor growth, movement, and survival of Yellowstone cutthroat trout and brook trout throughout the Spread Creek drainage. Considerable differences existed in frequencies of movements between species and among tributaries. Significant differences existed among growth rates of trout in three tributary streams. Preliminary results suggest the observed differences were driven by the complex interactions of streamflows, fish densities, and prey abundances, rather than stream temperatures. We discuss our results in the context of maintaining diversity of life-

history patterns within watersheds as a means to increase metapopulation resiliency. Our findings provide critical information needed to refine climate risk assessments and to better direct limited resources to ensure the long term persistence of the subspecies.

✦ INTRODUCTION

Yellowstone cutthroat trout is an integral part of natural ecosystems across the native range as a key resource for terrestrial and avian species and a recreational resource with strong socioeconomic values (Gresswell and Liss 1995; Wengeler et al. 2010). Relative to the historic distribution and abundance, Yellowstone cutthroat trout has experienced considerable declines as a result of habitat fragmentation and degradation and the introduction of non-native species (Gresswell 2011). Ultimately, understanding how anthropogenic-related disturbances influence Yellowstone cutthroat trout is an important step in prioritizing future restoration and directing management and conservation efforts.

In addition to current limiting factors, Yellowstone cutthroat trout is likely to be significantly influenced by global climate change, particularly given the narrow thermal tolerances of this species (Williams et al. 2009). However, the large elevational and latitudinal gradients suggest the effects of global climate change are likely to vary considerably across basins. Major basins across the intermountain West have experienced a consistent decrease in summer discharge and increase in stream temperatures over the past 50 years (Isaak et al. 2012). The concurrent

effects on biotic factors such as non-native species distributions (Wenger et al. 2011a; 2011b) and macroinvertebrate prey (Harper and Peckarsky 2006) will also play a major role in shaping future cutthroat trout distributions.



Figure 1. A picture of a resident Yellowstone cutthroat trout in Spread Creek. Note the PIT-tag used for addressing research questions.

While there has been work describing how climate change may influence spatial patterns of salmonids (e.g., Wenger et al. 2011a, 2011b), there continues to be a paucity of information linking salmonid life-history patterns and demographic rates to climate. To address the conservation and management needs of Yellowstone cutthroat trout (Figure 1), we conducted research to increase our understanding of the life-history patterns and the potential effects of habitat fragmentation and climate change on this native salmonid. Our specific objectives were to: 1) Monitor the Yellowstone cutthroat trout population connectivity and spawning locations of migratory Yellowstone cutthroat trout after the removal of an existing migration barrier, 2) Identify how stream temperature, stream flows, and food availability influence life-history characteristics of Yellowstone cutthroat trout, and 3) Quantify Yellowstone cutthroat trout demographic and vital rates across different portions of the stream network in the Spread Creek drainage, and how these factors differ with and without non-native brook trout *Salvelinus fontinalis*.

STUDY AREA

The study area for this research includes portions of the stream network within the Spread Creek drainage in northwestern Wyoming (Figure 2). Spread Creek is a relatively large drainage with over 200 km of fish-bearing streams. Prior to 2010, an

impassible barrier in the form of a diversion dam existed approximately 7.2 km upstream from the confluence with the Snake River. In the fall of 2010, collaborative efforts by state and federal agencies and Trout Unlimited helped remove this barrier and reconnect the Spread Creek drainage with the Upper Snake River.

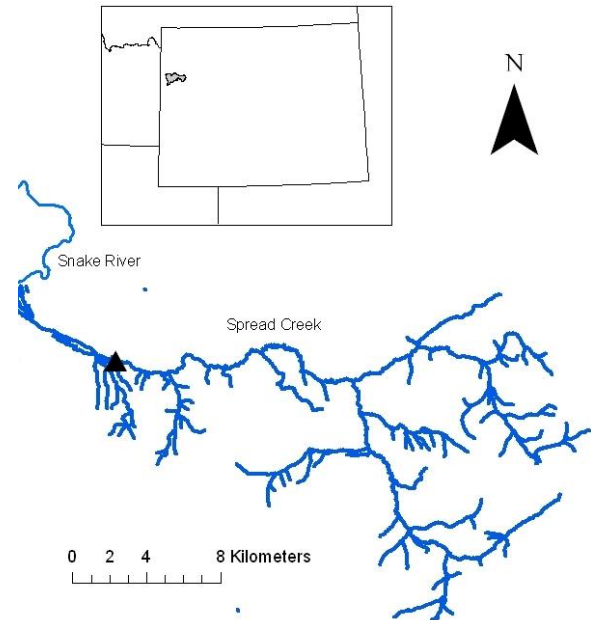


Figure 2. The location of the Spread Creek drainage in Wyoming and the stream network and former diversion dam (black triangle) location in the drainage.

Spread Creek hosts a variety of native fishes in addition to Yellowstone cutthroat trout, including bluehead sucker (*Catostomus discobolus*), Utah sucker (*C. ardens*), longnose dace (*Rhinichthys cataractae*), mottled sculpin (*Cottus bairdii*), and Paiute sculpin (*C. beldingi*). Non-native brook trout also exist in the Spread Creek drainage.

◆ METHODS

Fish sampling

Our study area included portions of Spread Creek, South Fork Spread Creek, Grouse Creek, Leidy Creek, and Rock Creek. Additional reaches were added to the 2011 sampling framework to increase sampling coverage. The additional reaches were chosen based on gaps in stream length not covered by the 2011 framework and were identified using ArcGIS. Once the reach was located, we began sampling at the nearest pool tail; the length of each reach varied by size of stream: Spread Creek = 200 m; SF Spread

Creek = 200 m; and 100 m for Grouse, Leidy, and Rock Creeks.

Fish sampling consisted of a summer and fall component in the tributaries and a single summer event in South Fork Spread Creek and mainstem Spread Creek. Summer sampling in the tributaries began the first week of July and was completed the third week of July. Fall sampling was conducted between September 22 and October 5. South Fork Spread Creek and Spread Creek were sampled between July 20 and August 3. Fish were captured exclusively with backpack electrofishing units in the tributaries and a combination of electrofishing and angling in Spread Creek and South Fork Spread Creek. We conducted one-pass surveys in the majority of the sample sites. However, to estimate capture efficiency, we block netted (20-mm mesh) and conducted 3-pass electrofishing surveys in 3 reaches in each tributary. No three pass surveys were conducted in Spread Creek or South Fork Spread Creek this year.

Once captured, individuals were placed in a stream-side holding container and identified to species. For all non-salmonids and salmonids <80 mm, we recorded lengths and weights and immediately returned individuals to the stream. For abundant species (i.e., sculpin), we only recorded length and weight information for the first 15 individuals per reach, then enumerated individuals. We anesthetized all salmonids >80 mm with a diluted solution of clove oil, recorded length and weight measurements, and inserted passive integrated transponder tags (PIT-tags; half duplex, Oregon RFID) ventrally and anterior to the pectoral fins. For all salmonids between 80 and 120 mm we inserted 12 mm PIT-tags and fish >120 mm we used 23 mm PIT-tags. We inserted PIT-tags into a small incision (2-4 mm) made with a scalpel. After tagging, we placed all fish in a flow-through recovery tank placed in the stream channel. Once fish regained equilibrium, we used hand nets to return fish to slow-water sections within the sampled reach. Animal capture protocols have been approved by Montana State University's Institutional Animal Care and Use Committee (IACUC).

Salmonid biomass

We estimated average reach widths using three width measurements equally spaced throughout each reach. Average depths from the July flow measurement were then used with the average widths to estimate the volume per reach. We estimated average salmonid biomass for Grouse, Leidy, and Rock Creeks. We adjusted the total biomass caught in

each reach based on the average capture efficiency per stream that was estimated from the three pass electrofishing events (see results section), and adjusted biomass estimates from each site for the entire stream and divided by the average volume per 100m reach in each stream.

Summer growth

Growth was estimated for all individuals recaptured during the fall sampling event. Daily growth rate was standardized for mass using the equation

$$G_s = (W_t^b + W_0^b) * (bt)^{-1}$$

where G_s is mass-standardized growth rate, W_t is mass at recapture, W_0 is mass at initial capture, t is time between capture and recapture, and b is the allometric growth constant (YCT= 0.472, BKT= 0.485). The allometric growth constant was estimated from the slope of the regression of natural log of specific growth and natural log of mass as described by Ostrovsky (1995). The mass value used in the regression was estimated using the iterative process suggested by Elliott and Hurley (1995).

Movement and capture-recapture

Prior to fish sampling, we installed passive instream antennae adjacent to the formal diversion structure on Spread Creek and at the mouths of Grouse, Leidy, and Rock Creeks (Figure 3). Each antennae array, including the one positioned in the irrigation canal, consisted of two channel-wide loops. Having multiple loops in each channel allows for quantifying directionality of fish movement. A half-duplex reader (Oregon RFID multiplexor) was used to record movements at each antenna. The system at the old diversion site was powered by two solar panels, which together with the reader and rechargeable batteries were located between the current diversion structure and the Spread Creek Channel. Antennae located in the tributaries were powered by a single solar panel each.

After completion of fish sampling, we used mobile PIT-tag antennae to provide recapture information and information regarding movement for all PIT-tagged individuals. We used continuous surveys in each of the three tributaries and conducted a single continuous survey from the mouth of Leidy Creek on South Fork Spread Creek downstream to the old diversion site on Spread Creek. We conducted the mobile surveys using 2 -3 portable antennae, which included hoop antennae (~0.3 m diameter) attached to

a pole and mobile rectangular PVC frames (1 m x 3 m). During the mobile surveys, we covered the entire stream channel in a manner analogous to backpack electrofishing. Movement distances were calculated in ArcMap10.1 with the Origin-Destination Cost Matrix function. Movement estimates represent the distance from the midpoint of the sampling reach where the fish was tagged to the point where it was detected. The estimates have a maximum resolution of 50m so any movement estimate less than that is considered within-reach movement.



Figure 3. Montana State University graduate student Patrick Uthe installing a PIT-tag antenna on Leidy Creek.

Entrainment within the diversion structure

In addition to observations from PIT-tag antennae within the diversion structure, opportunistic field sampling in October 2012 occurred in response to the observation of entrained fish within the diversion ditches. In response, biologists from Wyoming Game and Fish (WGF), Grand Teton National Park, and the USGS sampled the diversion structure and below the diversion in the proximate diversion ditches using backpack electrofishing on September 26-27, October 4th, and October 18th. In addition, biologists from Wyoming Game and Fish sampled the Elk Ranch Reservoir using a floating gill net (0- 2 m), which was set for nearly four hours. All fish captured were measured for length, checked for PIT-tags and returned to Spread Creek below the diversion structure.

Temperature and streamflow

We deployed continuous stream temperature loggers at numerous locations in the study area. Temperature loggers consisted of a combination of Onset Pendants and Onset V2 temperature loggers. (Dunham et al. 2005) In addition to temperature loggers, we deployed pressure-transducers to continuously measure stream flow height (i.e., stage) and develop stage-discharge relationships. We installed the pressure transducers in Rock Creek, Leidy Creek, Grouse Creek, South Fork Spread Creek and North Fork Spread Creek above the confluence, and at the site of the historic diversion structure on Spread Creek. Pressure transducers in tributaries were deployed at a site near the mouths and at a site above the top site on each stream. A temperature logger was deployed at the midpoint of each of the three tributaries. Pressure transducers were placed in a perforated 5 cm PVC pipe, partially buried in the substrate and attached to rebar. To establish stage-discharge relationships, we measured discharge at each location during the summer and fall. To avoid losing pressure transducers due to ice, we removed the pressure transducers in early November, and will replace these prior to the spring runoff.

Food availability

We measured food availability bi-weekly from July-September at a fixed sampling site (located between the mouth and the lowest site in Grouse, Leidy, and Rock Creeks. Each sampling event consisted of a morning sample starting at one hour after sunrise and an evening sample starting at one hour prior to sunset. This regiment was chosen to capture the beginning of the crepuscular increase in drift density that is an important feeding period for salmonids.

Two drift nets (25 x 45cm, 500 μ m) were deployed adjacently in the thalweg of a fast-water channel unit. Nets remained in the channel for one hour to maximize the volume of water sampled without risking backflow due to clogging. Nets were deployed at least 2cm off the substrate to prevent benthic macroinvertebrates from crawling into the nets. Nets were always deployed so that the tops were above the water surface to capture drifting terrestrial invertebrates. Flow and water depth were measured directly after setting the nets and prior to retrieving them. This was used to calculate the volume of water sampled over the hour. The contents of the nets were transferred to storage jars and preserved with 95% ethanol. Samples will be identified to the lowest possible taxa and converted to energy content estimates using dry-mass to energy equivalents from published literature.



Figure 4. Drift nets used to quantify stream productivity through macroinvertebrate drift.

◆ **PRELIMINARY RESULTS**

Fish sampling

We sampled 67 reaches 69eticula 8,754 km during the 2012 summer field season. During the fall, the 49 tributary reaches were resampled. During the summer sampling a total of 61 brook trout and 368 Yellowstone cutthroat trout were captured. Two brook trout and 16 Yellowstone cutthroat trout were recaptured individuals. We implanted 55 brook trout and 320 cutthroat trout with PIT tags. During the fall sampling season we captured 90 brook trout and 484 cutthroat trout. Of these, 19 brook trout and 53 Yellowstone cutthroat trout were recaptured individuals. We implanted 67 brook trout and 324 Yellowstone cutthroat trout with PIT tags. The first documented presence of brook trout in Leidy Creek occurred when we captured a single individual (101mm) during fall sampling. Size distributions varied among the tributaries during both sampling seasons. Some reaches in Grouse Creek exhibited a considerable shift in species composition between the summer and fall sampling events (Figure 5). In addition to salmonids, we captured a total of 2 longnose dace, 459 cottids, and 2 catostomids. The estimated capture efficiency was 0.69 (95% CI ± 0.23) in Grouse Creek, 0.53 (95% CI ± 0.24) in Leidy Creek, and 0.70 (95% CI ± 0.06) in Rock Creek.

Salmonid biomass

Biomass varied considerably across streams. We estimated average biomass as 16.4 g/m³ in Grouse Creek, 12.3 g/m³ in Rock Creek, and 6.0 g/m³ in Leidy Creek.

Summer growth

We estimated growth over the summer growing season for 11 trout in Leidy Creek, 18 trout in Rock Creek, and 33 trout (19 brook, 14 Yellowstone cutthroat trout) in Grouse Creek. Average mass-standardized growth rates varied among the three streams (Figure 5). Growth rates were not significantly different between species in Grouse Creek. Trout in Rock Creek had significantly lower growth rates than trout in Grouse and Leidy Creeks (Figure 6).

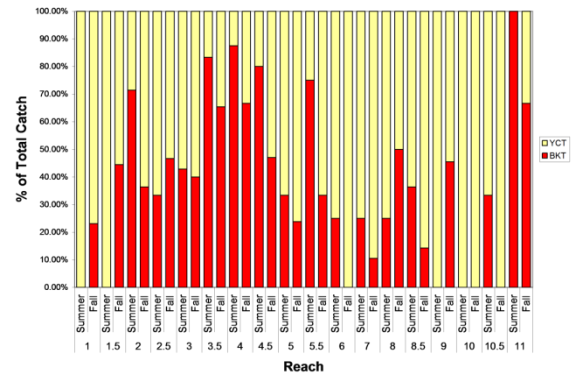


Figure 5. Seasonal changes in species composition of Yellowstone cutthroat trout (yellow) and brook trout (red) from electrofishing surveys in sample reaches in Grouse Creek during 2012. Reach numbers (i.e., 1-10) correspond to locations within Grouse Creek with the lowest number near the mouth of Grouse Creek and the highest reach corresponding to the uppermost sample reach.

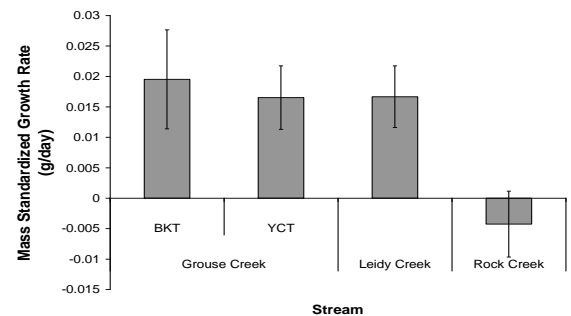


Figure 6. Average relative growth rates among Grouse, Leidy, and Rock Creeks. Growth rates calculated as relative growth in mass over the period between summer and fall sampling occasions. Estimates shown with 95% confidence intervals.

Movement and capture-recapture

The antennae on Spread Creek were installed on April 26, but were dislodged during runoff and re-installed on June 20. They remained operational until they were removed on November 2nd. The antennae in the diversion ditch operated from April 26 to the end of August, when it was removed during maintenance on the irrigation canal. The antennae detected a total of 11 trout throughout the operational period. Three of the fish were detected passing into the irrigation canal during the summer. One moved back out of the canal and proceeded downstream past the antennae in the main channel. The tagging locations of fish moving past the antennae were distributed throughout the Spread Creek basin. All the fish were Yellowstone cutthroat trout and ranged in size from 139-362mm.

The antennae on the tributaries were installed after peak runoff and remained operational throughout the summer and most of the fall (Grouse Creek, May 25 – November 6; Leidy Creek, May 24 – November 6; Rock Creek June 7- October 29). The number of fish passing over the antennae varied substantially across streams. Grouse Creek was the only stream that had an increase in downstream movement during the late fall.

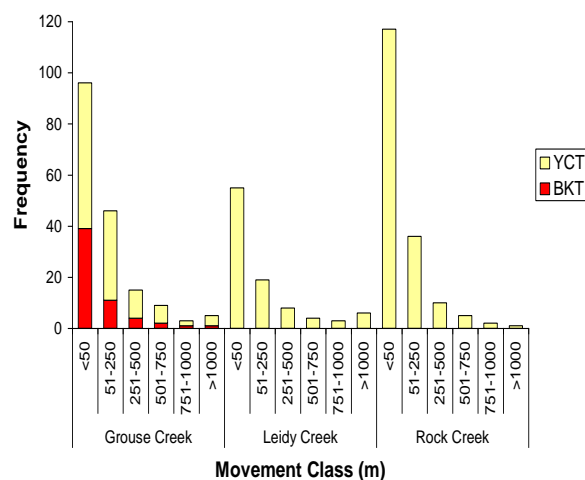


Figure 7. Frequency histograms of movement distances from three mobile PIT-tag surveys in Grouse Creek, Leidy Creek, and Rock Creek in 2012. Movements less than 50m are considered within-reach movement.

We surveyed a total of 38 km with mobile PIT-tag readers. Mobile tracking on South Fork Spread Creek and Spread Creek consisted of one event conducted during the middle of August. The mobile surveys on the tributaries were conducted at the end of June, July, and beginning of November. Overall, we detected 385 different trout for a total of 478 detections over the course of all mobile tracking events. Frequencies of movements varied across

species and streams (Figure 7). Yellowstone cutthroat trout in Grouse creek exhibited the highest displacement rates with approximately 49% of total detections from fish remaining in the reach they were tagged in. Within reach detections accounted for 58% of total detections in Leidy Creek and 68% of total detections in Rock Creek.

Entrainment within the diversion structure

From the 4 days of sampling the diversion structures, 310 Yellowstone cutthroat (median length = 200 mm; range = 48 – 390 mm) were captured and transported to lower Spread Creek (Figure 8). In addition to cutthroat trout we captured one mountain whitefish, two longnose dace, and 25 Paiute sculpin. No fish were captured in Elk Ranch Reservoir from the one gillnet survey; however, capture probabilities during daylight hours for visual predators is likely low and further work is needed to identify fish within the reservoir.

Temperature and streamflow

Stream temperatures and stream discharge were considerably different between 2011 and 2012. Average August stream discharge in Spread Creek (above the diversion structure) during 2011 (2.61 m³/s) was 55% higher than observed in 2012 (1.68 m³/s); during September this pattern was exacerbated with 2011 discharge (1.69 m³/s) nearly 70% higher than observed in 2012 (1.07 m³/s; Table 1). Average stream temperatures in Spread Creek in August in 2011 were 11.6 °C and were over 2 degrees higher in 2012 (13.7°C).

Table 1. The average (Standard deviation) discharge (m³/s) for Spread Creek above the diversion structure for August and September in 2011 and 2012.

	August		September	
2011	2.61	(0.86)	1.69	(0.34)
2012	1.68	(0.41)	1.07	(0.19)

Across the three tributaries, we observed considerable differences in discharge but relatively similar temperatures during the summer months. Stream discharge was considerably higher in Grouse Creek and Leidy Creek than in Rock. Average summer discharge (July through September) was highest in Leidy Creek (0.44 m³/s; SD = 0.52), intermediate in Grouse Creek (0.31 m³/s; SD = 1.32), and lowest in Rock Creek (0.07 m³/s; SD = 0.11). Stream temperatures were relatively similar across the three tributaries, but we observed substantial differences in

the lapse rates (i.e., how temperatures change within changing elevations: Table 2). Upper Grouse creek demonstrated the lowest stream temperatures across all sites

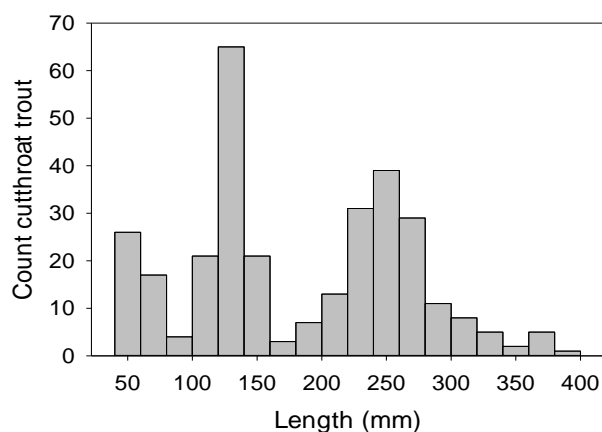


Figure 8. A histogram of the count and length of Yellowstone cutthroat trout entrained and captured in the diversion sediment trap and diversion ditches during four sampling occasions (four days) in late September and early October 2012.

Table 2. The maximum average weekly temperature (MWAT), maximum weekly average maximum temperature (MWMT), and the overall instantaneous maximum temperature (MDMT; as per Dunham et al. 2005) (Celsius) for locations within Spread Creek.

	MWAT	MWMT	MDMT
Lower Grouse Creek	13.2	18.3	19.4
Upper Grouse Creek	7.4	10.8	11.2
Lower Leidy Creek	11.5	16.7	17.7
Upper Leidy Creek	15.5	16.9	17.9
Lower Rock Creek	12.9	16.2	17
Upper Rock Creek	12.5	15.0	18.4
SF Spread Creek	12.9	16.8	17.9
NF Spread Creek	11.6	16.7	18.3
Spread Creek	15.1	18.7	20.4

Food availability

We collected six morning and evening samples between July and September in Rock, Leidy, and Grouse creeks. Two sampling occasions occurred in July, three occurred in August, and one occurred at the end of September. Samples have not yet been processed.

◆ MANAGEMENT IMPLICATIONS

The life-history patterns of Yellowstone cutthroat trout in headwater tributaries appear to be complex. Both resident and migratory life-history forms are apparent in the Spread Creek drainage. Although preliminary, we found Yellowstone cutthroat trout growth to vary substantially across tributaries, suggesting the need to include measures of fish density and movement with growth to gain a better understanding of how climate-driven attributes (e.g., streamflow) can influence fish behavioral characteristics.

While the removal of the historic Spread Creek dam eliminated upstream barriers, our results suggest considerable entrainment still exists. Our results also suggest the need for additional sampling to better understand the extent of entrainment across a year. Our preliminary results indicate a diversion screen may be warranted in the future.

◆ ACKNOWLEDGEMENTS

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SPATIO-TEMPORAL EVOLUTIONARY DYNAMICS IN NATURAL BUTTERFLY POPULATIONS (2012 FIELD SEASON)

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✦ INTRODUCTION

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

The focal species, *Lycaeides idas*, is one of five nominal species of *Lycaeides* butterflies that occur in North America (Figure 1; Nabokov 1949; Guppy and Shepard, 2001; Gompert et al. 2006). These species are descended from one or more Eurasian ancestors that colonized North America about 2.4 million year ago (Vila et al. 2011). *Lycaeides idas* 73eticulate with a second species, *L. 73eticul*, in the GYA (Gompert et al. 2010, 2012). *Lycaeides idas* is a 73eticulat species that is found in Alaska, Canada, and the central and norther Rocky Mountains of the contiguous USA (Scott 1986). *Lycaeides idas* is univoltine and adults generally fly from mid-July to early August. In the GYA *L. idas* populations often occupy mesic forest and montane habitat at elevations ranging from 2000-3500 m above sea level. Most populations of *L. idas* in the GYA feed on *Astragalus miser* as larvae, but some populations feed on other native legumes (most notably, other species of *Astragalus* and *Lupinus*; Gompert et al. 2010). We selected *L. idas* as the focal species for this study because of our experience with this species, extensive data on the location and natural history of *L. idas* populations, the availability of genomic resources for this species, and several key aspects of this species's natural history (e.g., *L. idas* have non-overlapping generations with one generation per year, well-defined populations, and modest genome sizes, and *L. idas* are found in various habitats that might experience different environment-dependent selection pressures).

The specific goals of this study are to: 1) quantify genetic variation and molecular evolution in *L. idas* and their relationship with population size and environmental variation across space (i.e., different populations) and through time (i.e., from generation to generation) and 2) test the hypothesis that the nature

and strength of environment-dependent selection varies among populations and over generations and that this variation is sufficiently large to contribute to the maintenance of genetic variation in *L. idas*. This report documents the results from the first year of this study (2012), during which time we began collecting *L. idas* for DNA sequencing and conducted a pilot project to quantify population sizes (population size is an important parameter for our evolutionary models).

Figure 1. Photograph of a *L. idas* butterfly perched on an Aster.



◆ METHODS

We began this long-term study in July of 2012. Consequently, this report covers the first year of the study. We collected 379 adult *Lycaeides idas* butterflies from 11 locations (Table 1). We are storing these whole adult butterflies for DNA extraction and sequencing at -80°C . In addition, we conducted a pilot study to evaluate a distance sampling protocol to estimate adult population densities and sizes in *L. idas*. Distance sampling involves counting individuals and recording their distance from a transect line or point (Buckland *et al.*, 2001). This distance information is used to estimate a detection function that accounts for imperfect detection away from the transect line. We included four sites in the pilot study: Bull Creek (BCR), Blacktail Butte (BTB), Bunsen Peak (BNP), and Garnet Peak (GNP). We haphazardly designated linear transects at each of the four sites (Figures 2 and 3; BCR: 6 transects, total length = 487.7 meters [m]; BTB: 7 transects, total length = 579.1 m; BNP: 6 transects, total length = 502.9 m; GNP: 5 transects, total length = 411.5 m).

Two trained observers slowly walked along each transect (about one pace per second) and measured and recorded the distance of each observed *L. idas* perpendicular to the transect line. We also observed and recorded the sex of each butterfly and the presence or absence of the larval host plant

(*Astragalus miser*) near the transect line. We conducted these population surveys from July 18th until July 30th, and we only performed transect counts between 10:00 am and 2:00 pm under sunny or partly sunny skies.

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

Population		Latitude	Longitude	Sample size
Big Ice Cave		45° 10' N	108° 24' W	6 m, 12 f
Blacktail (GTNP)	Butte	43° 38' N	110° 41' W	25 m, 25 f
Bull Creek		43° 18' N	110° 33' W	30 m, 28 f
Bunsen Peak (YNP)		44° 56' N	110° 43' W	25 m, 25 f
Garnet Peak		45° 26' N	111° 13' W	25 m, 25 f
Grassy Lake Road		44° 08' N	110° 47' W	16 m, 6 f
Hunt Mountain		44° 45' N	107° 45' W	13 m, 21 f
Natural (YNP)	Bridge	44° 32' N	110° 27' W	7 m, 10 f
Rendezvous Mountain (GTNP)		43° 36' N	110° 53' W	15 m, 15 f
Riddle Lake (YNP)		44° 22' N	110° 33' W	15 m, 15 f
Tibbs Butte		44° 57' N	109° 27' W	16 m, 4 f



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

We estimated population densities (adult butterflies per square kilometer) using the *distsamp* function in the *unmarked R* package. We binned the

detection distances of butterflies into 1 meter bins prior to analysis (e.g., 0 to 1 m, 1 to 2 m, etc.). We used a half-normal detection function and estimated the detection function and density model parameters using maximum likelihood (Royle 2004). This model assumes the latent transect-level abundance distribution is Poisson and that the detection processes is multinomial with a different detection probability for each distance class or bin.

◆ RESULTS

We observed and recorded distances for 121 butterflies across the four sites and 24 linear transects. Based on these observations our estimates of adult *L. idas* population density were: 0.0151 butterflies per square meter (standard error [se] 0.00333) at BCR, 0.0166 butterflies per square meter (se 0.00315) at BTB, 0.0105 butterflies per square meter (se 0.00256) at BNP, and 0.00292 butterflies per square meter (se 0.000843) at GNP. We converted these density estimates to estimates of peak census population size based on rough estimates of each population's range (we identified suitable habitat from ground surveys and satellite images). Peak population size estimates were 1340 butterflies (BCR), 2380 butterflies (BTB), 720 butterflies

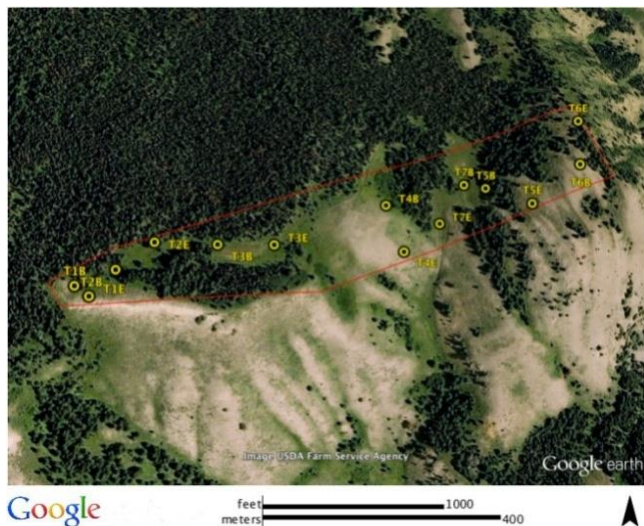


Figure 3. This google earth image shows the approximate boundary of the *L. idas* BTB population (red polygon) and the start and end points of transects (yellow circles; transects are numbered T1 to T7 and the letters B and E denote the start and end points, respectively).

(BNP), and 206 butterflies (GNP). Because adult *L. idas* eclose (i.e., emerge following pupation) over a period of several weeks, these peak population size

estimates are underestimates of the total adult population size at each site (perhaps by a factor of about three or four times given a one month flight season and a rough estimate of adult survival time in the wild of seven to ten days).

◆ DISCUSSION

Because we have just begun this long term study and we have not yet sequenced the DNA from the sampled butterflies, we cannot yet make any conclusions about the rates or causes of molecular evolution in these study populations. But we have already learned a few things from the pilot distance sampling surveys and analyses. These initial analyses indicate that the four focal sites sustain adult *L. idas* populations of hundreds to thousands of individuals. These are the first population size estimates for this butterfly species. Based on these moderate population size estimates we predict that both genetic drift and selection are important drivers of evolution in this system (Lynch, 2007). The population density standard errors were neither particularly small or large (they were about one-quarter the size of the density estimates). Thus, whereas these density estimates provide valuable baseline data, this study would benefit from more precise population size estimates which could readily be obtained by increasing the number of transects we survey at each site. We will continue this study during the 2013 summer field season. During this and subsequent field seasons we will increase the number of sites that we visit for DNA samples and population density surveys (we hope to visit 10 to 12 sites each year). We will also begin collecting weather and habitat data that will be useful for fitting causal models of molecular evolution. We plan to begin DNA sequencing of the collected *L. idas* after one or two additional field seasons.

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



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✦ INTRODUCTION

The benefit of a complex, intact community for maintaining ecosystem health in the face of emerging infectious disease risk has not been deeply explored. The diversity and distribution of haemoparasites in potential host mammal fauna are virtually unknown, and many diseases endemic to North America are not well understood in terms of transmission factors, prevalence, and contagion. Many of these tick and rodent borne pathogens nowadays are considered to be potential emerging infectious diseases that could spread to adjacent areas and new hosts, including humans, with climate change, land-use shift, and the expansion of distributions of the natural vectors of such haemoparasites. This study examines the effect of mammal community complexity in maintaining ecosystem health with respect to rodent/tick-borne diseases which have a high value for human public health as zoonotic diseases as well as for the unknown natural history of the mammalian community network.

At this point, a crucial step towards understanding the influence of parasites on mammal populations and emerging infectious disease (EID) risk is simply to describe the distribution of parasites within the entire mammal community and characterize the interconnections between pathogens, ectoparasite vectors, hosts species and land-use.

The work described in this brief report will provide the basis for the second and third chapters of the dissertation of doctoral student Leticia Gutiérrez, which will be an integrative study of mammal species that are connected through trophic and parasitic networks. The Greater Yellowstone Ecosystem

(GYE), which is the last example of a well-conserved temperate ecosystem in the northern hemisphere, will provide the setting for a first step towards characterizing the haemoparasite community in a mammal community with a full complement of top predators. This work will help to clarify the influence of carnivores and large herbivores, and other less known interactions, on parasite infection dynamics in local rodent communities. One direct benefit will be recommendations for decreasing the risk of human EIDs transmitted by ticks. Thus, the results of this study might reduce the negative perception of the local community of ranchers toward carnivores. The present report covers resources required to characterize blood-borne pathogens in a large sample of rodents captured in paired locations around the GYE contrasting high and low human disturbance involving ranching and recreation.

✦ HYPOTHESIS

Land use intensity is directly related to complexity of communities of mammalian host species which, in turn, influences the overall health of the ecosystem by moderating disease risk and pathogen transmission.

✦ PREDICTION

Areas protected from human disturbance will sustain a higher diversity of mesocarnivores, large carnivores, and, in general, large vertebrates, which will negatively affect the abundance of rodent species. As a consequence, tick-borne diseases will be less prevalent in undisturbed areas compared to areas with high levels of human disturbance.

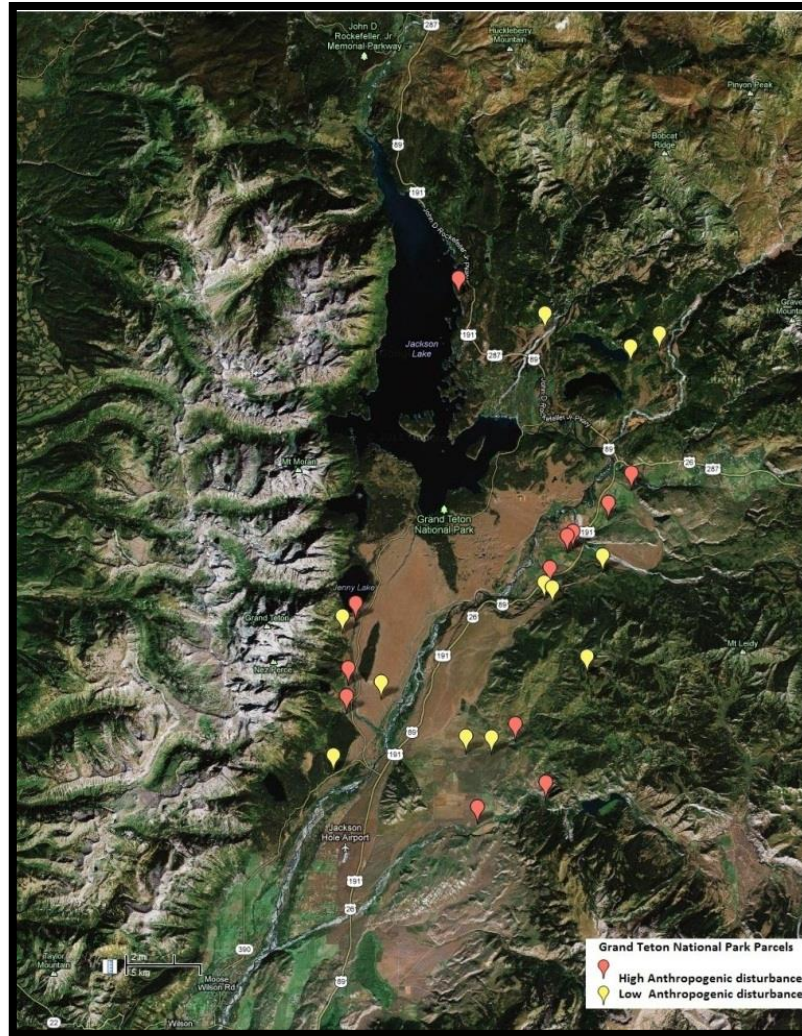


Figure 1. Grand Teton National Park rodent trapping showing high showing areas of high and low anthropogenic disturbance.

◆ OBJECTIVES

- 1) Determine the variety, abundance, and distribution of tick-borne pathogens of rodents in the GYE.
- 2) Determine the patterns of disease prevalence and interactions in the host-parasite-vector network.
- 3) Determine the direct and indirect effects of maintaining a complex trophic structure in the local mammalian fauna on disease risk indicators and overall ecosystem conservation, particularly with respect to habitat alteration and patterns of land use.

◆ STUDY AREA

The field study is located in the GYE, in Grand Teton National Park (43°44'0"N 110°48'12"W) (Figure 1).

◆ MAMMALIAN TRAPPING AND BLOOD SAMPLE COLLECTION

During summer 2012, twenty-four parcels were chosen for this purpose, divided by anthropogenic disturbance and land-use/vegetation cover: 4 grazing plots, 4 horse/cattle ranches, and 4 settlements as part of the highly disturbed areas lacking large mammals and 4 pristine meadows, 4 pristine sagebrush plots, and 4 pine forest plots as part of the undisturbed areas where a complex trophic structure in the mammalian community is expected to occur (Figure 1). During the 2012 field season at GTNP, 1,208 rodent samples (Figure 2) were added to the data source. This effort was achieved by doctoral student Leticia Gutiérrez as project leader, and three additional undergraduate field assistants.

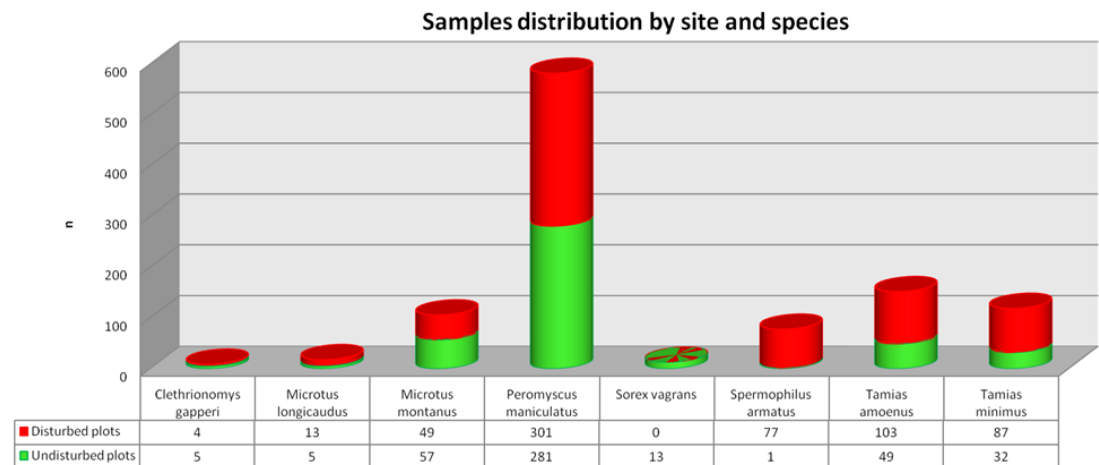


Figure 2. Rodent blood samples collected within Grand Teton National Park during summer 2012, $n=1,208$:

Teams of two people each sampled two sites each five days, over a period of eleven weeks, making it possible to access twenty-four new plots during the three month summer at GYE. Oats, sunflower seeds and dry raisins were used as bait. Traps were baited at sunset and checked the following morning at sunrise. Traps were closed during the day, and at night they were provided cotton pads to avoid hypothermia. Trapping was done during four consecutive nights. All traps were numbered; all sites were marked using colorful flagging and were GPS georeferenced. All individuals captured were identified with numbered ear tags, weighed, and sexed.

From each Isoflurane anesthetized mammal, blood was collected in a 40- μ l capillary tube from the sub-mandibular vein or saphenous vein. Part of the sample was preserved in Elute FTA cards/ Longmire's lysis buffer and part was used to make a smear. Serum samples also were collected. This blood collection protocol was chosen since this method is the least invasive among others described for small size mammals. Each trapped mammal was checked through direct visual inspection, and ectoparasites were collected with anatomical fine tweezers. Ectoparasites (ticks and flies) were kept in Eppendorf vials for 24 hrs in order to let the blood meals with the host DNA be thoroughly digested. The parasites were preserved in 1 ml 70% ethanol, frozen and subsequently lyophilized. Hence, it will be possible to preserve the ectoparasite DNA until it can be processed in the PI's lab.

Parasite DNA isolated from mammalian blood samples is subjected first to a reverse line blot (RLB, see Table 1) assay to identify, in a cost-effective manner, bacterial and piroplasma haemoparasites. 5'-

end amino-link species-specific probes are blotted in lines using a Miniblotter 45 (Immunetic, Cambridge, MA). Results are detected using a chemiluminescent substrate in autorad film. Being able to screen 43 samples against 42 different probes at one time makes this an excellent tool for the first stage of the molecular analysis. DNA of the detected pathogens will be amplified by multiplex PCR using biotin-labeled general primers for eubacteria and piroplasma. Oligonucleotide sequences of bacterial and piroplasma probes used in RLB assay are: *Anaplasma phagocytophilum*, *Arsenophonus sp.*, *Borrelia afzelii*, *B. burgdorferi sensu lato*, *B. burgdorferi sensu stricto*, *B. burgdorferi sensu lato* 16S, *B. lonestari*, *B. valaisiana*, *B. garinii*, *Ehrlichia canis/ovis/muris*, *E. ewingii*, *E. chaffeensis*, *Francisella endosymbiont of Dermocentor variabilis*, *F. philomiragia*, *F. tularensis subsp. tularensis*, *F. tularensis + F. philomiragia*, *Rickettsia amblyommii*, *R. amblyommii + Rickettsia sp.*, *Rickettsia endosymbiont of Dermocentor variabilis*, *R. rickettsii*, *Babesia bigemina*, *B. bovis*, *B. caballi*, *B. canis 1*, *B. canis 2*, *B. catch-all 1*, *Babesia catch-all 2*, *B. divergens*, *B. felis*, *B. microti 1*, *B. microti 2*, *B. ovis*, *B. rossi*, *B. vogeli*, *Hepatozoon catch-all*, *Theileria annae*, *T. annulata*, *T. buffeli*, *Theileria catch-all*, *T. equi*, *T. parva* and *Theileria/Babesia catch-all*.

In addition, PCR will be carried out using taxon-specific primers. In the case of positive infections, 18S rDNA, 16S rDNA, mitochondrial cytochrome b, or other specific genetic markers will be sequenced for parasite identification. According to objectives established in this project, we will identify *Plasmodium*, *Rickettsia*, *Babesia*, *Borrelia*, *Ehrlichia*, *Hepatozoon*, *Anaplasma*, *Theileria*, and *Francisella* haemoparasites. DNA sequencing will be done by the

DNA Service at the Genomics Core Facility at PennState.

It is important to point out that this is the first survey of parasites to detect *B. burgdorferi*, the agent of Lyme disease, outside of the Northeast, Upper Midwest and California distribution range described for this highly pathogenic zoonotic disease. This novel finding can contribute to the study of climate change (e.g. expansion in tick vector, host shift and disease distribution ranges) and to understanding the protective role of rich trophic networks.

This preliminary data shows strong evidence of specific rodent borne diseases associated with disturbed areas (p-value = 0.009). Individual characteristics such as species, sex and age seems to be important regarding haemoparasite prevalence. For instance, *Borrelia burgdorferi* prevalence appears to be influenced by the host species (p-value = 0.01) and also by the interaction of sex and age of the individuals (p-value = 0.004). In this particular case, all the infected individuals with *B. burgdorferi* were trapped in disturbed areas. Surprisingly, 45% of them belong to the species *Tamias minimus* (least chipmunk) and just 22% to the species *Peromyscus maniculatus* (white-footed mouse). In addition, 22% of the individuals correspond to female-adults, 56% to male-adults and 22% to male-juveniles. These novel findings might unravel new host species as more competent disease reservoirs.

More extensive genetic studies will be focused on the Lyme disease population distribution and expansion. In addition to RLB assay, DNA extracts from hosts and vectors will be screened by PCR with genus-specific *flaB* primers. PCR amplicons will be directly sequenced. Sequence diversity and genetic diversity will be assessed. Sequence variants at *flaB* will delimit *Borrelia* species and subtypes among species. Published pathogen sequences in GenBank will be used as alignment template; MEGA 5 will be used to determine genetic distances. Maximum likelihood phylogenetic tree building will be made for each pathogen species found using Geneious. Phylogenetic tree will be visualized with FigTree software.

In order to understand the spread of Lyme disease through the continent it is necessary to explore the population structure of *Borrelia burgdorferi* correlated with the spatial distribution of sequence types. Multilocus sequence analysis of eight chromosomal housekeeping genes (*clpA*, *clpX*, *nifS*, *pepX*, *pyrG*, *recG*, *rplB* and *uvrA*) of the spirochete strains will elucidate the phylogenetic relationship of the newly described *B. burgdorferi* isolates. The MLST data will be analyzed regarding spatial distribution of sequence types (STs), correspondence between spatial distribution of STs and geographic location through permutation test and Bayesian analysis of the population structure will assess the relatedness of the *B. burgdorferi* strains.

Data analysis will be based upon haemoparasite prevalence among rodent species. Cluster analysis will be used to assess the geography of disease prevalence. Then, univariate analysis will be performed to assess disease prevalence differences among clusters and land use. Finally, logistic regression will be used to take into account the different host and environmental variables, and their interactions, which might influence inter- and intraspecific disease prevalence.

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

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

STUDIES OF PARASITIC WASPS (HYMENOPTERA: BRACONIDAE) IN ASSOCIATION WITH MOUNTAIN PINE BEETLE OUTBREAK



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✦ ABSTRACT

A survey of parasitoid wasps (Hymenoptera: Braconidae) in Grand Teton National Park reveals undiscovered (but not unexpected) diversity, as well as changes in diversity associated with the bark beetle epidemic and the unusually warm, dry year. Our 2012 survey found nearly the same number of Braconidae subfamilies (18 vs 19) as a 2002 survey (Shaw 2002); a remarkable amount of diversity given that the 2002 survey was based upon five times as many specimens. Eleven species found in this study are new distribution records for the Greater Yellowstone Ecosystem (GYE), which points to much undiscovered local diversity. Differences from previous studies are possibly due to the unusual warmth and dryness of spring 2012, along with some influence from beetle kill. We provide a list of parasitoids and predators associated with mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in the Greater Yellowstone Ecosystem (GYE), a stepping stone for further research to determine the role of natural enemies in bark beetle outbreak dynamics in the GYE.

✦ INTRODUCTION

Our study was focused on three questions: 1) Is there significant diversity of braconid parasitoids in GYE undiscovered by previous studies? 2) How have bark beetle infestations affected the make-up of the parasitoid community? 3) Which natural enemies of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) are present in the lodgepole pine (*Pinus contorta*) forests of GYE?

The first goal of our study was to conduct general sampling of parasitoid wasps as follow-up to two previous studies of parasitoid diversity in the GYE (Lockwood et al. 1996; Shaw 2002). These previous studies resulted in the discovery of 100 new distribution records for braconid wasps, and at least ten undescribed species. Based on these results, along with the paucity of hymenopteran research in this region, we expected to find a high proportion of new distribution records, thus adding to our knowledge of insect diversity in this area of the Rocky Mountains. Finding a high proportion of unrecorded species would indicate a much greater diversity than is already known and would point to the need for further studies.

The second goal was to provide an initial assessment of how parasitoid faunas are changing over time in response to the bark beetle epidemic. The current bark beetle epidemic in the GYE is part of a large-scale historical event that may affect biodiversity well into the foreseeable future. In the current, early post-epidemic period, increases in insects that utilize early stages of decaying wood, large numbers of bark beetles, and an associated decline in insects utilizing living pine trees are expected, along with a parasitoid insect fauna that reflects these changes (Stephen and Dahlsten 1976). Over the years, this stage may be followed by a succession of changing resources and conditions extending through time until reaching a new equilibrium, one that may or may not resemble the forest before the beetle epidemic, and which can present new challenges for forest management. Research in both biological and sociological parameters is essential to understand this succession, and to successfully meet the resulting new management challenges (Progar et al. 2009).

The third goal was to survey and inventory parasitoid wasps and other natural enemies associated with the mountain pine beetle. Comparatively little is known about bark beetle/natural enemy associations in the GYE, except by inference from studies in other Rocky Mountain habitats. Understanding the role of natural enemies in bark beetle population dynamics in the GYE begins with knowing which natural enemies are present. Our western forests are experiencing historically unprecedented bark beetle epidemics that have been largely ascribed to climate change and other anthropogenic changes (Bentz et al. 2010; Lundquist and Bentz 2009). Experience is validating modeling predictions that mountain pine beetle epidemics will continue to climb elevational and latitudinal gradients (Amman, 1973; Hicke et al. 2006). However, climate change is one of many factors – the lodgepole forest in the Jackson Hole Valley did not appear to have sustained as much beetle kill as some surrounding areas, mostly at higher elevations (personal observation), for reasons that are not clear. It is known that many factors, including natural enemies, play a role in the dynamics of bark beetle epidemics (Raffa et al. 2008), and that better information and models are required to predict the future risk and to make appropriate management decisions (Bentz et al. 2008).

◆ METHODS

Insects were collected in lodgepole forests with two Townes-style Malaise flight-intercept traps at ground level in the same locations on the AMK Ranch as in Shaw's 2002 study. We chose to replicate the 2002 study as closely as we could for reasons of comparison. In addition, we placed canopy Malaise traps in four lodgepole pines, two at the AMK ranch where there was little evidence of beetle activity, and two in an area of much higher beetle activity approximately one quarter mile west of the Potholes parking area along Teton Park Road; both forested areas are at nearly the same elevation, and were visually matched for density and maturity (closed canopy with some openings and open understory). The canopy traps were placed adjacent to tree trunks approximately eight feet off the ground to be in the region of the trunk attacked by mountain pine beetle and high enough to avoid damage from wildlife. A Malaise flight intercept trap is a tent-like structure with a sheer fabric barrier that flying insects bump into, while additional barriers in the trap direct the insects into a collecting jar filled with alcohol (or other killing agent). We chose Malaise traps for our study because many previous studies have demonstrated the utility of this kind of trap for sampling Braconidae in forested areas (Lewis and Whitfield 1999; Mazon and

Bordera 2008; Shaw 2002; Noyes 1989). Although we did not find any reference to using Malaise canopy traps for sampling bark beetle associates, we believed the method would work because of its demonstrated effectiveness for sampling flying insects.

Trapping was conducted from July 23 to Aug 10, 2012 and the traps were serviced weekly (insect samples were removed and collection jars refilled with fresh alcohol). On completion of field work, samples were brought to the University of Wyoming, and insects of interest were sorted from the samples, and then chemically dried and mounted for taxonomic study.

Approximately 200 specimens of family Braconidae were prepared and mounted. This family was chosen for study because their hyperdiversity, wide range of hosts, and indirect connections to an even broader spectrum of organisms through their hosts, makes them good indicators for a range of ecological measures (Anderson and Purvis 2008; Anderson et al. 2010; Barbieri Junior and Dias 2012; Lewis and Whitfield 1999; Ueno 2013); and because Dr. Scott Shaw is a specialist in the taxonomy of that group. Specimens were identified to subfamily and genus using keys provided by Goulet and Huber (1993), Shaw (1995), and Wharton et al. (1997). A lack of recent revisions for a large proportion of the Braconidae taxa makes further identification of many specimens difficult (Shaw 2002) so we relied on sorting to morphospecies and comparison with previously identified specimens, a practice that has been validated (Derraik et al. 2010) and which was used in previous surveys. We took a conservative approach to using morphospecies to identify new distribution records, so our proportion of reported new records is likely low.

Three sources of information were used to determine the presence of bark beetle natural enemies in the GYE: our 2012 survey, a literature search, and study of specimens in the University of Wyoming insect collections. To our knowledge, this is the first time anyone has compiled a list of bark beetle natural enemies in the GYE.

◆ RESULTS AND DISCUSSION

In our current study we identified at least 49 braconid wasp species in 18 subfamilies with eleven of those species being new distribution records for the GYE (see appendix for complete list of subfamilies

and species). The scope of the current study limits comparisons between this and previous surveys to mostly qualitative analysis. We hope for the opportunity for more quantitative analyses in a future study.

Comparison to Previous Studies: We believe our most striking result to be the finding that 20% of the Braconidae species that we collected were new distribution records for Grand Teton National Park despite the near duplication of Shaw's 2002 survey (same time period and location) – obviously there is still much braconid diversity to be discovered. Climate change along with the unusual 2012 weather may have contributed to this result by altering the temporal distribution of the insects such that some species that were present previously were not present in this time period, and some which hadn't been present previously were present in 2012 during the collection period.

Also striking was a much lower collection rate for Braconidae than in the 2002 survey. Given that we used more traps, we were expecting more insect samples; instead we collected about 20% of the previous number of Braconidae specimens. This result was likely mostly weather related. During 2012, March and April temperatures averaged 6.1 degrees and 4.1 degrees higher than the respective 2002 monthly averages, which likely resulted in earlier than normal breaking of winter dormancy (see table 1). Also note that June 2012 was much drier and warmer than June 2002, which likely caused an early end to growth and reproductive cycles for many plants and insects. Almost nothing was blooming at the research station during late July of 2012 and much of the vegetation appeared dried out before the start of sampling. Braconid numbers and diversity are directly related to the diversity and density of host species, which in turn are dependent directly or indirectly on vegetation quality. Another important effect of the weather was the lack of nectar sources, upon which many adult braconids depend (Jervis et al. 1993; Williams and Hendrix 2008).

New Distribution Record: *Symphya* sp: The known hosts of members of this genus are agromyzid fly larvae in the genus *Phytobia*, which are tree cambium-boring insects (Wharton 1997).

Subfamily Doryctinae: Doryctines are parasitoids of woodboring beetle larvae (Marsh 1965; Wharton et al. 1997). Among the evidence of changes in the parasitoid community due to beetle kill was the finding of three previously unrecorded doryctines in GTNP during 2012.

New Distribution Records: New records are discussed below by subfamily.

Four of the eleven new distribution records are parasitoids of wood-boring insects. Two other new records of special interest are species in the rare genera *Holdawayella* and *Paradelius*.

Subfamily Alysiinae: Alysiines are parasitoids of immature stages of flies, and are one of the most important natural control agents of fly populations.

Table 1. Weather records for time periods preceding 2002 and 2012 insect surveys show that the spring and early summer of 2012 were much warmer and drier than during 2002. (Weather records are from the Burro Hill weather station located approximately +450 feet elevation and 14 miles ESE of the AMK Ranch. This is the nearest weather station with records going back to 2002.) Precipitation is expressed as inches and temperature is in degrees Fahrenheit.

	2002 precip in inches	2012 precip in inches	2002 ave temp degrees Fahrenheit	2012 ave temp degrees Fahrenheit
March	0.78	0. 79	25. 1	32.2
April	1.79	0. 62	35. 3	39.4
May	0.79	1. 84	44. 8	44.4
June	1.02	0. 35	55. 6	60
July	1.21	1. 16	65. 4	64.2
August	0.39	0.03	58. 9	64.3
12 month totals		9.	9.5	7.5
ending August 15	56		6	5

New Distribution Record: *Ecpnylus* species near *pacificus* Marsh: The known hosts of members of the genus *Ecpnylus* are the larvae of various bark beetles and wood-boring beetles (Marsh 1965; Wharton et al. 1997). A total of six specimens were collected in canopy traps placed in lodgepole pines with active bark beetle infestation. Hosts are not known, but may be mountain pine beetle or a secondary bark beetle. Previous studies did not find any members of genus *Ecpnylus* (Lockwood et al.

1996; Shaw 2002). If these specimens are *E. pacificus*, they may represent previously unseen morphological variability in this species. Alternatively, these wasps may prove to be an undescribed species.

New Distribution Records: *Herospilus* sp. 2 and *Heterospilus* sp. 3: Genus *Heterospilus* is associated mostly with wood and bark boring larvae (Marsh 1965) (Wharton et al. 1997). A single specimen of *Heterospilus* sp. 1 was collected in YNP in 1990 – a comparison shows this specimen is different from either of the two collected in 2012. These were not keyed to species due to lack of a recent revision of the Nearctic species of this genus.

Subfamily Braconinae: This subfamily contains the genus *Coeloides*, many of which are important parasitoids of bark beetles, including *C. rufovariegatus* Provancher and *C. sympitys* Mason, which are considered to be among the most important parasitoids of the mountain pine beetle (Amman 1984; Bellows et al. 1998; Mason 1978). Also in this subfamily is the genus *Atanycolus* whose hosts are almost entirely larvae of wood and bark inhabiting beetles, (Wharton 1997). Given previous records in the GYE and the current bark beetle outbreaks, it was a surprise that neither of these genera were seen in 2012. However, not surprisingly, at least three species of the very speciose genus *Bracon* were found, including two new distribution records.

New Distribution Records: *Bracon* sp 1, *Bracon* sp 2 (Hymenoptera: Braconidae: Braconinae): Members of the subfamily Braconinae are parasitoids on a variety of hosts, mostly lepidopterous and coleopterous larvae in concealed situations. The genus *Bracon* is very large and diverse; recorded hosts for the genus *Bracon* are mostly Lepidoptera and Coleoptera, including the larvae of some woodboring beetles (Marsh 1979; Quicke and Sharkey 1989; Muesebeck 1925). Two of the three species of *Bracon* found in 2012 were not seen previously; this may be due in part to beetle-kill, but is more likely due to the temporal disjunct in developmental cycles caused by the unusual weather patterns last year, and the fact that *Bracon* is such a large and diverse genus.

Subfamily Euphorinae: Euphorines are unusual in that they attack adult insects – most braconids attack larval stages or pupae (Shaw 2004). Although widespread and diverse, they are often sparsely dispersed throughout the environment and many are rarely collected (Wharton et al. 1997). The 2012 material adds one new distribution record in this subfamily; it should also be noted that, although not a new record, two specimens of a rare species in this

subfamily were collected: *Myiocephalus boops* Wesmael. *M. boops* is a Holarctic species that is associated with ants, but its biology is unknown (Muesebeck, 1936; Shaw 1985). One of the current specimens was collected in a canopy trap, which may offer a clue to its biology, or it could be a random occurrence – all previous specimens from GYE were collected in ground-based Malaise traps.

New Distribution Record: *Holdwayella* probably *tingiphaga* Loan: This is another seldom collected species, and has not been reported from the GYE before. Loan et al. (1971) described the genus *Holdawayella*, including its biology. The two known species are apparently not distinguishable morphologically, but have a different biology and attack different hosts. *H. tingiphaga* attacks lace bugs (Tingidae) that live on alder, while the other species attacks tingids on walnut trees. Our sampling location was close to the shore of Jackson Lake, with riparian trees including alder, which supports the identification of *H. tingiphaga*. Additional field work is needed to confirm our identification.

Subfamily Adeliinae: This is a small subfamily of diminutive wasps represented by only two genera and five described species in North America. Though distributed widely, they are rarely collected, probably in part because of their small size. As far as known, they are parasitoids of leaf-mining moths (Wharton et al. 1997; Whitfield 1988).

New Distribution Record: *Paradelius* sp.

Subfamily Agathidinae: Agathidinae is a large subfamily with at least 99 species in America north of Mexico (Sharkey 2004). They are recorded as parasitoids of lepidopterous larvae in cases where hosts are known (Wharton et al. 1997).

New Distribution Record: *Agathis* sp. This is only the second species of *Agathis* found in the GYE (Shaw 2002).

Subfamily Orgilinae: Members of the subfamily Orgilinae attack Lepidoptera and were one of the most abundant groups in previous surveys of GYE, making up 14% of the specimens caught in Malaise traps (Shaw 2002). Interestingly, their relative abundance did not change from earlier surveys, though the relative abundances of Cheloninae and Microgastrinae, also parasitoids of Lepidoptera, dropped considerably in 2012.

New Distribution Record: *Orgilus* sp. near *lateralis* Cresson: *Orgilus lateralis* is widespread,

having been recorded from coast to coast in the US. Muesebeck (1970) believed *O. lateralis* to possibly be a cluster of separate, related species so this is possibly an undescribed species. This same species has been collected previously in Medicine Bow Routt National Forest in eastern and central Wyoming.

Subfamily Rogadinae: This is a very large subfamily, with some members being quite common. Hosts are caterpillars of Lepidoptera (Wharton *et al.* 1997).

New Distribution Record: *Aleiodes medicinebowensis* Marsh and Shaw was originally described from eastern Wyoming (Marsh and Shaw 2001). This record extends its known range to the western part of the state.

Some other notable changes seen in the current survey: The proportion of specimens of the subfamily Microgastrinae was much lower in 2012 (approximately 30% of specimens) than in 2002 (over 50% of specimens). This was probably a result of the anomalous spring weather in 2012 which resulted in much lower populations of host plants that support caterpillars – Microgastrinae are the most common parasitoids of caterpillars. One species of Microgastrinae that was quite numerous in previous surveys, *Sathon neomexicanus* Muesebeck (Williams 1988), was completely absent.

Also notable was the absence of the important bark beetle parasitoids in the genus *Coeloides* found in previous surveys – these include *Coeloides rufovariegatus* Cushman, and *Coeloides sympitys* Mason. These parasitoids may not have been present during the sampling period in 2012 due to temporal shifts in the wasps' and/or the beetle's life cycles, possibly driven by climate change, and/or by the unusual spring weather of 2012.

Table 2. Test and CI for Two Proportions

Sample	X	N	Sample p
1	8	10	0.800000
2	2	10	0.200000
Difference = p (1) - p (2)			
Estimate for difference: 0.6			
95% lower bound for difference: 0.305760			
Test for difference:			
Fisher's exact test: P-Value = 0.012			

Parasitoid Fauna in Association with Bark Beetle Epidemic: Our study found moderately strong

evidence of bark beetle-associated changes in parasitoid communities. Firstly, 35% of the 2012 new distribution records (four of eleven) are parasitoids of bark or wood boring insects. Secondly, the proportion of wood and bark borer parasitoids was much higher (eight of ten) in the canopy trap sample from beetle infested trees than in the sample (two of ten) from healthy trees. We compared these proportions using a pooled p and Fisher's exact test to adjust for small sample size (see Table 2).

With this adjustment, our analysis estimates that the likelihood of our result being due to chance is about 1.2%. This is strong evidence for an effect on the parasitoid community in the immediate vicinity of tree trunks, but these samples probably do not account for the majority of the parasitoid diversity, which demonstrably resides closer to the ground among the wider variety of understory plants (in our survey, four canopy traps caught 20 braconids, and two ground-based traps caught 180).

✦ CONCLUSIONS & RECOMMENDATIONS

Significant diversity of the braconid community remains to be discovered. We strongly believe that a large proportion of the braconid parasitoid diversity in GYE remains to be discovered because our sampling has mostly been limited to a single habitat, lodgepole forest, at one elevation, over short time periods. We recommend a comparative quantitative analysis of biodiversity measures be applied to future surveys; we are quite certain that such an analysis would support the above conclusion. We also recommend continuing inventories of GTNP insects; it is apparent from the rate of discovery of new records that more species records will likely be discovered in the future.

Braconid diversity is affected by beetle kill. We found fairly strong evidence to support this conclusion, though studies that more directly focus on this question are required to better measure this effect. Ground-based Malaise traps placed in beetle killed stands would collect a much more generalized sample and would give a clearer picture of the changes in the parasitoid community. Future surveys should be conducted periodically to monitor forest recovery in areas most hard-hit by beetle kill, as an understanding of the forest response to beetle kill will be needed to guide future management practices.

Natural enemies play a role in bark beetle dynamics. As a first step in understanding the role of natural enemies of bark beetles in the GYE we have created a list of natural enemies of the mountain pine

beetle in the GYE lodgepole forests. (Table 3) Although this list includes important natural enemies known from other Rocky Mountain forests, there may be local differences that can only be detected by more extended sampling and more applicable sampling methods. Given the very small sample we collected in our canopy traps, we judge that canopy traps are not an effective method of surveying bark beetle associates, so we recommend that future surveys adopt methods proven for the purpose, including emergence traps, and sticky traps (for examples, see Amman 1984 and Stephen and Dahlsten 1976). We also recommend studies of the biology of natural enemies, for only by understanding the relationships between bark beetles and their predators and parasitoids can we hope to develop management practices that can enhance the impact of those natural enemies on bark beetle outbreak dynamics. The absence of the common and important bark beetle enemies *Coeloides* sp. in our current survey also warrants further study, as this finding may indicate changes in the effectiveness of natural enemies due to climate or other changes.

Table 3. Natural Enemies of Mountain Pine Beetle known to occur in GYE

Species	Order and Family	References for Biology and Distribution
<i>Coeloides dendroctoni</i> Cushman = <i>C. rufovariegatus</i> Provancher	Hymenoptera: Braconidae	(Amman 1984; Bellows <i>et al.</i> 1998; Mason 1978)
<i>Coeloides sympitys</i> Mason	Hymenoptera: Braconidae	(Mason 1978)
<i>Rhopalicus pulchripennis</i> Crawford	Hymenoptera: Pteromalidae	(Adams and Six 2008)
<i>Enoclerus spehegeus</i> Fabricius	Coleoptera: Cleridae	(Amman 1984; Bellows <i>et al.</i> 1998; Shmid 1970)
<i>Thanasimus undatulus</i> Say	Coleoptera: Cleridae	(Amman 1984; Bellows <i>et al.</i> 1998)
<i>Temnochila chloridia</i> Mannerheim	Coleoptera: Trogossitidae	(Bellows <i>et al.</i> 1998)
<i>Medetera aldrichii</i> Wheeler	Diptera: Dolichopodidae	(Pollet <i>et al.</i> 2004; Bickel 1985)

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Appendix: List of Subfamilies and Species Found in this Survey

Subfamily Adeliinae

Paradelius sp. (new distribution record)

Subfamily Agathidinae

Agathis sp. (new distribution record)

Subfamily Alysinae

Aspilota sp.

Chorebus sp.

Dacnusa sp.

Dinotrema sp. 1

Dinotrema sp. 2

Symphya sp. (new distribution record)

Subfamily Aphidiinae

Aphidius sp.

Binodoxys sp.

Ephedrus sp.

Praon sp. 1

Praon sp. 2

Subfamily Blacinae

Blacus sp.

Subfamily Braconinae

Bracon sp. 1 (new distribution record)

Bracon sp. 2 (new distribution record)

Bracon sp. 3

Subfamily Cheloninae

Archiochelonus sp. 2

Ascogaster near *borealis* Shaw

Ascogaster near *rufa* Muesebeck & Walkley

Chelonus (*Microchelonus*) sp. 1

Chelonus (*Microchelonus*) sp. 2

Subfamily Doryctinae

Doryctes near *fartus* (Provancher)

Ecphylus near *pacificus* Marsh (new distribution record)

Hetrospilus sp. 2 (new distribution record)

Hetrospilus sp. 3 (new distribution record)

Ontsira imperator Haliday

Subfamily Euphorinae

Centistes laevis Cresson

Holdawayella probably *tingiphaga* Loan (new distribution record)

Myiocephalus boops Wesmael

Subfamily Helconinae

Wroughtonia probably *frigida* Cresson

Subfamily Hormiinae

Hormius sp.

Subfamily Macrocentrinae

Macrocentrus incompletus Muesbeck

Macrocentrus sp. 2

Subfamily Meteorinae

Meteorus near *dimidiatus* Cresson

Subfamily Microgastrinae

Apanteles sp. 1

Apanteles sp. 2

Cotesia sp.

Microplitis sp.

Subfamily Neoneurinae

Neonuris sp.

Subfamily Opiinae

Opius sp. 1

Opius sp. 2

Opius sp. 3

Subfamily Orgilinae

Orgilus near *lateralis* Cresson (new distribution record)

Orgilis sp. 1

Orgilis sp. 2

Subfamily Rogadinae

Rhysipolis platygaster Spencer

Aleiodes medicinebowensis Marsh and Shaw (new distribution record)

Aleiodes near *scrutator* Say

A CASE FOR INCREASED FORAGING SUCCESS UNDER HIGH CONSPECIFIC DENSITIES IN THE NEW ZEALAND MUDSNAIL, *POTAMOPYRGUS ANTIPODARUM*

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✦ ABSTRACT

An animals' fitness can be positively or negatively affected by the density of conspecifics. While density dependent increases in fitness, or Allee effects, have been a key focus of the management of declining populations of native organisms, they may also be exploited for the purpose of invasive species management. Although most Allee studies focus primarily on mate location, a threshold density of conspecifics may also be required for effective foraging. *Potamopyrgus antipodarum* is a successful invader that can reach very high densities. Previous studies have demonstrated that *P. antipodarum* benefits from certain high densities through increased reproduction and activity. To determine whether conspecific density positively affects the foraging ability of *P. antipodarum*, I conducted laboratory experiments with three increasing levels of density (one, five and 15 individuals, control targets were alone). Because the presence of interactors may also affect the type of food individuals choose, I also included two food options differing in the amount of phosphorus, which is an important nutrient known to be limited in one invaded stream. Although food choice was unaffected by conspecific density, *P. antipodarum* were more likely to feed and fed longer in the higher density treatments; target snails in the treatment containing 15 conspecifics fed three times as long as targets in the treatment with five conspecifics. These results provide further insight into the ecology of *P. antipodarum*, and their success as invaders. Further work is needed to determine how this species uses high density to locate food resources.

✦ INTRODUCTION

Invasive species, non-indigenous species that cause ecological or economic harm, are one of the leading causes of global biodiversity loss (Sala *et al.* 2000). As a result, there is increasing interest in identifying the mechanisms that lead to successful invasion (Sakai *et al.* 2001, Taylor and Hastings 2005). Successful invasions require minimum founding populations for the establishment and growth of viable populations, and the spread of these populations through the invaded region (Parker *et al.* 1999). Invaders that are able to reach high population densities will be more likely to dominate, negatively affecting native ecosystems (Hall *et al.* 2006, McKenzie *et al.* 2013). Although high invader densities can result in both intra- and interspecific competition for space and nutrients (Schloesser 1996, Strayer 1999), high densities may provide fitness benefits for some invaders through increased mating opportunities, predator avoidance and improved foraging strategies (Kramer *et al.* 2009). These types of density-dependent increases in fitness (Allee 1931) should be particularly strong during early stages of invasion, when the probability of locating mates affects the likelihood of extinction in the invaded range (Taylor and Hastings 2005, Lockwood *et al.* and references therein 2007, Tobin *et al.* 2011). Although they have received much less attention, Allee effects that are not directly related to mate location (hereafter non-reproductive Allee effects), such as predator avoidance and food location, may profoundly affect the success of an invader. Because asexual invaders do not require mates, they are ideal for studying non-reproductive Allee effects.

Potamopyrgus antipodarum (Hydrobiidae, Mollusca; Gray 1843) is a freshwater snail native to New Zealand. While both sexual and asexual populations are found in the native range (Winterbourn 1970, Lively 1987), only the parthenogenetic females are known invaders (Jacobsen and Forbes 1997, Alonso and Castro-Diez 2008). *Potamopyrgus antipodarum* have successfully invaded multiple habitat types, world-wide, likely resulting from their ability to tolerate a wide range of temperatures and salinities (Winterbourn 1969, 1970), and high relative growth rates (Hall et al. 2006, Tibbets et al. 2010). The high growth rates of *P. antipodarum* suggest that these snails should have high nutrient demands (Elser et al. 2000). However, the resources in which they live are often nutrient limited (Cross et al. 2005, Tibbets et al. 2010), suggesting that *P. antipodarum* populations should be sensitive to nutrient availability. Despite often living in environments with low nutrient availability, invasive *P. antipodarum* can occur in very high population densities (500,000/m² in one stream, Hall et al. 2006), making them ideal for studying invasion biology (Alonso and Castro-Diez 2008, Liess and Lang 2011) and potential non-reproductive Allee effects. My experiment investigated whether *P. antipodarum* benefits from high conspecific densities through more effective foraging.

Potamopyrgus antipodarum may increase individual fitness in the presence of multiple conspecifics. Two laboratory experiments showed that individual *P. antipodarum* substantially increased reproductive output in the presence of high conspecific densities (Brenneis et al. 2010 and Neiman et al. 2013). Additionally, *P. antipodarum* increased overall activity (Liess and Lange 2011) and were more likely to feed (Hansen 2013) in the presence of many conspecifics. I conducted laboratory behavioral trials with field-caught *P. antipodarum* to determine whether feeding activity or choice of food is positively affected by high conspecific density.

✦ METHODS

Study Animals

In June 2012, I collected adult *P. antipodarum* (3.5 – 5 mm length) from lower Polecat Creek near Flagg Ranch (Rockefeller National Parkway, WY) with aquatic nets. All snails in the GYE are members of the US1 clonal lineage (Dybdahl and Drown 2011). Snails were housed in aquaria in the UW Zoology and Physiology Animal Facility, at 23° C on a 12 hour light cycle, and allowed to acclimate to the laboratory environment for one week

prior to the start of experiments. During the acclimation period, I fed snails an *ad libitum* diet of organic leaf lettuce, goldfish flakes and algae pellets.

Experimental Diet

For the experimental diet, I cultured the green algae, *Scenedesmus acutus*, with a nutrient medium containing identical N and either low (C:P ~ 1,119) or high (C:P ~ 203) amounts of P (Dobberfuhl and Elser 1999). I manipulated phosphorus level because *P. antipodarum* is known to be limited by the availability of phosphorus (Tibbets et al. 2010). After cultures grew for one week, I concentrated the algae in a centrifuge. I pipetted 0.25 mL of concentrated algae into aluminum weigh boats (3.5 mm diameter) and placed them in a 60°C drying oven for 24 hours. To ensure that algal cells would adhere to the inside of the weigh boats, I scuffed the inner surface of each using a Dremel (120 grit bits) prior to adding food.

Experimental Design

I asked two related questions: 1) Is the probability of feeding and time spent feeding (foraging activity) influenced by the number of conspecifics and 2) is food choice affected by increasing density of conspecifics. To address these questions, I placed two food boats, one containing high P and one containing low P algae, in the center of each 300 mL (~10 cm diameter) experimental chamber with all snails (targets and conspecifics) equally spaced from the two food options. Each experimental treatment included 25 replicates. I fasted target snails for three days to increase motivation for feeding. Each replicate ran for five hours and was recorded using a high definition video camera. I analyzed video data for the total time each target spent on each food type.

To address question 1, whether *P. antipodarum* increased feeding activity in the presence of increased conspecific densities, I measured the amount of time a single target snail (> 3.5 mm) fed with zero (control), one, five or 15 similarly-sized (3 – 5 mm) conspecifics. Because chamber size and water volume was identical among treatments, I defined density as the number of animals per chamber. I painted the target snails with nail polish so that I could observe individual behavior. I compared the probability of feeding among density treatments using a Fisher's Exact Test. To assess whether the presence of any conspecifics affected foraging activity, I first compared the controls (no conspecifics) to the combined density treatments using a t-test. Then, to determine whether varying densities of conspecifics

affected foraging activity, I omitted controls and used a one-way ANOVA to determine whether density of conspecifics affected foraging activity. I used a square root transformation of the total time feeding (minutes) to achieve homoscedasticity. For both probability of feeding and foraging activity, I omitted replicates where no feeding occurred and I combined data from both food types. I defined feeding events as any time that a target snail was inside of a food boat. Finally, I conducted another Fisher's Exact Test to learn whether different conspecific densities affected the probability of choosing high quality food. All statistics were conducted using the R statistical package (R Development Core Team, 2012).

◆ RESULTS

The number of target snails that fed on either food type differed among treatments (Fisher's Exact Test, $p = 0.006$) such that the number doubled between one and five conspecifics and tripled from five to 15 conspecifics. However, the total amount of time *P. antipodarum* spent feeding did not differ between controls and all treatments of conspecific densities combined ($t_{20} = 0.2104$, $p = 0.835$). Among density treatments, the amount of time that target snails fed differed ($F_{2, 15} = 2.91$, $p = 0.085$; Figure 1) such that snails fed ten times longer with five conspecifics relative to one conspecific, and twice as long with 15 conspecifics relative to five.

However, I found no effect of varying conspecific density on the probability of choosing high P or low P food (Fisher's exact test, $p = 0.115$).

◆ DISCUSSION

Identifying the traits that characterize successful invaders is critical to predicting likely invaders, and to minimizing the impacts of established invasive populations. *Potamopyrgus antipodarum* is a successful aquatic invader, and has been shown to negatively affect native grazers in field (Riley et al. 2008) and laboratory experiments (Thon and Krist in prep.). High relative growth rates and percent body phosphorus (Tibbets et al. 2010) suggest that *P. antipodarum* should have a high P demand (Elser et al. 2003). However, because P is often limiting in benthic resources (Cross et al. 2005), it is not clear how *P. antipodarum* is able to maintain high population densities in invaded habitats. Although my results suggest that increased conspecifics do not improve the ability of snails to choose food that is high in P, they

do suggest that greater numbers of conspecifics may improve the foraging activity of this snail. While the threshold for a positive effect on foraging may occur with fewer than 15 conspecifics (e.g. ten), under my experimental conditions more target *P. antipodarum* fed and spent the most amount of time feeding when 15 conspecifics were present. It is possible that even higher densities of conspecifics will have a stronger positive effect of *P. antipodarum* foraging behavior.

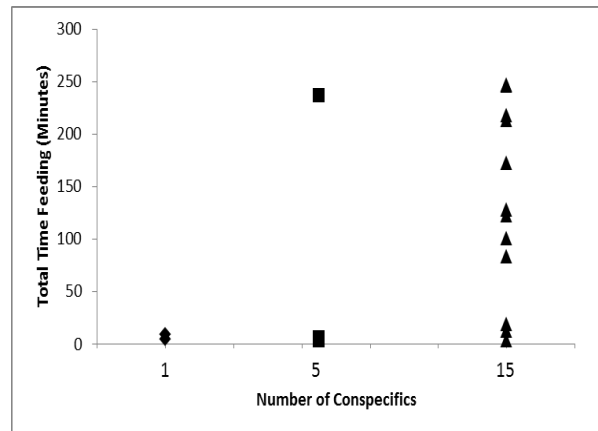


Figure 1. The invasive snail, *Potamopyrgus antipodarum*, altered foraging activity (measured as the amount of time feeding by a target snail) in the presence of three levels of conspecific density ($F_{2, 15} = 2.91$, $p = 0.085$). When the high outlier from the treatment with five conspecifics, and the three smallest outliers from the treatment with 15 conspecifics were removed, there was no apparent difference between treatments containing one and five conspecifics, but target snails from both spent significantly less time feeding than targets with 15 conspecifics (Tukey-Kramer: $p = 0.0002$ and $p < 0.0001$ respectively).

My results are similar to other work that suggests *P. antipodarum* benefits from high densities of conspecifics through increased reproductive output (Brenneis et al. 2010, Neiman et al. 2013) and activity (Liess and Lange 2011). In addition, growth of *P. antipodarum* was much less affected than a native snail, *Fossaria*, by very high densities of conspecifics in a laboratory experiment (Thon and Krist in prep.). Although I did not examine very high densities, my results demonstrate that *P. antipodarum* is more likely to feed with at least 15 conspecifics present. Increased probability of feeding by *P. antipodarum* may be explained by chemical cues produced by feeding individuals, which attract conspecifics to food patches. This response has been shown in many social animals (Aguilar and Sommeijer 2001, Saleh et al. 2007), and in asocial rattlesnakes (Clark 2007). It is also possible that, similar to some hermit crabs (Laidre 2010), *P. antipodarum* locates food visually, based on the presence of conspecifics on food resources.

The lack of an effect of increased conspecifics on food choice may suggest that *P. antipodarum* is unable to distinguish differences in food quality. Perhaps *P. antipodarum* lack the sensory ability to locate resources based on nutrient quality. Furthermore, the increase in the probability of feeding at higher densities could mean that *P. antipodarum* was unable to successfully locate the algae by olfaction. If this snail cannot detect algae, an increase in density simply increased the probability of an individual randomly finding the food, with additional individuals following the chemical or visual cues of the successful snail. Although one study did identify preference for certain food types by *P. antipodarum* (Haynes and Taylor 1984), their experimental chambers contained 250 animals and their results did not distinguish between individual choice and conspecific facilitation. It is also possible that *P. antipodarum* can distinguish between different types of resources, such as plant and animal material (Haynes and Taylor 1984), but not differences in quality of one specific species, as in my experiment.

Because I showed that some densities positively affect the foraging behavior of *P. antipodarum*, my results highlight the importance of including Allee effects in future invasion studies. Because invasive species require a minimum population size for establishment and spread, identifying and exploiting density-dependent traits of invasive species may facilitate management of established populations. Identifying the minimum population size necessary for the establishment of *P. antipodarum* would advance our understanding of how Allee effects contribute to the invasion success of this species.

◆ ACKNOWLEDGEMENTS

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

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♦ ABSTRACT

The Snake River is an essential feature of Grand Teton National Park, and this dynamic fluvial system maintains diverse habitats while actively shaping the landscape. The complex, ever-changing nature of the river make effective characterization difficult, however; traditional field methods are ill-suited for this task. Remote sensing provides an appealing alternative that could facilitate resource management while providing novel insight on the controls of channel form and behavior. This study continued our ongoing assessment of the potential to measure the morphology and dynamics of large, complex rivers such as the Snake via remote sensing (Figure 1). More specifically, we acquired hyperspectral images and bathymetric LiDAR data in August 2012 and are now comparing the depth retrieval capabilities of these sensors; *in situ* observations of water column optical properties inform this analysis as well. In addition to bathymetry, we are investigating the feasibility of using these data to infer bottom reflectance and hence delineate various substrates, such as gravel and submerged aquatic vegetation. Another new aspect of our research focuses on estimating flow velocities from the hyperspectral images and high-resolution digital aerial photography acquired simultaneously. Extensive field measurements of velocity will help us develop this approach. Similarly, measurements of sediment grain size on exposed bar surfaces will be used to assess whether particle size can be inferred from the high-resolution photography. Remotely sensed data also are being used to identify areas of erosion and deposition and hence quantify the sediment flux associated with changes in channel morphology. Additional

hyperspectral and bathymetric LiDAR data will be acquired in 2013, along with field measurements of depth, velocity, and bottom type.

♦ INTRODUCTION



Figure 1. Cataraft used for measuring field spectra along the Snake River. Photo by Brandon Overstreet.

A defining feature of the Teton landscape, the Snake River plays an important role in the geomorphology and ecology of Jackson Hole and provides visitors to Grand Teton National Park with abundant recreational opportunities. This dynamic fluvial system collects water and sediment from a large, mountainous drainage basin and conveys these materials across the valley floor via various mechanisms of flow and sediment transport. These processes interact to produce coherent patterns of sediment transfer and storage that are manifested as distinctive landforms - channels, bars, floodplains, and

terraces. These geomorphic surfaces are colonized by vegetation but eventually reclaimed as the river shifts laterally, incises new channels, or reoccupies former flow paths. This perpetual reworking of the riparian zone creates a patchy mosaic of habitat conditions that supports a diversity of terrestrial and aquatic organisms, including such iconic species as bald eagles, beaver, native trout, and moose. The potential to view such wildlife, along with the unique scenery in part created by the Snake, makes this fluvial environment a source of considerable enjoyment by the public, for whom the river and surrounding National Park have been protected and preserved.

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

Remote sensing techniques could provide such a capacity by enabling more efficient measurement of several key river attributes. A

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

Research on the application of remote sensing to rivers has progressed rapidly over the past decade (Marcus and Fonstad, 2010). For example, our earlier work demonstrated the feasibility of mapping flow depth from optical data (Legleiter et al., 2004, 2009). Field measurements and digital aerial photography collected along the Snake River in August 2010 also indicated that reasonably accurate depth estimates could be derived from relatively basic images of this kind (Legleiter, in press). A subsequent study demonstrated that river bathymetry could even be mapped from space, with high-resolution multispectral images from the WorldView2 sensor (Legleiter and Overstreet, 2012). Our results thus suggest that integrated, spatially explicit analysis of remotely sensed data could enable scientists and managers to more efficiently characterize complex river systems like the Snake.

Research hypothesis and specific aims

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

1) Obtain field measurements of reflectance, water column optical properties, water depth, flow velocity, and substrate composition to assess the feasibility of retrieving key geomorphic parameters such as bathymetry, velocity, and particle size from optical image data.

2) Extend our image time series through 2012 by acquiring hyperspectral data, high-resolution digital aerial photography, and both near-infrared topographic LiDAR and water-penetrating bathymetric green LiDAR.

3) Quantify the sediment flux associated with channel change by measuring volumes of erosion and deposition volumes from repeat LiDAR coverage acquired in 2007 and 2012.

◆ STUDY AREA

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

Our 2012 field campaign involved extensive data collection along the Snake River and

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

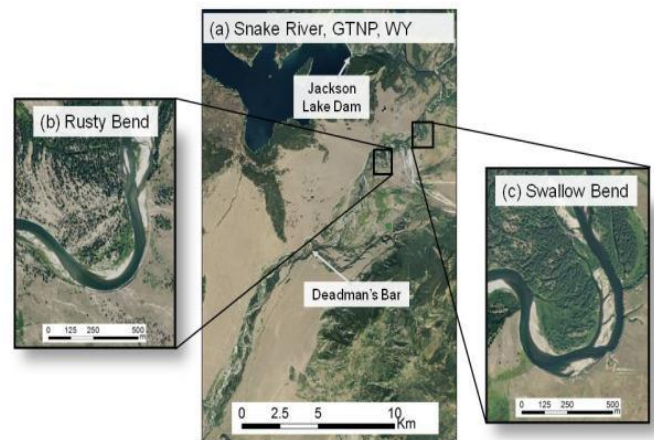


Figure 2. WorldView2 satellite image of the Snake River acquired 13 September 2011 showing the locations of our two primary study reaches: Rusty and Swallow Bends.

◆ METHODS

For 2012, the general strategy of our investigation was to 1) make field measurements of flow conditions, bed material composition, and optical properties along the Snake River, 2) obtain various types of remotely sensed data from the riparian corridor, 3) develop and evaluate image processing methods for retrieving key geomorphic and habitat parameters from these image data sets, and 4) combine newly acquired and archival LiDAR coverage to examine channel changes occurring between 2007 and 2012. The data acquired in 2012 also provide a basis for planning future remote sensing missions, with additional flights scheduled for August 2013. This project thus involved a combination of geospatial data analysis and field work; these two components are described below.

Remotely sensed data and image processing

Our previous research on the Snake River has demonstrated the feasibility of mapping water depth from publicly available aerial photography (Legleiter,

in press) and satellite images (Legleiter and Overstreet, 2012), but in 2012 we focused on two new types of remotely sensed data. In collaboration with the National Center for Airborne Laser Mapping (NCALM), we acquired airborne hyperspectral images, high resolution digital aerial photography, and both near-infrared LiDAR for measuring sub-aerial topography and green LiDAR for measuring channel bathymetry. These data sets are illustrated in Figures 3 and 4.

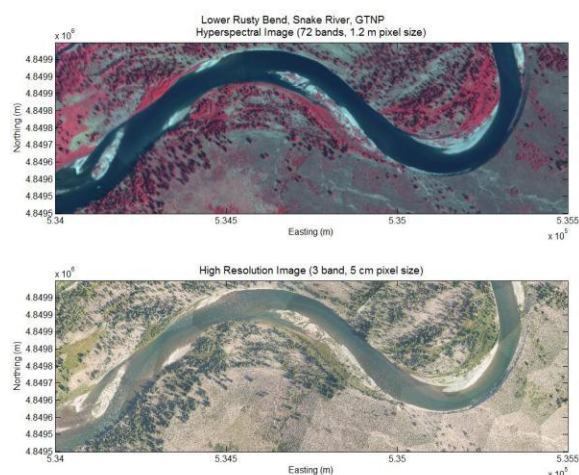


Figure 3. Hyperspectral image data and high-resolution aerial photography acquired from our Rusty Bend study site in August 2013, though a collaboration with the National Center for Airborne Laser Mapping (NCALM).

The hyperspectral images were acquired with a CASI 1500 sensor deployed at several different altitudes and aircraft velocities to yield data with pixel sizes ranging from 0.6 to 1.2 m, with up to 72 spectral bands. These data were only recently delivered by NCALM, with a single 1.2 m-resolution image having been processed to date, so our analysis of these images remains in a very early stage. Although the images we received were radiometrically calibrated and geo-referenced by NCALM, alignment with our field measurements was unacceptable and we are now re-processing the raw data acquired during the flight to achieve closer co-registration with our field data. The high-resolution aerial photography shown above was obtained with a DIMAC LiGHT+ medium format digital aerial camera system that provided 5 cm pixel sizes with a standard, three-band, true color spectral configuration. These data were geo-referenced and assembled into a mosaic by NCALM, and alignment with our field-based data sets is much better than for the hyperspectral images. The primary issue with the aerial photography is the seams evident where the individual frames were combined into a mosaic.

NCALM specializes in LiDAR data

collection, processing, and analysis, and acquired two types of LiDAR data for our project. Their standard Optech Gemini system operates at a NIR wavelength (1064 nm) and features a high scan frequency that yields a dense coverage of elevation measurements from exposed surfaces. For the channel proper, however, the NIR laser pulses are strongly absorbed by water and do not reach the bottom. A second, green (532 nm) LiDAR, the Optech Aquarius, is specifically intended for measuring bathymetry in addition to topography, although the system had been deployed only in coastal settings prior to this study of the Snake River. The two LiDAR data sets are shown in Figure 4, with the additional in-stream detail provided by Aquarius clearly evident. Deliverables from NCALM included both gridded, 1 m resolution digital elevation models and the original, raw point clouds in a LAS file format. Because these data sets were provided only recently, our analysis of the LiDAR is an early stage as well. Nevertheless, the remotely sensed data acquired in 2012 extend our time series from 2009 through the present and thus help to advance our ongoing investigation of channel change.

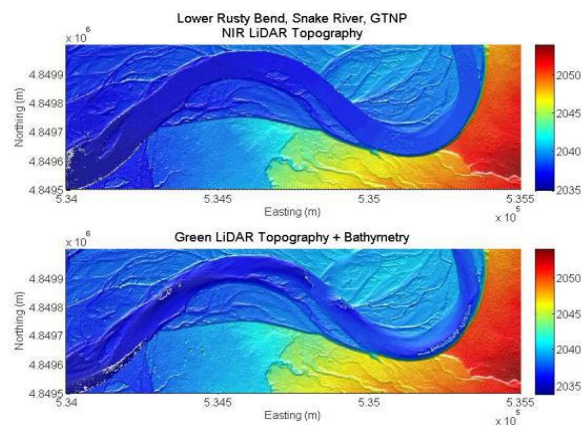


Figure 4. LiDAR data acquired by NCALM from the Snake River in August 2013.

Field data collection

In addition to the remote sensing component described above, our study also involved extensive field work intended to validate image-derived river information and support our geomorphic research. As part of our overall effort to advance the remote sensing of rivers, the development of which has been hindered by a lack of *in situ* observations, we made direct field measurements of several optical characteristics of the Snake River. Reflectance spectra were recorded above the water surface using an Analytical Spectral Devices (ASD) FieldSpec3 spectroradiometer. A 100% reflectant Spectralon calibration panel was used to establish a white reference prior to each round of

measurements. The spectroradiometer was mounted on a specially designed cataraft and configured to record spectra once each second as we traversed the river on a series of channel-spanning transects and longitudinal profiles (Figure 1). Flow depths were recorded simultaneously using the survey instrumentation described below. This protocol thus provided paired observations of depth and reflectance needed to develop and refine bathymetric mapping algorithms. Moreover, these data extended the range of river conditions under which spectra have been measured from shallow, wadable streams (Legleiter et al., 2009) to a deeper, larger channel with more diverse bottom types. For example, our Swallow and Rusty Bend study sites were up to 3 m deep and featured submerged aquatic vegetation and bright-colored clay bedrock substrates, respectively. In previous field seasons we collected spectra only along cross-sections located in our two primary study sites, but the addition of downstream profiles in 2012 further extended the range of river conditions we have observed and provided a greater sample size as well.

In addition to bathymetry, the composition of the streambed also might be mapped via remote sensing. To further explore this possibility and build upon the spectral library of different substrate types we measured directly with the ASD in 2011, we collected a series of substrate images. A GoPro camera with a waterproof housing was mounted beneath our raft during spectral data collection and configured to automatically acquire an image every second. By combining the time stamps for these images with those of the spectra and GPS positions, we obtained paired, geo-referenced observations of depth, reflectance, and substrate composition. An example substrate image from Swallow Bend is shown in Figure 5.

The optical properties of the water column impose an important constraint on remote mapping of bathymetry and/or bottom type, and we collected field data on several characteristics of Snake River water. We developed and implement several innovative field methods for collecting such data during our 2012 campaign, and the increased efficiency allowed us to acquire a larger data set spanning a broader range of conditions. For example, we designed a measurement crane for positioning a waterproof, upward-facing detector connected to the spectroradiometer at various depths within the water column at which we recorded the amount of downwelling radiant energy propagating to each depth (Figure 6). These data were used to calculate a diffuse attenuation coefficient at each wavelength following the procedure outlined by Mishra et al. (2005). In addition, we used a new WetLabs ac-s to directly measure two key inherent

optical properties of the water column, the absorption and attenuation coefficients, a and c . A second WetLabs instrument, called the EcoTriplet, also provided observations of the scattering coefficient b , turbidity, and concentrations of chlorophyll and colored dissolved organic matter (CDOM). A Eureka Environmental Manta 2 multi-probe was used to measure blue-green algae concentrations as well. These optical data were collected on several dates at discrete sites along the Snake River (for the irradiance profiles and ac-s measurements) and along the path of the raft, for the EcoTriplet and Manta 2 sensors. Ancillary data in support of these measurements included water samples analyzed for suspended sediment concentration.

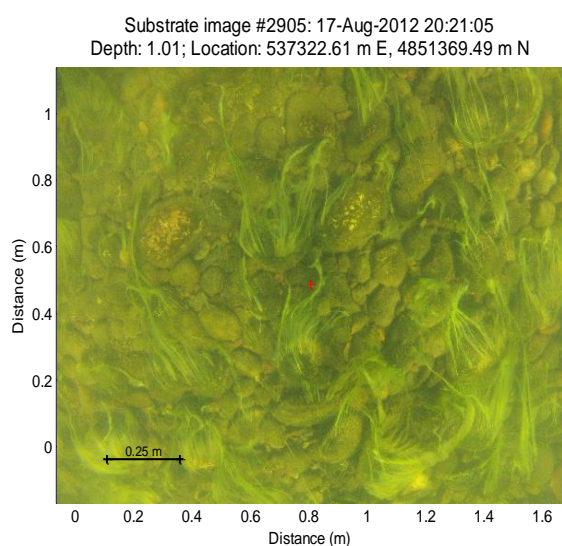


Figure 5. GoPro substrate image from Swallow Bend showing submerged aquatic vegetation present on the bed.

A second key component of our field effort was a survey of channel bed topography. These data were collected using a high-precision (sub-centimeter) real-time kinematic GPS receiver that was attached to a survey rod for measuring terrestrial surface elevations. Survey points were arranged along cross-sections traversing exposed bars and shallow areas of the active channel and selected so as to emphasize important breaks in slope, such as the top and base of stream banks. For areas that were too deep to wade safely, the GPS receiver was mounted on the cataraft and configured to record water surface elevations while communicating with an echo sounder that measures flow depths; subtracting the depth from the water surface elevation yielded measurements of the bed elevation. Over 22 km of the Snake River was surveyed in this manner. Measurements were obtained along a series of 6 transects in our detailed study sites as well as longitudinal profiles recorded as we

progressed downstream each day. These field measurements allowed us to establish relationships between depth and reflectance, both from field spectra and, eventually, hyperspectral images.



Figure 6. Measurement crane used to facilitate measurements of the downwelling radiant energy at different depths within the water column.

In an effort to expand the range of river attributes that can be derived from remotely sensed data to include information on flow velocity, we measured flow conditions within the Snake River using an acoustic Doppler current profiler (ADCP). This instrument was deployed from a kayak outfitted with a specialized mounting system (Figure 7) and recorded flow velocities in a series of cells distributed vertically throughout the water column. The ADCP measured streamwise, cross-stream, and vertical velocity components at a frequency of once per second and thus provided a very detailed characterization of the flow field. We also used the ADCP to measure river discharge by integrating the product of depth and velocity as we moved across the channel. In addition to cross-sections located in our two primary study sites at Swallow and Rusty Bends, we recorded velocities along profiles oriented down the river. The ADCP also recorded flow depths and thus provided an additional source of field data for evaluating remotely sensed bathymetry.



Figure 7. Flow velocities were measured with an acoustic Doppler current profiler (ADCP) deployed from a kayak, shown here during a September deployment intended to characterize the flow field at a lower discharge.



Figure 8. Measurement crane used to acquire digital photographs of bar surfaces that will be used to estimate sediment grain size. We also intend to explore the possibility of mapping grain size from the high-resolution digital aerial photography shown in Figure 3.

In addition, data acquired with the ADCP will support future work on the interactions between flow processes, bed material transport, and the evolution of channel form. To pursue this more general geomorphic research objective, we made a second round of flow measurements in late September at a lower discharge than during our primary field

campaign in August. The latter data set will allow us to more closely examine the influence of bar-pool topography on flow patterns through meander bends at a range of flow stages (Legleiter et al., 2011). To further expand this range, we have just (June 2013) completed a third set of measurements at a higher discharge more likely to mobilize bed material and lead to scour and fill.

The geomorphic processes responsible for channel change are highly sensitive to sediment grain size, but this type of information was not readily available for the Snake River. To facilitate our analysis of the river's sediment budget, we used the measurement crane shown in Figure 8 to elevate a camera and obtain photographs of bar surfaces. Grain size information will be derived from these images using established procedures (Warrick et al., 2009). To scale up this type of grain size mapping, we will also evaluate the possibility of inferring particle size from image texture metrics derived from the high-resolution digital aerial photography.

◆ RESULTS

Our previous work has focused on spectrally-based depth retrieval from remotely sensed data and field-based characterization of the optical properties of the water column. Although this work is ongoing, these topics have been addressed in annual reports from 2010 and 2011. For this summary of our 2012 activities, we shift our focus to several new, but related aspects of our research, keeping in mind our overall research objective of developing an advanced, operational capacity for deriving various kinds of river information from remotely sensed data. Here, we describe some preliminary results from our current efforts to: 1) map river bathymetry from NIR and green LiDAR, 2) identify different bottom types on the basis of their unique spectral characteristics, 3) infer flow velocities from hyperspectral images, and 4) quantify volumes of erosion and deposition associated with bank failure and channel change.

Measuring river bathymetry with green LiDAR

Whereas our earlier work has emphasized mapping bathymetry from passive optical image data based on relationships between depth and reflectance, in 2012 we began exploring a new means of characterizing channel morphology. LiDAR has become the preferred method of measuring terrestrial surface elevations for Earth science applications, but the NIR laser pulses emitted by standard LiDAR systems are strongly absorbed by water, implying that

these sensors cannot detect the channel bed. One solution to this problem, advocated in a previous study (Legleiter, 2012), is to combine depth estimates derived from optical images with LiDAR topography for exposed bars and floodplains to obtain a complete topographic representation of the riparian landscape. Recently developed green LiDAR systems, however, might provide a more efficient means of obtaining such data. Because the shorter-wavelength green laser does penetrate through water to some finite depth, submerged as well as sub-aerial topography can be measured with a single instrument.

Data acquired by NCALM's new Aquarius sensor in August 2012 along the Snake River allowed us to evaluate the potential for mapping channel morphology via this new technology. NIR topographic LiDAR were obtained as well, and we combined the two data sets to calculate water depths as the difference between the elevations recorded by the NIR LiDAR, which represent the water surface, from the elevations from the green LiDAR, which presumably were based on returns from channel bed. The resulting bathymetric map is shown in Figure 9A, which depicts our Rusty Bend field site. For the most part, depths inferred from the two LiDAR data sets are hydraulically reasonable, spatially coherent, and in good agreement with the field-based measurements shown in Figure 9B.

Also prominent in the bathymetric map, however, are a number of gaps, most notably in the deepest part of the bend at the upper end of the reach and in the center of the reach where the channel curves to the left. These gaps represent areas from which no green LiDAR returns were recorded and coincide with the deepest pools at this site. These depth retrieval errors are expressed as large positive residuals, defined as the field-measured depth minus the LiDAR-derived depth, in Figure 9C. The distribution of residuals in Figure 10 shows that although errors were minimal for much of the channel, a tendency to underestimate depth was indicated by numerous positive residuals; the mode at 2 m was associated with the data gaps in the pools.

These observations suggest that the LiDAR system as configured during this flight was not capable of resolving the full depth of pools on the basis of discrete return data. Because one of the purported advantages of green LiDAR is enhanced penetration depth relative to passive optical remote sensing, these results were unexpected and disappointing. Earlier research has shown that accurate depth estimates could be obtained for pools exceeding 2 m in depth from satellite images, implying that the hybrid optical/NIR

LiDAR strategy might be more reliable than green LiDAR. Our colleagues from NCALM also were surprised by these results and are currently exploring a different processing strategy that takes advantage of the full waveform of the laser pulse rather than discrete returns. This approach could yield more reliable bathymetry across a broader range of depths, but further testing is required.

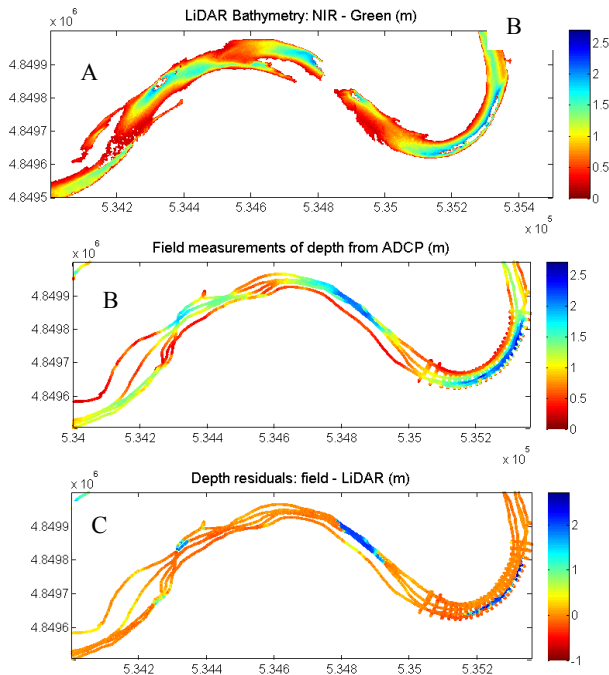


Figure 9. (A) Bathymetric map derived from NIR and green LiDAR from Rusty Bend; (B) field measurements of depth; and (C) depth retrieval residuals. Flow from right to left.

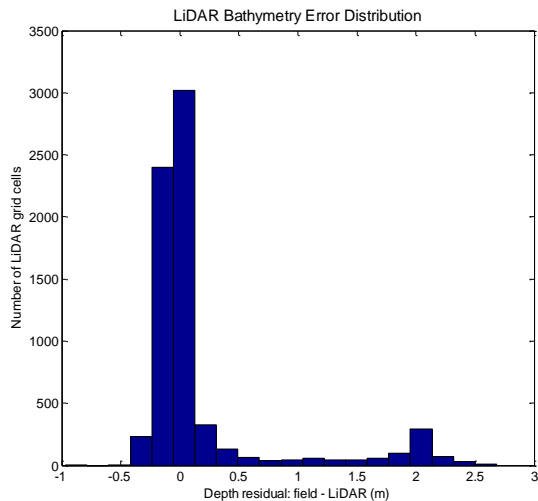


Figure 10. Distribution of depth retrieval residuals, defined as the difference between field-measured and image-derived depths, for Rusty Bend.

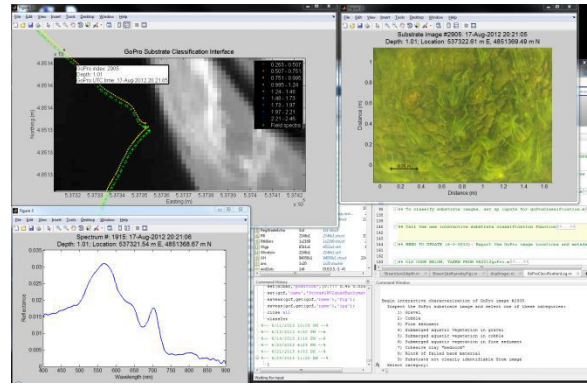


Figure 11. Graphical user interface for classifying substrate images of the Snake River and inspecting the spectral characteristics of different bottom types.

Mapping the riverbed via optical remote sensing

Another potential advantage of passive optical remote sensing is the availability of multiple spectral bands that might be used to infer other river attributes in addition to depth. For example, if the influence of the water column on the reflectance signal can be accounted for and removed, the bottom reflectance can be isolated and used to delineate various substrate types. Although this approach has been applied in coastal environments, we are not aware of any previous studies that have attempted to extend this approach to the fluvial environment. Our efforts to do so are in an early stage, but we have acquired a valuable field data set for pursuing this objective. By deploying the echo sounder, ASD spectroradiometer, and GoPro camera from our cataraft, we obtained paired observations of depth, reflectance, and bottom composition. Because each of these measurements were recorded once each second during multiple passes down the Snake River, we have thousands of spectra and substrate images to process. To facilitate this process, we have developed a user interface, shown in Figure 11, for selecting points from a map, querying the nearest substrate image and reflectance spectrum, and assigning the substrate at that location to one of several classes: gravel, cobble, or fine sediment with or without submerged aquatic vegetation, cohesive clay bedrock, and failed bank material. For the gravel and cobble classes, the user is also prompted to measure a representative particle size on the image, which can efforts to do so are in an early stage, but we have acquired a valuable field data set for pursuing this objective. By deploying the echo sounder, ASD spectroradiometer, and GoPro camera from our cataraft, we obtained paired observations of depth, reflectance, and bottom composition. Because each of these measurements were recorded once each second during multiple passes down the Snake River,

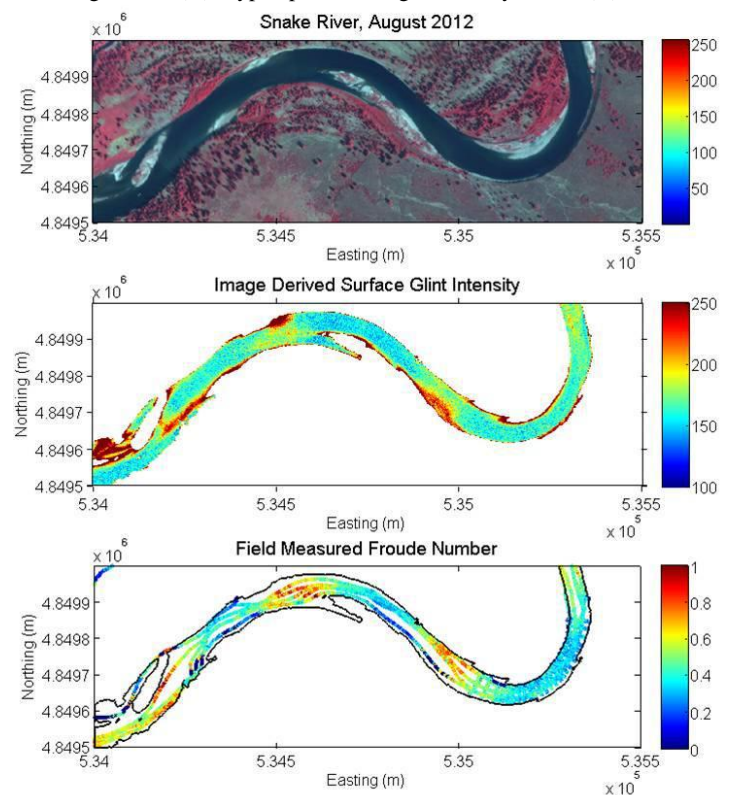
we have thousands of spectra and substrate images to process. To facilitate this process, we have developed a user interface, shown in Figure 11, for selecting points from a map, querying the nearest substrate image and reflectance spectrum, and assigning the substrate at that location to one of several classes: gravel, cobble, or fine sediment with or without submerged aquatic vegetation, cohesive clay bedrock, and failed bank material. For the gravel and cobble classes, the user is also prompted to measure a representative particle size on the image, which can be converted to units of millimeters based on the known image scale. For images with submerged vegetation, an ordinal ranking of stem density is made as well. These data will thus form the basis for new algorithms for discriminating fine from coarse sediment, identifying vegetation, and potentially estimating algal biomass.

Inferring flow velocity from hyperspectral images

A second attribute that potentially could be inferred from high-resolution hyperspectral image data is flow velocity. The basis for this approach is the common field observation that areas of faster flow tend to have rougher, more irregular water surfaces, with white water in rapids being an extreme case. The texture of the water surface in turn exerts a primary control on the reflectance characteristics of the air-water interface. As the roughness of the water surface increases, surface reflectance also tends to increase because more of the individual facets of the irregular surface are oriented toward the sun and produce stronger specular reflections. If the surface component of the total reflectance signal can be identified and isolated, a correlation between surface reflectance and flow velocity could be established. Although this innovative method has not been tested for actual image data from real rivers, a recent study conducted in an outdoor flume showed a strong connection between the reflectance of the water surface and the texture (i.e., microtopography) of that surface, which was in turn related to flow velocities (Legleiter and Overstreet, In press).

We are now attempting to scale up this approach by isolating the water surface reflectance, or glint, from the hyperspectral image data acquired in 2012, shown in Figure 12A. The intensity of this glint signal is derived from the image spectra by measuring the depth of an absorption feature at a wavelength of 760 nm associated with oxygen gas in the atmosphere. For pixels with a greater contribution from the surface, such atmospheric effects are more prominent in the reflectance signal. In rivers, the texture of the water surface is influenced by the combination of flow depth

d and velocity v , two variables that are used to define a non-dimensional quantity known as the Froude number: $Fr = v/(gd)^{1/2}$, where g is the acceleration due to gravity. Portions of the channel with higher Froude numbers (i.e., higher velocities and/or shallower depths) such as riffles tend to have a rougher water surface texture and presumably a greater surface reflectance. To examine this relationship, we produced a surface glint intensity image based on the oxygen absorption band (Figure 12B) and computed the Froude number from our ADCP field measurements (Figure 12C). Comparison of these two maps indicates a consistent spatial pattern, with areas of greater glint intensity coinciding with higher Froude numbers. These initial results imply a relationship between surface reflectance, surface texture, and flow velocity that might enable river hydraulics to be inferred from hyperspectral images, in addition to morphology. Figure 12. (A) Hyperspectral image of Rusty Bend. (B) A



map depicting the glint intensity, or strength of the reflectance from the water surface, derived from the original hyperspectral image based on an absorption feature associated with oxygen in the atmosphere. (C) Field measurements of flow depth and velocity were used to calculate the Froude number, with areas of faster and/or shallower flow having higher Froude numbers. The similar spatial patterns in (B) and (C) imply a connection between surface reflectance, surface texture, and flow hydraulics.

Further work will be required to verify this connection and develop efficient algorithms for

mapping velocities from hyperspectral images.

Channel change: quantifying erosion and deposition

In addition to our interest in developing remote sensing methods for characterizing large, dynamic river systems such as the Snake, our work also seeks to better understand the geomorphic history of this particular river and gain insight on the processes that have directed the channel's evolution over time. These two goals are highly complementary, as archives of remotely sensed data provide valuable, synoptic documentation of changes occurring along the river. The image data sets acquired in 2012 extend our annual time series from 2009 through the present, with additional image acquisition scheduled for August 2013.

Our previous annual report described riparian land cover classifications developed from successive images in this time series using a spectrally-based decision tree algorithm. This approach allowed us to identify portions of the valley floor that experienced a transition from one land cover type to another during the time period between images and infer the operative geomorphic process. For example, an area classified as floodplain during time 1 but active channel during time 2 would have experienced erosion, whereas a transition from active channel to gravel bar would imply deposition. These land cover transitions thus provide information on the areal extent of erosion and deposition, but calculating the volume of material involved requires additional information on the depth of scour or the thickness of sediment deposited. Repeat coverage of LiDAR topographic data are well-suited to this purpose and we obtained an existing 2007 LiDAR data set for the Snake River corridor to complement the new NCALM data acquired in 2012.

Ultimately, we intend to scale up this analysis to encompass the Snake River throughout Grand Teton National Park, but initially our efforts have focused on Swallow Bend. This reach is peculiar in that a large bar is located on the outside of the bend, whereas curved channels typically feature a point bar on the inner bank. The unusual morphology of Swallow Bend is shown in the 2012 image on the right side of Figure 13, but an aerial photograph from 1994 shows that the bar on the outside of the bend is relatively recent. Although we have several hypotheses as to what might have led to the deposition of this bar, with an 18-year gap between images identifying when this pronounced morphologic change occurred is not possible; this is

why the annual time series we have now begun to accumulate is so valuable.

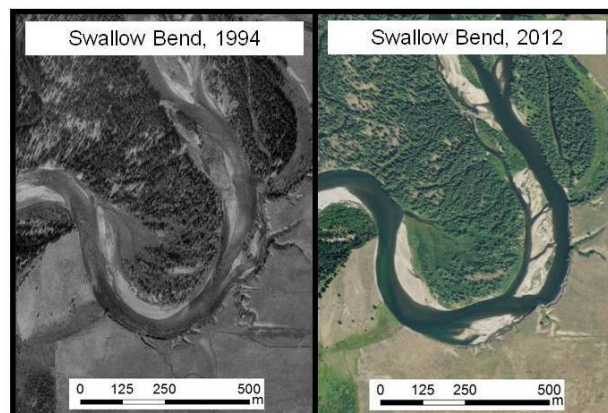


Figure 13. Historical and recent images of Swallow Bend, with the 2012 scene highlighting the large bar deposited along the outer bank.

Similarly, repeat LiDAR coverage, with 2007 and 2012 data sets already available and a new acquisition planned for 2013, allows sediment volumes to be quantified as well. By comparing sequential topographic data sets, a digital elevation model (DEM) of difference (DoD) can be produced and used to determine the depth of scour or thickness of fill. Multiplying these depths by the cell size of the DEM yields a volume. For Swallow Bend, a comparison of the 2007 and 2012 LiDAR data sets indicates that the terrace protruding into the channel along the outer bank near the entrance to the bend has retreated by several meters, with over 10 m of vertical erosion occurring during this time period in some locations. Movement of this eroded material downstream could lead to sediment accumulation on the bar along the outer bank, with the protruding terrace acting to deflect the flow toward the inside of the bend and allowing deposition in the zone of weaker flow below the constriction. Our future work will focus on incorporating this type of quantitative information into a sediment budgeting framework that explicitly accounts for inputs from bank erosion and storage of sediment on bars. This analysis will help refine existing sediment budgets, which are based on bedload transport measurements on the Pacific Creek and Buffalo Fork tributaries and the Snake River but do not incorporate sediment fluxes associated with bank erosion or bar deposition (Erwin et al., 2011). The resulting, refined sediment budget will help advance our understanding of the processes driving the Snake River's dynamics.

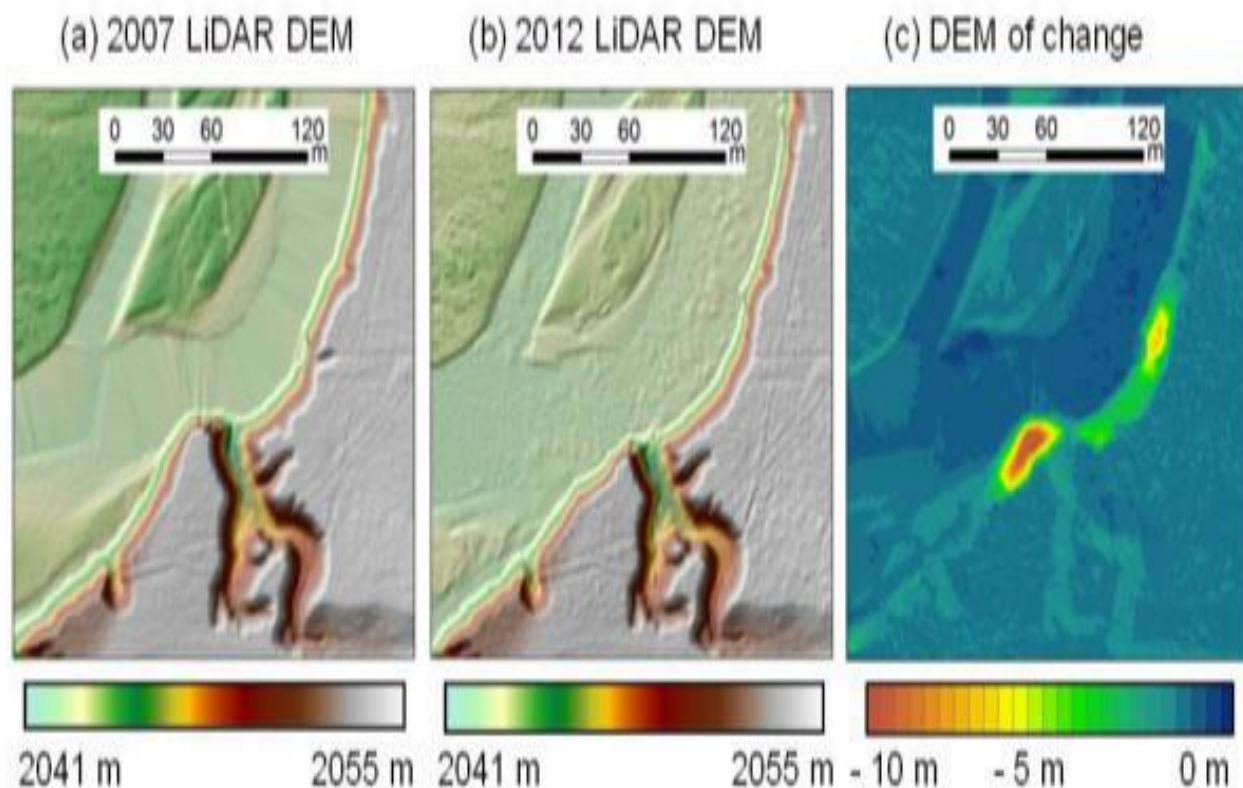


Figure 14. LiDAR topography from 2007 and 2012, with a DEM of difference highlighting erosion of the outer bank.

◆ MANAGEMENT IMPLICATIONS

could provide a powerful tool for assessment and monitoring of riverine resources throughout the region. The 2009 Craig Thomas Snake River Headwaters Act designated the river above Jackson Lake as a Wild River and the segment from Jackson Lake Dam to Moose, along with the Pacific Creek and Buffalo Fork tributaries, as Scenic Rivers in recognition of their ecological, aesthetic, and recreational value. This legislation provides these streams with protected status as part of the National Wild and Scenic Rivers System and ensures the free-flowing condition of these waterways. Along with this designation comes the task of determining how best to preserve this remarkable fluvial system.

Accordingly, the Park Service has set out to develop a new river management plan, which will involve documenting these unique natural resources and identifying effective strategies for their protection. Park managers are thus obligated to characterize the form and behavior of the Snake River, along with the associated habitat conditions and recreational opportunities. Our primary objective is to derive such information from remotely sensed data; this continuing project will thus directly inform the Park's

This ongoing study directly contributes to the Park Service's current management priorities and river management plan. Moreover, the techniques developed as part of this investigation could be applied to other streams throughout the Snake River headwaters, both those that have already been awarded Wild and Scenic status and others that might merit such consideration in the future. Although remote sensing clearly offers significant potential to facilitate a number of river-related applications, this potential has not been realized in practice, and the capabilities and limitations of a remote sensing-based approach must first be established. By demonstrating the utility of these methods, and also acknowledging their deficiencies, this study of the Snake River could lead to more widespread, effective use of remote sensing in river research and management.

◆ ACKNOWLEDGEMENTS

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sensed data were acquired through collaboration with the National Center for Airborne Laser Mapping, with Juan Fernandez-Diaz and Michael Sartori leading the project. We are grateful to Kathy Mellander, Susan O'Ney, Sue Consola-Murphy, and Linda Franklin of the National Park Service for their support of our study.

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SEDIMENT TRANSPORT AND BEDLOAD LITHOLOGY IN STREAMS OF THE TETON RANGE, WYOMING

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♦ ABSTRACT

The ability of streams to erode bedrock and transport sediments is controlled by discharge. Yearly snowmelt, bedrock, and nearby rockfall deposits influence the flow of water and the sediments available for transport. Discharge and bedload sediments were observed over two summers to understand the impacts of precipitation and lithology on five stream channels in the Teton Range. Discharge was higher and bedload clast sizes were larger when more snowfall fell in the preceding winter months. All streams were able to transport sand to small gravel sediments. The type of lithology observed in the bedload was mostly controlled by bedrock available throughout the entire catchment.

♦ INTRODUCTION

Stream erosion plays an important role in the evolution of mountain landscapes by incising into bedrock and transporting materials from talus or glacial till deposited on valley floors (Whipple et al., 2000; Kirby and Whipple, 2001). Recent investigations show that sediments carried by streams provide tools for streambed abrasion. Maximum erosion occurs when coarse-grained sediment is transported over partially exposed bedrock. Fine-grained sediments in streams (clay, silt, and sand) abrade channel beds less effectively because they are transported by suspension (Sklar and Dietrich, 2001). Therefore, larger clasts (gravel, pebbles, cobbles, and boulders) play a more important role in stream abrasion and incision. The mean and median grain sizes, as well as sediment volume, can quantify the potential incision efficiency in mountain streams (Tomkin et al., 2003; Torizzo and Pitlick, 2004).

Efficient erosion and downstream changes in channel geometry are mostly due to increasing discharge

during high flow or flood-like conditions (Leopold and Maddock, 1953). As discharge increases, streams are more likely to incise into the bedrock (Park, 1977). Mountain streams with steep, confined valleys and high colluvial input from adjacent hillslopes are likely to display different patterns of downstream channel geometry than those of lowland alluvial streams (Wohl, 1998), however these channels receive relatively little attention compared to those in more alluvial environments (Montgomery and Gran, 2001). Thirty percent of eroded sediment is transported through the length of the stream system to the mouth (Walling, 1983). Because the mineralogy or lithology of materials moved by streams can be compared to the bedrock sources to determine patterns of erosion, incision and transport in these channels can be evaluated.

The erosional efficiency of streams in the Teton Range was investigated by analyzing stream discharge, sediment sizes and clast lithology in five different watersheds. Bedload sediments were described by their size and lithology to determine how catchments vary in the materials they transport. Changes from upstream to downstream sediment transport in mountain streams were studied to provide more insight on downstream discharge and colluvial controls. The stream channels in this study were classified as mixed bedrock-alluvial channels, which are common in actively incising terrain (Howard, 1998).

STUDY AREA

The Teton Range in northwestern Wyoming runs 64 kilometers north to south and 24 kilometers east to west and is the youngest of the Rocky Mountains, dated at five million years. The geologic history of the Teton Range is marked by many events, including Cretaceous and Neogene faulting, Quaternary glaciation,

and volcanism associated with the nearby Yellowstone hotspot (Love et al, 2003).

Uplift began with the Laramide orogeny 80 to 55 million years ago (Roberts and Burbank, 1993). Basin and Range extension formed the Teton normal fault, and Quaternary movement has averaged 1.3 mm/yr (Pickering White et al., 2009). The western fault block is being uplifted and tilted westward. Greatest uplift is on the eastern edge and creates the asymmetrical mountain range with high peaks and steep mountain front along the eastern margin. The fault block east of the Teton Fault is subsiding, forming modern day Jackson Hole (Love et al., 1992).

Although the Teton Mountains are a young range, the rocks making up the core of the mountains are much older. Sedimentary, igneous, and metamorphic rocks can all be found in the range (Figure 1). In the catchments observed in this study, the oldest exposed rocks are Archean gneisses (Reed and Zartman, 1973) composed mostly of quartz, feldspar, biotite, and hornblende (Love et al., 2003). The backbone of the Teton Peaks is composed of Mount Owen Quartz Monzonite, which is a granitic rock containing 30-40% quartz, equal proportions (20-35%) of both potassium-rich and sodium/calcium-rich feldspar, 5% or less biotite and traces of muscovite (Reed and Zartman, 1973). Irregular intrusions of pegmatite contain crystals that are upwards of several centimeters to half a meter in diameter and contain the same feldspars found in the Mount Owen Quartz Monzonite plus muscovite, biotite and brown and red garnets (Love et al., 2003). The youngest Precambrian formations are black, fine to medium grained diabase dikes (Reed and Zartman, 1973; Love et al., 1992).

Sedimentary rocks aged 510 million to 90 million years are also present in several east-draining catchments (Craighead, 2006). One of the most notable sedimentary formations observed is the Gros Ventre Formation, which is subdivided into the Death Canyon Limestone, the Wolsey Shale, the Flathead Sandstone, the Gallatin Limestone, and the Park Shale units (Foster, 1947). Also included in the sedimentary stratigraphy of the Teton Range are the cliff-forming units, the Bighorn Dolomite and the Madison Limestone formations (Love et al., 2003).

The Cambrian Flathead sandstone is white, tan, brown, or maroon sandstone, with interbedded shale. The Gros Ventre formation consists of two shale members and a limestone member. The Death Canyon Limestone is blue, gray, brown or tan and the Gallatin Limestone is dark gray and mottled tan. The Bighorn

Dolomite is a light to dark gray, fine-grained dolomite (Love et al., 1992).

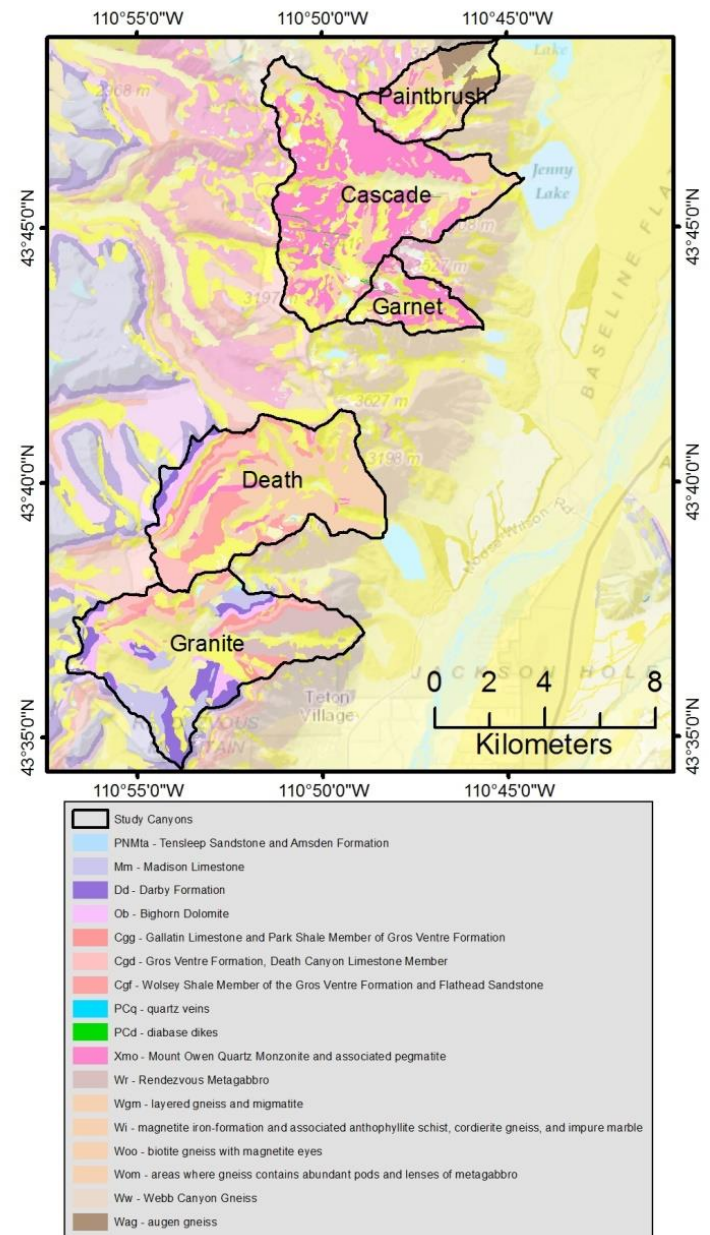


Figure 1. Geology of the Teton Range from Love et al. (1992). The geology units shown are limited to the bedrock observed in the 5 study catchments.

Glaciers in the Teton Range played an important role in shaping the landscape during two glacial episodes in the Quaternary period. The Bull Lake glaciation occurred between 160,000 to 130,000 years ago and the Pinedale glaciation began more than 30,000 years ago and lasted to 14,000 years ago. Evidence of these glacial episodes in drainage basins is preserved in moraines, U-shaped valleys, and polished rock faces.

Alpine glacial moraine deposits left behind in the Jackson Hole valley created natural dams that formed Phelps, Jenny, and Bradley lakes (Love et al., 2003).

Although the bedrock is old and resistant, joints and fractures create some weakness in the slopes. Fractured rock faces, temperature variations and freeze-thaw cycles cause the rocks to crack and detach, forming talus fans on canyon floors. Streams flowing over talus deposits transport these sediments to lakes in Jackson Hole (Love et al, 2003).

Precipitation controls stream discharge and sediment transport in the Teton Range because the water source of mountain streams is primarily snow melt, rain, and melting glacial ice. Estimates of precipitation in each Teton canyon were taken from a model using the parameter elevation regressions on independent slopes model (PRISM), which predicts the precipitation expected with increasing elevation. Foster et al. (2010) applied an algorithm based on point climate measures from a network of weather stations and a digital elevation model (DEM) to create a continuous grid of precipitation using a linear climate elevation regression function. Their model showed maximum precipitation values at the topographic highs of the range, and decreased in a bulls-eye pattern away from the highest peaks. The expected relationship between mean annual precipitation from this model and the mean watershed elevation is shown in Figure 2.

◆ **METHODS**

Five Teton streams were studied to determine the sediment sizes that are transported and bedrock units that are most easily eroded. Field observations included stream discharge, water surface slope, clast sizes, and clast lithology. Fieldwork was completed over the summers of 2011 and 2012. Data were collected at approximately the same time of year in both field seasons, between July 25-August 13 of 2011 and July 27-August 5 of 2012, to minimize error due to changes in seasonal weather. Major east-flowing drainage systems of the Teton Range were measured and included Paintbrush, Cascade, Garnet, Granite, and Death canyons. Streams were selected based on catchment area (10-43 km²), bedrock variability, and accessibility (Figure 3).

Channel cross-section areas, flow velocities and sediment sizes were collected at upstream and downstream locations in each watershed. The cross-section area was calculated using the Reimann sum method of integration. Flow velocity and depth were measured with an FP101 global flow probe. The area was

multiplied by velocity to calculate the total discharge. The slope of the water and bed surfaces was observed with a Laser Inc. Technology Trupulse 360°B laser rangefinder. At each sampling location, 50 clasts were measured in the field to determine the range of sizes within the stream channel. Ten clasts were chosen at random across the channel to determine the lithology of cobbles present. Sand and finer grains were collected by scooping sediment which had accumulated in the channel. Sediment samples were cleaned, dried and sieved to 0.002 mm, 0.05 mm, and 2 mm at Illinois State University. Mineral compositions of 50 randomly selected grains were observed under a microscope. A 32 ounce water sample was collected and filtered to measure suspended solids.

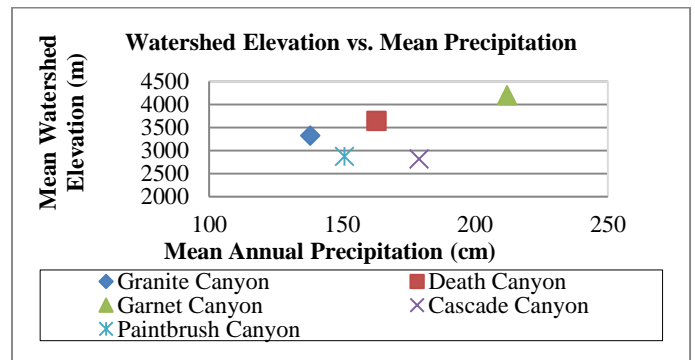


Figure 2. Mean annual watershed precipitation and mean watershed elevation created from data modeled in Foster et al. (2010).

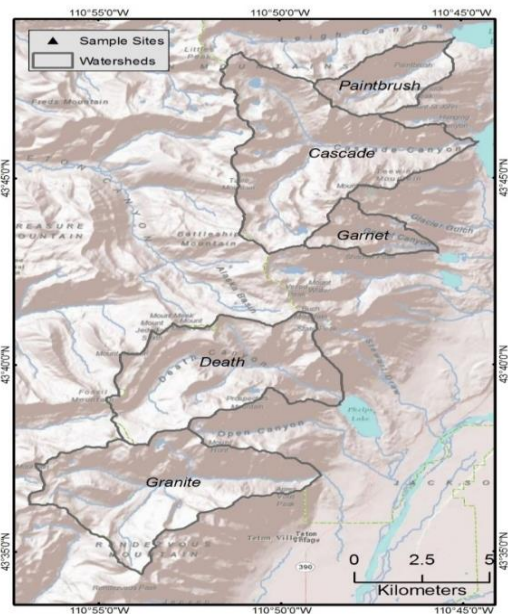


Figure 3. Watersheds studied and location of channel cross sections and sediment observations.

The largest particle size potentially carried by each stream was calculated based on basal and critical shear stresses. The basal shear stress, τ_b , is the force imparted on the streambed by moving water and was calculated with the equation:

$$\tau_b = \gamma_w * R * S$$

where γ_w is the specific weight of water (9800 N/m³), R is the hydraulic radius of water, and S is the slope of the water surface. Critical shear stress, τ_c , is the theoretical force required to pick up a grain of diameter (d) and was calculated by the equation:

$$\tau_c = \Theta_{cc} (\gamma_s - \gamma_w) d$$

where Θ_{cc} is the Shield's parameter for turbulent flow (0.044), γ_s is the weight density of the grain (26,000 N/m³), γ_w is the specific weight of water (9800 N/m³), and d is the grain diameter (m).

A comparison of shear stresses describes the sediment erosion and transport conditions in stream channels. If the basal shear stress were greater than the critical shear stress, then erosion, or entrainment, of the sediment grains would occur in the stream channel. If the basal shear stress were less than the critical shear stress then no erosion would occur and sediments would be deposited. The basal shear stress was set to equal the critical shear stress to solve for the maximum grain diameter carried by each stream.

A digital elevation model (DEM) and the Hydrology tools in ArcGIS 10.0 were used to define the flow network and watershed boundaries in the study catchments. A geologic map of Grand Teton National Park (Love et al., 1992) was used to calculate the area of each bedrock unit within each catchment. The stream cobble and sediment mineral compositions were compared to the mapped bedrock areas to determine the primary source of sediments.

◆ RESULTS

Discharge

Stream discharges for 2011 were 35% higher than 2012 (Table 1). Snowfall in the preceding winter and spring was also higher in 2011 than in 2012 (Table 2). At Teton Village, 238 inches of winter snowfall was observed in 2011, while only 108 inches of snowfall was recorded in 2012 (total of monthly snowfall from October to May for both years reported on Weather Warehouse website: <https://weather-warehouse.com>).

Table 1. Summary of discharges measured at each channel cross section.

Canyon	Location	2011 Discharge (m ³ /s)	2012 Discharge (m ³ /s)
Granite	Upstream	-	1.45
	Downstream	-	2.63
Death	Upstream	-	-
	Downstream	8.78	2.2
Garnet	Upstream	1.45	1.08
	Downstream	2.12	0.86
Cascade	Upstream	2.29	0.71
	Downstream	12.26	8
Paintbrush	Upstream	-	1.8
	Downstream	4.72	1.37

In all but one stream, discharge increased downstream. Granite Canyon showed an 81% increase in discharge from upstream to downstream. Garnet Canyon showed a 26-46% increase in stream discharge from upstream. The combined discharge from the north and south forks of Cascade Canyon was 6.22 m³/s in 2011, which increased 97% to 12.26 m³/s at the downstream location when the two forks had joined. In 2012, the combined discharge from the north and south forks of Cascade Canyon was 2.03 m³/s, which increased 294% to 8.0 m³/s at the downstream location. Paintbrush Canyon had a 31% decrease in stream discharge from upstream to downstream, thus being the only stream to have a lower discharge at the downstream location.

Table 2. Summary of winter snowfall preceding summer field seasons. Snowfall values from Weather Warehouse website: <https://weather-warehouse.com>.

Month	Snowfall		
	2010	2011	2012
January		45.4	27.8
February		20.4	29.2
March		44.4	10.6
April		31.5	3
May		2	0.5
June		0	0
July		0	0
August		0	0
September	0	0	
October	7.1	0.2	
November	36.3	22.3	
December	50.8	14.2	

Although yearly snowfall influenced stream discharge, we also recognize that the amount of snowmelt also may have varied with time of day; as temperatures warmed throughout the day, more snow melted and increased discharge. Observations were collected at the same time of the year (July 25-August 10) during this study to reduce seasonal uncertainties, however the time of day often varied.

Sediment Size

The clast sizes entrained by each stream were estimated from basal shear stress, critical shear stresses and the median, 25th percentile (Q1), and 75th percentile (Q3) sizes were modeled at each location (Figure 4). The maximum predicted D50 (50% of the clasts are equal to or smaller than this value) was 128 mm in the north fork of Cascade Canyon. The smallest predicted D50 was 19 mm in upper Garnet Canyon (Table 3).

Calculated and measured clast sizes were compared to determine how well the basal and critical shear stress calculations predicted sediment sizes that could be transported. Table 3 shows the predicted D50 clast sizes compared with the actual measured values at each sampling location and percent error of each. Predicted D50 sizes were all larger than the measured D50 sizes. The difference between the lowest D50 size was only 2 mm. Overall, at higher discharges, larger clasts (D50) were found in the streambed (Figure 5).

Table 3. Predicted (Pred) and measured (Meas) D50 clast sizes for each stream cross section. D50 % Error is the percent error between the equation-predicted and field measured clast sizes.

Canyon	Pred D50 (mm)	Meas D50 (mm)	D50 % Error
Lower Granite Canyon (2012)	45	38	17
Upper Granite Canyon (2012)	64	49	27
Lower Death Canyon (2011)	32	24	29
Lower Death Canyon (2012)	23	22	4
Lower Garnet Canyon (2011)	32	31	3
Upper Garnet Canyon (2011)	45	33	31
Lower Garnet Canyon (2012)	23	20	14
Upper Garnet Canyon (2012)	19	17	11
South Fork Cascade Canyon (2011)	32	26	21
North Fork Cascade Canyon (2011)	128	92	33
South Fork Cascade Canyon (2012)	23	18	24
North Fork Cascade Canyon (2012)	39	32	20
Lower Paintbrush Canyon (2011)	64	26	84
Lower Paintbrush Canyon (2012)	32	26	21
Upper Paintbrush Canyon (2012)	23	18	24

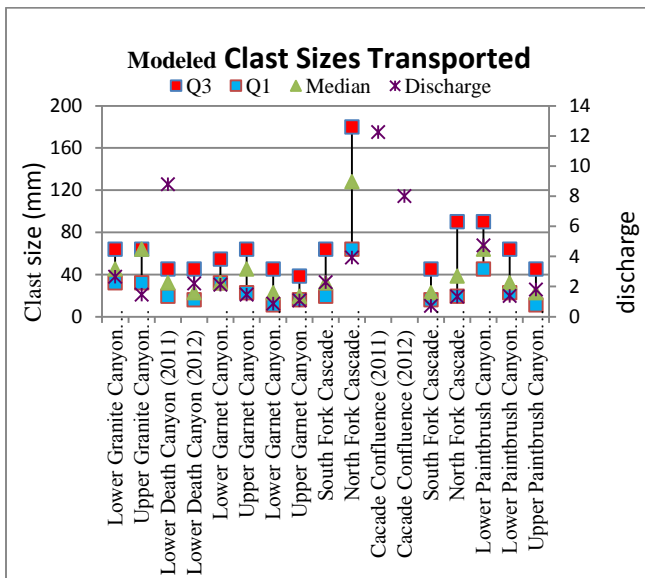


Figure 4. Stream discharge plotted with 25th percentile (Q1: 25% smaller), 75th percentile (Q3: 75% smaller) and median clast sizes.

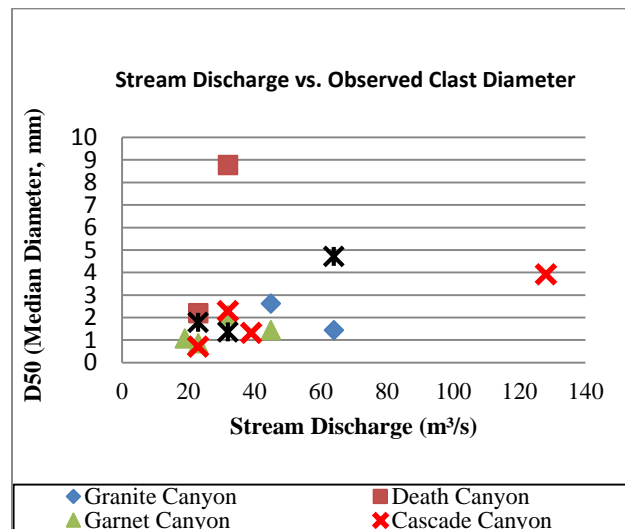


Figure 5. The relationship between stream discharge and measured clast diameters for both.

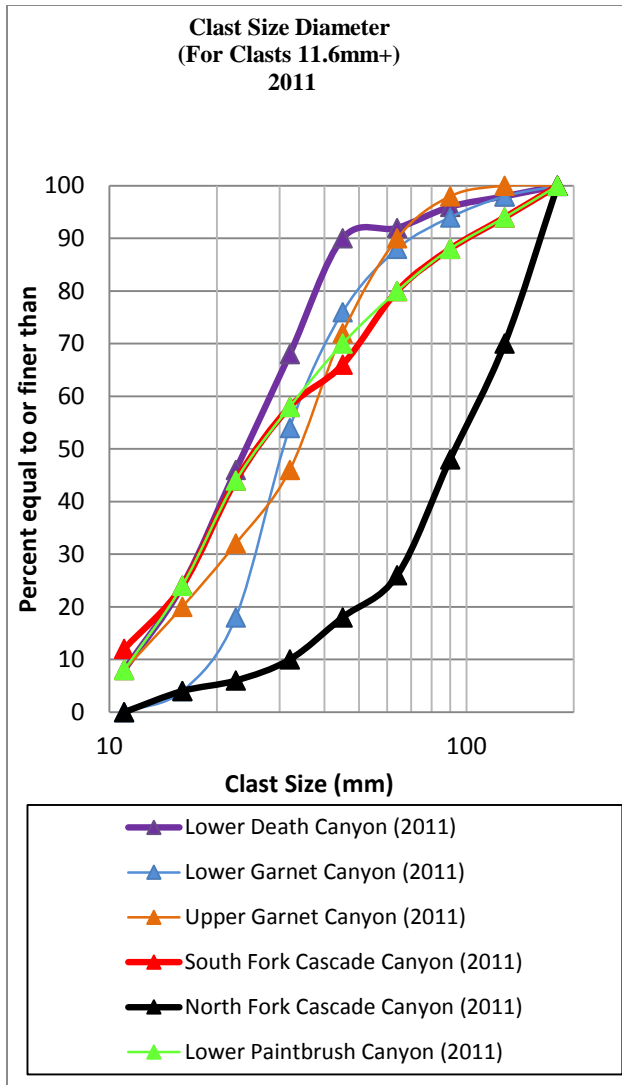


Figure 6. Cumulative sediment size curves for clasts equal to or greater than 11.6 mm in 2011. Bold lines represent larger watersheds.

Cumulative percent curves illustrate the bedload size distribution for clasts greater than 11.6 mm (Figures 6 and 7). In 2011, the north fork of Cascade Canyon had the largest clast sizes, with a measured value of 92 mm. Watershed size did not show a strong relationship to sediment size in the 2011 observations. The summary of sediment sizes observed in cross sections in 2012 shows a stronger trend of larger watersheds containing larger bedload clasts. Both upstream and downstream sample locations in Granite Canyon (D50 of 49 mm for Upper Granite Canyon and D50 of 38 mm for Lower Granite Canyon) and the north fork of Cascade Canyon (D50 of 32 mm) were the three locations with the largest clasts sampled in 2012. The stream showing the smallest clasts, Upper Garnet Canyon, had a D50 value of 17 mm.

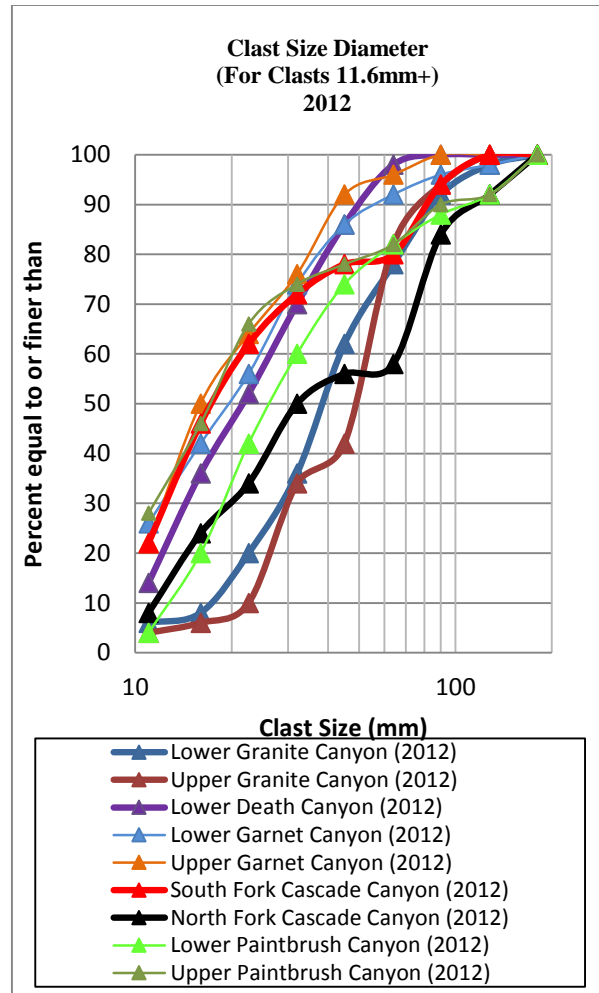


Figure 7. Cumulative sediment size curves for clasts equal to or greater than 11.6 mm in 2012. Bold lines represent larger watersheds.

Lithology

Primary bedrock units are comprised of granites, gneisses, and quartz monzonite with major sedimentary units in the southern end of the range (Granite and Death Canyons). In four of the five canyons that were observed, the primary bedrock composition was also the most frequently observed lithology in the active stream channel (Table 4 and Figure 8). In Paintbrush Canyon, more gneiss was mapped throughout the catchment, however, more quartz monzonite was observed in the stream. This observation may have been due to the similarities between the granitic textures in some bands of the gneissic rocks in parts of Paintbrush Canyon. Additional work will be done to look at a greater number of samples from each stream and investigate the source of minerals based on mineral properties and ages.

Table 4. Percentages of lithology observed in stream bedload and mapped as exposed bedrock. Bedrock measurements were estimated from the geologic map by Love et al. (1992).

Canyon	Location	Lithology percentages				
		Quartz Monzonite	Gneiss	Carbonate	Diabase or Metagabbro	Sandstone
Granite	Stream	40	0	60	0	0
	Bedrock	<1	6	64	20	10
Death	Stream	39	61			
	Bedrock	6	50	28	0	16
Garnet	Stream	77	23			
	Bedrock	69	30	0	1	0
Cascade	Stream	58	36		6	
	Bedrock	71	26	1	<1	1
Paintbrush	Stream	62	38			
	Bedrock	27	73	0	0	0

Carbonate rocks were most frequently observed in the Granite Canyon stream as was expected due to 64% of the mapped area containing limestone or dolomite. Although carbonate rocks were also mapped over a considerable area in Death Canyon (28%), no carbonate clasts were found in the Death Canyon stream, where stream clasts were primarily composed of gneiss and quartz monzonite. In Garnet, Cascade, and Paintbrush canyons the majority of clasts were granite, quartz monzonite, and gneiss. The minerals observed in the stream sediments were primarily quartz at every location both years. As was expected, a high percentage of quartz was observed in sediment samples because quartz is present in many of the mapped bedrock units and is resistant to weathering. The suspended solids collected from the water samples showed that there were more particles in suspension in all of the canyons in 2011 than in 2012, although concentrations were low in both years.

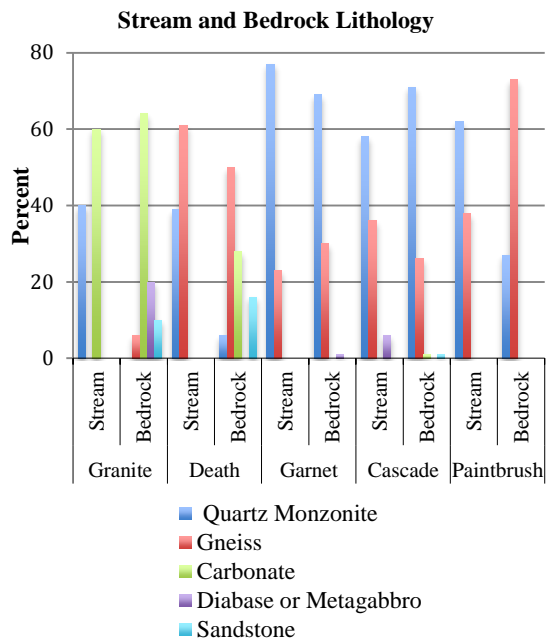


Figure 8. Distribution of lithologies observed in stream bedload and mapped bedrock units for each canyon.

◆ SUMMARY

The study of discharge in Teton streams allowed us to evaluate how watershed area, elevation, and annual precipitation influence materials transported and eroded within stream channels. Precipitation has a direct impact on the volume of water flowing through the stream channels in Grand Teton National Park. When annual precipitation increased, the streams during late summer flow carried a higher volume of water. High snowfall over the winter months in 2011 resulted in higher July-August stream discharges as compared to 2012, when snowfall was almost half as much as the previous year and discharges were much lower.

It was hypothesized that the highest precipitation watershed would have the largest clasts moving through the stream channel. In 2011, the north fork of Cascade Canyon had the largest clasts, while in 2012, Granite Canyon had the largest clasts. Cascade Canyon had the second highest precipitation as modeled by Foster et al., 2010 while Granite Canyon had the lowest precipitation of the five canyons. This shows that the watershed with the highest elevation and precipitation did not produce the stream with the largest clasts, but that watershed area was a bigger factor in determining clast size. Overall, the consistently larger clasts observed in 2011 indicates higher discharge related to late season snowmelt enhanced the ability of streams to carry gravels.

Although the predicted median sediment sizes are larger than the actual median sediment sizes, the values are similar. When graphically compared, a best-fit line indicates a positive correlation between actual and predicted sediment sizes (Figure 9). The error between the observed and predicted was highest in Paintbrush Canyon and the North Fork of Cascade Canyon where large boulders obstructed the stream near the cross section site. Nearby bridges may also have influenced the observed sediment sizes in Paintbrush and Death Canyon.

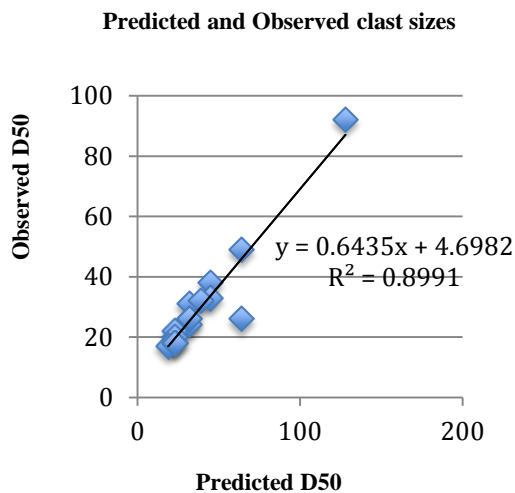


Figure 9. Clast sizes predicted from equations were compared to the clasts measured in the stream bedload. All predicted and stream observations from Table 3 are included in this graph.

In both years, the median clast sizes observed in the stream channels were pebble to cobble sized gravels. This indicates that fine debris deposited in the stream channel from rockfalls onto the valley floor can be moved throughout most of the observed catchments. This has important implications for studies using detrital minerals for analyses of erosion rates or patterns. Often detrital apatite, zircon, or quartz techniques require sampling sand sized sediments ranging from 63 micrometers to 2 millimeters. The results of this study indicate that the sediments of interest for detrital methods are moved, and are therefore likely to represent processes occurring throughout the entire catchment.

In most catchments, the lithology indicates a similar result related to the efficiency of the stream to transport sediments. The clasts used to observe lithology were typically cobble-sized or larger (minimum of ~64 mm). The primary bedrock lithology was frequently the dominant stream bedload lithology, however there were some exceptions. The large grains observed for lithology may have been more representative of the material

comprising local bedrock or nearby talus deposits. This may explain the higher concentration of quartz monzonite observed in Paintbrush Canyon and the lack of carbonate rocks in Death Canyon. The proximity of the stream to potential bedrock sources is also an important control on the distribution of carbonate rocks in Death Canyon. Many carbonate units are positioned above a ledge that does not interact with the active stream channel, therefore these rocks cannot be transported to the stream channel.

◆ ACKNOWLEDGEMENTS

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LOW NEUTRAL GENETIC DIVERSITY IN AN ISOLATED GREATER SAGE GROUSE (*CENTROCERCUS UROPHASIANUS*) POPULATION IN NORTHWEST WYOMING

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✦ ABSTRACT

Habitat loss is well recognized as an immediate threat to biodiversity. Depending on the dispersal capabilities of the species, increased habitat fragmentation often results in reduced functional connectivity and gene flow followed by population decline and a higher likelihood of eventual extinction. Knowledge of the degree of connectivity between populations is therefore crucial for better management of small populations in a changing landscape. A small population of greater sage-grouse (*Centrocercus urophasianus*) exists in northwest Wyoming within the Jackson Hole valley, including Grand Teton National Park and the National Elk Refuge. To what degree the Jackson population is isolated is not known as natural dispersal barriers in the form of mountains and anthropogenic habitat fragmentation may limit the population's connectivity to adjacent populations. Using 16 microsatellite loci and 300 greater sage-grouse samples collected throughout Wyoming and southeast Montana, significant population differentiation was found to exist among populations. Results indicated that the Jackson population was isolated relative to the other sampled populations, including Pinedale, its closest neighboring large population to the south. The one exception was a small population immediately to the east of Jackson, in which asymmetric dispersal from Jackson into Gros Ventre was detected. Both Jackson and Gros Ventre populations exhibited significantly reduced levels of neutral genetic diversity relative to other sampled populations. More work is warranted to determine the timing at which Jackson and Gros Ventre

populations had become isolated and whether it was primarily due to recent habitat fragmentation or more historic processes. Due to its small population size, continual monitoring of the population is recommended with the goal of at least maintaining current population size and, if possible, increasing suitable habitat and population size to levels recorded in the past.

✦ INTRODUCTION

Habitat degradation and fragmentation due to human mediated activities are considered primary factors contributing to global biodiversity decline (Sala et al. 2000; Fahrig 2003; Baillie 2004). As habitat is lost, populations become increasingly distant from each other leading to reduced gene flow and loss of genetic diversity through drift (Reed 2004; Frankham 2005; Ezard and Travis 2006; see also Johnson et al. 2003, 2004; Dixo et al. 2009; Delaney et al. 2010). This pattern is becoming increasingly pervasive throughout human inhabited environments with many species possessing isolated populations of various size and associated fitness related consequences (Westemeier et al. 1998; Madsen et al. 1999; Blomqvist et al. 2010; Fei et al. 2011). Isolated or peripheral populations may be more susceptible to environmental and demographic stochasticity due to factors limiting their distribution and other conditions such as minimal gene flow and small population size (e.g., Peterman et al. 2013). Therefore, these populations are of important conservation concern (Channell and Lomolino 2000) especially given that many isolated or peripheral populations often harbor unique genetic diversity

(Nielsen et al. 2001). Much work has focused on identifying recently isolated populations in an effort to help inform management and thereby mitigate potential fitness consequences that may contribute to local extirpation and ultimately species extinction (Kyle and Strobeck 2002; Segelbacher et al. 2003; Ratkiewicz et al. 2012; also see Henle et al. 2004; Prevedello and Vieira 2010).

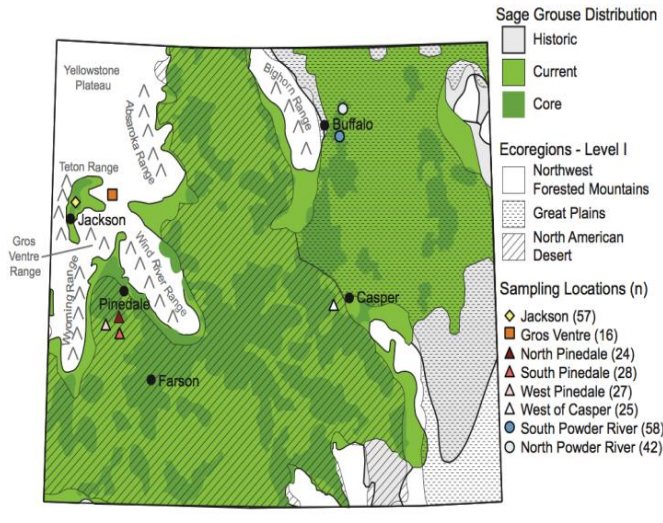
Sagebrush-steppe habitat in North America is one example where dramatic land-use changes over the past century have resulted in the isolation and decline of many sagebrush dependent species (Knick et al. 2002, 2003; Rowland et al. 2011). The sagebrush biome (*Artemisia* spp.) was once a dominant habitat type across much of northwest United States, but has been recently altered by human-mediated practices including agriculture, livestock grazing, infrastructure development, energy exploration and extraction for oil and gas, invasive species (e.g. cheatgrass, *Bromus tectorum*), and changes in fire regime (Knick and Connelly 2011). Many of these factors have a cumulative effect, resulting in sagebrush habitat fragmentation, degradation, and loss. Accordingly, animals considered sagebrush obligates, including Brewer's sparrow (*Spizella breweri*), pygmy rabbit (*Brachylagus idahoensis*), and pronghorn (*Antilocapra americana*), have responded negatively to habitat alteration and fragmentation and are of increasing conservation concern due to decreased abundance (Baker 1976; Knick and Rotenberry 2002; Rowland et al. 2006). For example, the pygmy rabbit has experienced a significant decline in population size and was listed as an Endangered Species in 2003 (USFWS 2003). Likewise, energy development activities have been shown to displace mule deer (*Odocoileus hemionus*), and increasing concern exists that the removal and disruption of migration corridors for mule deer and pronghorn may have negative impacts on their long-term population sustainability (Sawyer et al. 2005, 2006).

The greater sage-grouse (*Centrocercus urophasianus*, hereafter referred to as sage-grouse) is a sagebrush obligate that has also experienced range-wide population decline and contraction and now occupies approximately 56% of its pre-European settlement distribution (Schroeder et al. 2004). Populations of this species have become increasingly fragmented and isolated and, consequently, have received widespread political and conservation attention (Oyler-McCance et al. 2005; Walker et al. 2007; Aldridge et al. 2008). In 2010, the United States Fish and Wildlife Service determined that sage-grouse deserved protection under the Endangered Species Act, yet protection was precluded due to higher priority cases. It is currently a

candidate for protection under the Endangered Species Act with a final decision due by the end of fiscal year 2015.

Recent work investigating connectivity among sage-grouse populations throughout their entire geographic distribution identified a total of ten distinct population-level clusters based on genetic methods (Oyler-McCance et al. 2005). The majority of these clusters, however, were explained largely by isolation by distance (IBD) suggesting connectivity among the primary core regions (i.e., southeast Oregon, northeast Nevada, southern Idaho and much of Wyoming and eastern Montana; Oyler-McCance et al. 2005; see also Bush et al. 2011). Several small, isolated populations were also identified, located on the periphery of the species' current range in Colorado, Utah, Washington, and on the California/Nevada border, some of which had reduced genetic diversity compared to populations sampled in the core of the species' range (Oyler-McCance et al. 2005). Many of these isolated populations have resulted from recent habitat fragmentation (i.e. see Schroeder et al. 2004; Oyler-McCance et al. 2005). As sagebrush habitat is lost, isolated populations will continue to decline in size and lose genetic diversity by genetic drift, further reducing population viability and increasing risk of extirpation (Frankham 2005), a common theme among lekking grouse in general (i.e., extinction vortex; Soule and Mills 1998).

The primary objective of this study was to assess the degree of isolation and level of genetic diversity of a relatively small sage-grouse population located in the Jackson Hole valley of northwest Wyoming (herein referred to the Jackson population). The current Jackson sage-grouse population is estimated to be between 300 and 500 individuals, existing primarily on protected federal land (Grand Teton National Park and the National Elk Refuge) with an area of approximately 9,500 hectares of sagebrush habitat (B. Bedrosian, unpubl. data; see also Garton et al. 2011). To what degree this population is isolated from surrounding sage-grouse populations is not known, but potential dispersal barriers do exist surrounding this population, including forested mountains to the west, east and southeast, the city of Jackson to the south and Yellowstone plateau with more forested high elevation habitat to the north (Figure 1). Furthermore, recent anthropogenic habitat changes and increasing human presence (i.e., development and park visitation rates) have occurred in areas immediately adjacent to Jackson, potentially increasing the distance to larger sage-grouse populations to the south (i.e., Sublette County). This is Figure 1. Approximate locations of sage-grouse populations sampled throughout Wyoming with sample size in



parentheses. A population in southeast Montana was also sampled ($n=23$; not shown on map). Historic, current, and core sage-grouse distributions indicated in grey, light and dark green, respectively (adapted from Schroeder et al. 2004 and from the Sage-Grouse Core Management Areas Version 3 Map, see http://wyofile.com/wp-content/uploads/2011/08/sg_coreareas.jpg). Northwest Forested Mountains, North American Desert, and Great Plains level I ecoregions indicated with blank, striped, and dashed patterning, respectively (also see Olson et al. 2001 and ftp://ftp.epa.gov/wed/ecoregions/cec_na/NA_LEVEL_1.pdf). Major mountain ranges and geographic features near Jackson indicated in grey.

of concern because the current distance to the nearest sage-grouse population is much greater than the species' average dispersal distance (Knick and Connelly 2011).

Telemetry studies have not recorded any Jackson sage-grouse dispersing to other locations (B. Bedrosian, unpubl. data, Holloran and Anderson 2004). Thus, evidence suggests that current barriers to dispersal, whether natural or anthropogenic, may be sufficient to prevent gene flow between the Jackson sage-grouse population and other populations in Wyoming. Depending on current levels of genetic diversity and connectivity, the Jackson sage-grouse population may warrant immediate management to prevent its extirpation.

◆ METHODS

Tissue collection and DNA extraction

Blood samples were collected from yearling and adult sage-grouse over a five year period (2005-2010) between March and May from eight geographic locations in Wyoming and one in southeastern Montana (Table 1, Figure 1). Samples were collected from

Jackson Hole ($n = 57$) and Gros Ventre ($n=16$; Teton County), from three locations near Pinedale (Sublette County) designated north ($n = 24$), south ($n = 28$), and west ($n = 27$) Pinedale, west of Casper ($n = 25$; Natrona County), and in Powder River Basin east of Buffalo (Johnson County) designated north ($n = 42$) and south ($n = 58$) Powder River. Additional samples were collected in southeast Montana ($n = 23$; Carter County) and designated SE Montana. DNA was extracted from a total of 300 samples using the DNeasy Blood and Tissue Kit following manufacturer's protocols (QIAGEN Inc.).

Genotyping

Seventeen microsatellite loci were chosen based on previous sage-grouse population genetic studies (Oyler-McCance et al. 2005; Bush et al. 2011). Microsatellite loci were originally developed for greater sage-grouse (SGCA11.2, Oyler-McCance et al. 2011; reSGCA5, reSGCA6, and reSGCA9, Oyler-McCance pers. comm.), Gunnison sage-grouse (*Centrocercus minimus*; SGMS06.4, SGMS06.6, SGMS06.8, MSP7, MSP11, MSP18; Oyler-McCance and St. John 2010), capercaillie (*Tetrao urogallus*; TUD3, TUT3, TUT4, Segelbacher et al. 2000) and black grouse (*Tetrao tetrix*; TTD6, Caizergues et al. 2001; BG6, BG14, Piertney and Höglund 2001; TTT3, Caizergues et al. 2003). SGMS06.6 was a trinucleotide repeat and SGMS06.4, SGMS06.8, BG6, BG14, TUT3, TUT4, and TTT3 were tetranucleotide repeats; all remaining loci were dinucleotide repeats.

Polymerase chain reactions (PCR) were optimized and modified slightly from previously published methods that described protocols for each locus. A fluorescently labeled forward primer and an unlabeled reverse primer were used in PCRs. Each reaction was performed in 10 μ L final volume with final concentrations of 100 μ M each dNTP, 1x PCR buffer, and 0.1 μ L (0.5 units) GoTaq Flexi DNA polymerase (Promega). A final concentration of 1.0 mM of each primer was used for SGMS06.4, SGMS06.8, MSP7, MSP18, and SGCA11.2 and 0.25 mM for the remaining loci. $MgCl_2$ concentrations ranged from 1.0mM (SGMS06.8) to 1.5mM (SGMS06.4, MSP7, MSP18, and SGCA11.2) and 2.25 mM (remaining loci) per PCR reaction. Thermal profiles for all loci except TTD6 consisted of 2 min at 94°C, 35 cycles of 30 s at 94°C, 30 s at the specified annealing temperature described elsewhere (Segelbacher et al. 2000; Piertney and Höglund 2005; Oyler-McCance and St. John 2010; Oyler-McCance et al. 2011) with the exception of SGMS06.4, SGMS06.8, and TTT3 (59.9°C, 55.4°C and 58°C, respectively), and 30 s at 72°C, and a final 5 min extension at 72°C. The thermal profile for TTD6 followed that described in Caizergues et al. (2001). Each

amplified product was genotyped using an ABI 3130xl Genetic Analyzer and analyzed with the program GeneMarker v.1.6 (Soft Genetics, LLC.).

Statistical Analyses

Genetic diversity. -- Microsatellite genotypes were tested for linkage disequilibrium and departure from Hardy-Weinberg Equilibrium (HWE) within each population and locus using the program GDA v. 1.1 (Lewis and Zaykin 2001). Sequential Bonferroni corrections were used to correct for multiple simultaneous comparisons (Rice 1989). Mean number of alleles per locus (A), observed (H_o) and expected (H_e) heterozygosity, and inbreeding coefficient (f) were calculated using GDA, and allelic richness (AR) was estimated using FSTAT v. 2.9.3.2 (Goudet 1995). AR provides an estimate of allelic diversity that controls for differences in samples size (Leberg 2002).

To assess genetic variability among sampling locations, we compared AR , H_o , or H_e using a one-way analysis of variance (ANOVA) on ranked data, blocked by locus in order to control for interlocus variation ($\alpha=0.05$; SAS 9.3, SAS Institute, Cary, NC, USA). Significant findings were further analyzed using an *a posteriori* Student-Newman-Keuls multiple comparison test on ranked data to determine groups with means that did not significantly differ from each other. Values for f were considered significant if their 95% confidence interval as calculated with GDA did not overlap with zero.

Population connectivity.-- Principal Coordinate Analysis (PCoA) implemented in the Excel-based genetic analysis program GenAIEx v. 6.5 (Peakall and Smouse 2006) was used to visualize whether any patterns were observed that corresponded with sample location. The genetic distance (GD) matrix used in the PCoA was calculated using the *Distance* option (Peakall and Smouse 2006). One PCoA was conducted that included all populations, and two additional PCoAs were conducted corresponding to the identified clusters from STRUCTURE (see below; see also Figure 2).

To assess genetic differentiation between sampled sage-grouse populations, pairwise F_{ST} values were calculated following Weir and Cockerham (1984) as implemented in Arlequin v. 3.11 (Excoffier et al. 2005). Differences in population structure between sampling locations were tested using 1000 permutations among populations with Fisher's exact test. In addition, the Bayesian method of Pritchard et al. (2000) as implemented in STRUCTURE v. 2.3.4 was used to identify the most likely number of genetic clusters (K) among sampled individuals. This method identifies genetically distinct clusters based on maximizing Hardy-Weinberg equilibrium and linkage equilibrium among samples. Each simulation from $K=1$ to 10 was performed 20 times using a burn-in of 100,000 followed by 500,000 iterations while allowing for admixture, an individual α for each cluster, and a model of correlated allele frequencies that did not include prior information on population origin (see Falush et al. 2003). STRUCTURE was run to determine the most likely number of clusters for all populations.

Table 1. Measures of mean nuclear microsatellite genetic diversity for 16 loci for sage-grouse populations in Wyoming and southeast Montana. n , sample size; A , mean number of alleles; AR , allelic richness; H_e , expected heterozygosity; H_o , observed heterozygosity; f , inbreeding coefficient; N_e , effective population size. Letters as subscripts for AR , H_o and H_e indicate groups that are not significantly different ($\alpha = 0.05$).

Locality	n	A	AR	H_o	H_e	f	N_e (95% CI)
Jackson	57	7.0	6.1 _c	0.685 _b	0.732 _{bc}	0.065*	91 (68-131)
Gros Ventre	16	5.5	5.5 _c	0.660 _b	0.695 _c	0.052	21 (15-32)
North Pinedale	24	9.7	8.8 _{ab}	0.794 _a	0.806 _a	0.015	infinite (232-infinite)
South Pinedale	28	11.2	9.4 _a	0.779 _{ab}	0.807 _a	0.036	960 (205-infinite)
West Pinedale	27	10.5	9.1 _a	0.794 _{ab}	0.805 _a	0.013	infinite (2043-infinite)
West of Casper	25	9.8	8.5 _{ab}	0.780 _a	0.790 _a	0.013	infinite (-439-infinite)
South Powder River	24	9.6	7.7 _b	0.754 _{ab}	0.765 _{ab}	0.014	215 (193-infinite)
North Powder River	58	9.6	7.6 _b	0.748 _{ab}	0.774 _{ab}	0.034*	87 (71-111)
SE Montana	23	8.9	8.1 _{ab}	0.755 _{ab}	0.779 _a	0.03	188 (97-1543)

* inbreeding coefficient is significantly different from zero.

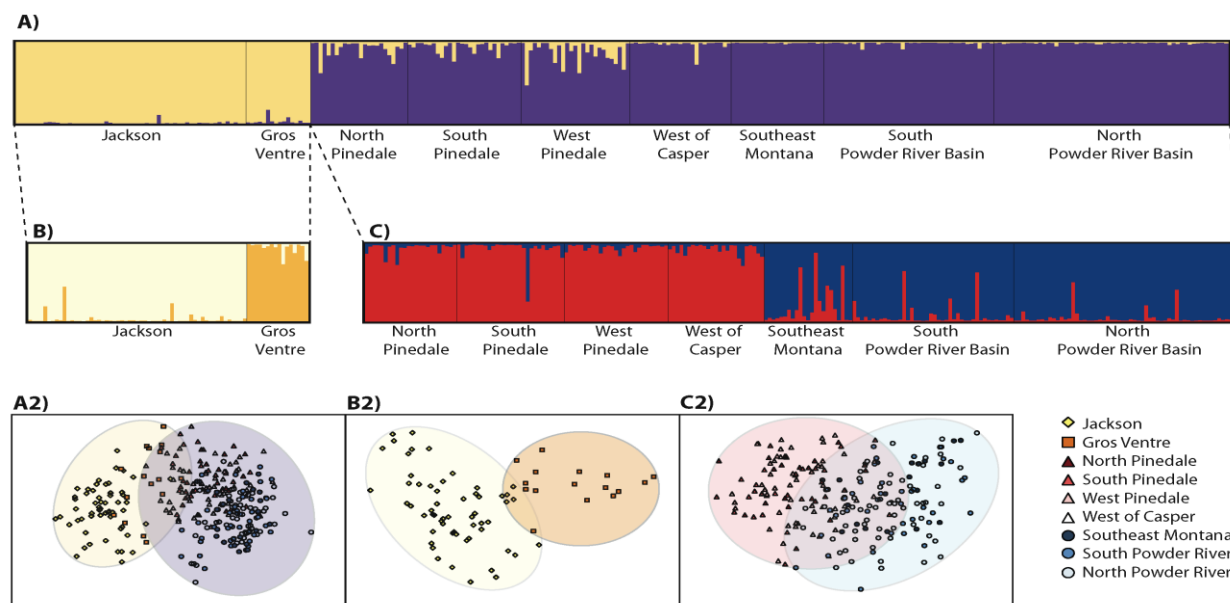


Figure 2. Bayesian clustering of sage-grouse using STRUCTURE based on 16 microsatellite loci in (A) eight sampling locations throughout Wyoming and one in Montana, (B) Jackson and Gros Ventre only, and (C) Pinedale, Casper, Powder River, and Montana sampling locations only. Each color represents a distinct cluster. Principal coordinate analysis (PCoA; A2, B2 and C2) corresponds to each of the sampling strategies used with STRUCTURE (A, B, and C, respectively).

Additional STRUCTURE analyses were performed to determine if further population structure existed within each of the initially identified clusters. STRUCTURE was also run with the exclusion of the Powder River and Montana populations to determine the relationship between Jackson, Gros Ventre, and Pinedale populations. The web-based program STRUCTURE HARVESTER v. A.1 (Earl and vonHoldt 2012) and the Evanno ΔK method (Evanno et al. 2005) were used to determine the mostly likely number of genetically distinct clusters (K). The program CLUMPP v. 1.1.2 (Jakobsson and Rosenberg 2007) was used to compile replicate runs results from STRUCTURE, and the program DISTRUCT v. 1.1 was used to visualize results (Rosenberg 2007).

Several modules within BAPS v. 5.3 (Corander et al. 2008b) were used as an additional method to identify genetic structure among sample locations. We ran ‘population mixture analysis’ with clustering of individuals with and without spatial coordinate information. Spatial information allowed the program to assign a non-random distribution based on biologically relevant population information thereby allowing for increased power to detect population structure (Corander et al. 2008b). We also ran population admixture analysis based on mixed clustering (Corander and Marttinen 2006; Corander et al. 2008a). Each module was run for $K=1$ to 10.

Correlations between genetic similarity (M) and geographic distances among populations (i.e. isolation by distance, IBD) were evaluated using the program Isolation By Distance Web Service v. 3.23 (IBDWS; Jensen et al. 2005). The program performs a Mantel test with pairwise matrices of geographic distance and Slaktkin’s (1993) measure of similarity, $M=[(1/FST)-1]/4$. Significance of IBD was tested with a Mantel procedure (10,000 permutations). Geographic distances between each population were measured using Google Earth.

To estimate the rates and direction of recent migration among populations, the Bayesian method for multilocus genotype data, BAYESASS v 3.0.3, was implemented (Wilson and Rannala 2003). Because simulation studies show that the method’s accuracy decreases with increased numbers of populations analyzed (Faubet et al. 2007), final analyses were conducted after combining sampling locations into four populations according to results obtained from STRUCTURE (see below). Specifically, data for the Pinedale and Casper locations were clustered into a single population, data for the Powder River/Montana locations were clustered into a single population, and Jackson and Gros Ventre were included as independent populations. Mixing parameters were adjusted according to the user’s manual to obtain acceptance rates between 20-60%. Specifically, default delta values for migration rates were kept at 0.10, while delta values for allele frequencies and inbreeding were

0.30. The program was performed with a burn-in of 7.0×10^6 generations, 2.7×10^7 iterations, and sampling frequency of 1000. To ensure consistent estimates, ten runs were conducted with different seed numbers. A rough 95% credible set around the posterior mean was calculated using the provided mean and standard deviation according to the user's manual.

Effective population size. -- Estimates of effective population size (N_e) were calculated for each population using the linkage disequilibrium method as implemented in LDNe v. 1.31 (Waples and Do 2008). Alleles with frequencies <0.02 were excluded (Waples 2006), and 95% confidence intervals for N_e were obtained using the jackknife option (Waples and Do 2008).

◆ RESULTS

Genetic diversity measures

All loci were polymorphic with a range of 2 to 24 alleles per locus in each population. After adjusting for multiple comparisons, the majority of loci possessed no significant deviations from HWE or showed signs of linkage. Locus TUD3, however, showed significant heterozygote deficiency in four populations (Jackson, North Pinedale, West Pinedale, and Casper), and was excluded from all subsequent analyses.

Significant differences in AR , H_o , and H_e were observed between sampled sage-grouse populations (Table 1). Overall, the Pinedale and Casper populations exhibited the highest measures of neutral genetic diversity, SE Montana and each of the Powder River populations possessed intermediate

levels, and Jackson and Gros Ventre had the lowest diversity values. Significant inbreeding coefficients (f) were observed for the Jackson and North Powder River Basin populations, while all other populations were not significantly different from zero.

Analyses of population structure

Multiple methods indicated that Jackson was isolated from all other sampled sage-grouse populations. The PCoA showed limited differentiation among the majority of sampled sage-grouse populations with the exception of the Jackson population, which formed a separate distinct cluster, and to a lesser degree the Gros Ventre population, in which approximately half the individuals clustered with Jackson and the remaining clustered in an overlapping zone between Jackson and the other sampled populations (Figure 2). When all populations were analyzed together, the first three coordinates accounted for 30.9, 15.8, and 14.9% of the variation, respectively.

Pairwise F_{ST} values showed evidence of population differentiation among sampled locations with the highest values observed between comparisons with Jackson (range: 0.070-0.111) and also Gros Ventre (range: 0.073-0.109; Table 2). Pairwise F_{ST} values were significant ($\alpha = 0.001$) for all populations except those between areas within Pinedale and between North Pinedale and the Casper population (Table 2).

Results from STRUCTURE also indicate that Jackson and Gros Ventre were significantly differentiated from all other sampled locations, with $K=2$ as the most likely number of genetic clusters when all nine sampling locations were analyzed as a

Table 2. Population pairwise F_{ST} comparisons based on 16 asterisk microsatellite loci. *, $P < 0.001$.

	Jackson	Gros Ventre	North Pinedale	South Pinedale	West Pinedale	West of Casper	S Powder River	N Powder River
Gros Ventre	0.088*	-						
North Pinedale	0.073*	0.084*	-					
South Pinedale	0.084*	0.079*	0.004	-				
West Pinedale	0.070*	0.073*	0.007	0.006	-			
West of Casper	0.093*	0.109*	0.009	0.021*	0.021*	-		
S Powder River	0.101*	0.104*	0.025*	0.034*	0.035*	0.035*	-	
N Powder River	0.103*	0.103*	0.027*	0.039*	0.036*	0.030*	0.008*	-
SE Montana	0.111*	0.107*	0.033*	0.037*	0.040*	0.046*	0.019*	0.023*

Significant values ($\alpha < 0.001$) are indicated by an asterisk.

single dataset (Figure 2). Specifically, Jackson and Gros Ventre formed a single cluster, and individuals from the remaining sampling locations formed the second cluster (see Figure 1). Within each cluster, further substructure was also observed, specifically between Jackson and Gros Ventre ($K=2$) and between Powder River Basin/Montana and Pinedale/Casper ($K=2$; Figure 2) when analyzed separately between Jackson and Gros Ventre ($K=2$) and between Powder River Basin/Montana and Pinedale/Casper ($K=2$; Figure 2) when analyzed separately.

Analysis with BAPS confirmed previous results that the Jackson population was isolated from other sampled populations. This result was consistent regardless of inclusion of spatial information or admixture in the model. When spatial information was excluded from the model, four main clusters were identified that corresponded with Jackson, Gros Ventre, Pinedale/Casper, and Powder River/SE Montana. When spatial information was included, two clusters were identified with Jackson clustering separately from all other populations, including Gros Ventre. When admixture was included, three main clusters were identified, with Jackson and Gros Ventre forming a single cluster, and Pinedale/Casper and Powder River/SE Montana forming the remaining two clusters.

Isolation-by-distance analyses

Using microsatellite data from all sampled locations, there was a significant relationship between geographic distance (km) and log genetic similarity ($r^2 = 0.175$, $P = 0.025$; Figure 3). However, all pairwise comparisons with Jackson and Gros Ventre possessed relatively low levels of genetic similarity regardless of geographic distance (Figure 3; see also Table 2). This

was further shown when Jackson and Gros Ventre were excluded from the analysis, by showing a stronger IBD relationship ($r^2 = 0.606$, $P = 0.001$; Figure 3).

Contemporary migration

Based on estimates from BAYESASS, a high proportion of individuals were derived from their own populations (> 0.96) for all clusters except Gros Ventre (0.82; Table 3). Accordingly, recent immigration rates among the majority the four clusters were low ($m < 0.03$) with the exception that a moderate portion of the individuals sampled in Gros Ventre were migrants derived from Jackson ($m = 0.10$).

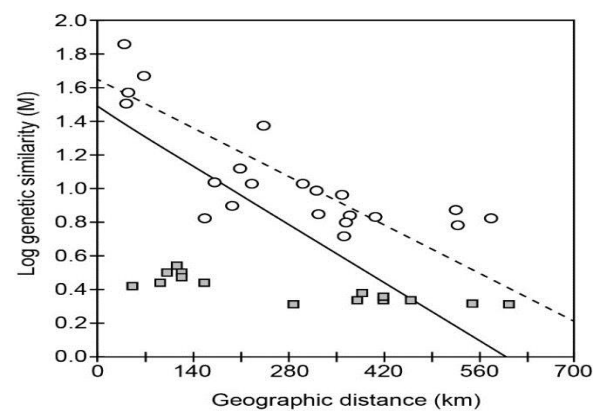


Figure 3. Analysis of isolation by distance (IBD) for microsatellite loci. Levels of log genetic similarity (M) are plotted against geographical distances (km) for pairwise comparisons of all nine sampled locations (solid line; $r^2 = 0.175$, $P = 0.025$) and all locations except Jackson and Gros Ventre (dotted line; $r^2 = 0.606$, $P = 0.001$). Pairwise comparisons including Jackson and Gros Ventre are shown with a grey square. P -values represent significance of IBD using Mantel's test (10,000 permutations).

Table 3. Migration rates among greater sage-grouse populations using the program BAYESASS. Values shown are the means of the posterior distributions of m , the migration rate into each population, and their respective 95% credible set in parentheses. Values along the diagonal (in bold) are the population of individuals derived from the source population each generation. Migration rates ≥ 0.100 are underlined. Populations are based on results from STRUCTURE with Pinedale/Casper and Powder River/SE Montana (MT) identified as separate populations.

Migration into:	Migration from:			
	Jackson	Gros Ventre	Pinedale/Casper	Powder R/SE MT
Jackson	0.983 (0.964-1.002)	0.006 (-0.006-0.018)	0.006 (-0.005-0.016)	0.006 (-0.005-0.016)
Gros Ventre	<u>0.100</u> (0.002-0.198)	0.865 (0.763-0.966)	0.018 (-0.016-0.052)	0.017 (-0.015-0.049)
Pinedale/Casper	0.006 (-0.004-0.015)	0.011 (-0.005-0.027)	0.963 (0.933-0.992)	0.021 (-0.004-0.046)
Powder R/SE MT	0.003 (-0.003-0.008)	0.003 (-0.003-0.009)	0.006 (-0.003-0.016)	0.988 (0.976-1.000)

Effective population size

Effective population sizes varied among sampled populations (Table 1). Jackson, Gros Ventre,

and North Powder River populations had relatively small N_e (i.e. < 100 , upper 95% CI < 140 individuals), while the remaining sampled populations were of large size with some exceeding the ability of the method to estimate N_e accurately and identified as infinity (Table 1; see Waples, 2006)

◆ DISCUSSION

Significant population genetic differentiation exists between Jackson and sampled sage-grouse populations in Wyoming and SE Montana, including those in close geographic proximity to Jackson (i.e., Pinedale and, to a lesser extent, Gros Ventre; Figure 2), while the remaining populations appear to show an overall IBD pattern of population structure similar to other studies investigating sage-grouse population connectivity using genetic methods (Oyler-McCance 2005; Bush et al. 2011; Figure 3). These results have important implications for the future management of sage-grouse in northwest Wyoming. The lack of genetic connectivity, coupled with small N_e , and low genetic diversity, suggest that Jackson and Gros Ventre may require immediate attention to prevent local extinction; however, depending on the timing of isolation (pre- vs. post-European settlement), differing management strategies are required for securing a long-term viable population.

In 1948 and 1949, a total of 359 sage-grouse (269 adults and 90 juveniles) were transported into the Jackson Hole valley from Eden Valley, WY (Sweetwater County), ca. 35km south of the south Pinedale sampling area (Patterson 1952). At the time, Patterson estimated a total population size of ca. 500 individuals based on total maximum lek counts. Lek counts collected during the present study period were approximately half as compared to lek counts collected by Patterson (1952). Estimates from 1950 and 1951, derived from band sightings of relocated grouse, suggested that 9.5% and 11% of the strutting birds had been relocated to Jackson Hole, respectively (Patterson 1952). Patterson suggested that few adults established in relocated areas, whereas released juveniles regularly established in the second season following their relocation. No systematic surveys or estimates were produced to estimate the percentage of relocated females ($n=95$) that bred. Our results suggest that either the relocated birds did not enter the effective breeding population or that the strength of genetic drift was sufficient to change the allele frequencies of the Jackson population relative to other populations within the past 60 years. Given the degree of genetic differentiation between Jackson and the surrounding regions, it is also possible that the Jackson

population has developed morphological or behavioral differences that resulted in the relocated birds being precluded from breeding, as has happened with the divergence of plumage and vocalizations in Gunnison sage-grouse from greater sage-grouse (Young et al. 1994). More data are needed to elucidate any differences in appearance, sound, or strutting behavior between populations.

In other areas, relocation has been used as a management tool to help boost genetic diversity, such as for sage-grouse populations in Utah (Baxter et al. 2008, 2013) and California (Bell and George 2012; see also Reese and Connelly 1997) and other lek-breeding species such as greater prairie-chicken (*Tympanuchus cupido pinnatus*) in Illinois (Westemeier et al. 1998). However, despite a large number of sage-grouse being relocated into Jackson from a larger population sixty years ago, the contemporary Jackson population is isolated, suggesting that the population may require supplementation indefinitely for long-term management of this population if it remains of small size similar to its current population size. For species with similar life history requirements that are also in decline, such as the greater prairie-chicken, translocation of birds into small isolated populations have caused initial increases in genetic diversity and fitness (i.e., hatching successes; Bouzat et al. 2009); however, in order to produce a self-sustaining population, long term management goals require an increase in habitat connectivity, quantity, and quality (Bouzat et al. 2009). This is likely the case with small recently isolated sage-grouse populations as well.

To what degree recent changes in the landscape near Jackson and surrounding areas have influenced sage-grouse dispersal patterns in northwest Wyoming is not known, but human mediated reduction in connectivity to the large core population in Pinedale may have contributed to the isolation detected in the current study. There is evidence to suggest that other species' dispersal and migration patterns to and from Jackson Hole have been affected over a similar time period. For example, a large annual historic elk migration event once extended through Jackson to southwest Wyoming during the fall and winter, but became restricted north of Jackson by the end of the 19th century to an area that is now designated as the National Elk Refuge largely due to an expanding human population and habitat alteration (Cromley 2000). Both Jackson and Gros Ventre sage-grouse populations are located approximately 130 km to the north of the most northern Pinedale population sampled in this study, which is less than half the distance between Pinedale and Casper populations (Figure 1). As geographical features such as mountains

likely act as the primary dispersal barriers for Jackson sage-grouse, it is possible that migration routes to the south of the valley existed before European settlement but have now been altered by human activity. For example, the city of Jackson, increased land cultivation, and/or fossil fuel development south of Jackson (i.e. Pinedale Anticline Project in Sublette County) may have been sufficient to disrupt the already limited dispersal routes between Jackson and Pinedale. In the 1950's, approximately 9,425 ha of sagebrush habitat was available for sage-grouse in the southern portion of Jackson, roughly 19% less than pre-settlement estimates of 11,579 ha. Currently, only 6,674 ha of sagebrush habitat exists and supports a population of roughly half that in the 1950's (Bedrosian et al. 2010). While the habitat loss within Jackson may or may not contribute to the overall genetic isolation of the valley, reduction in habitat and/or altered connectivity with core populations may be an important factor in reducing population size and increased inbreeding.

Despite significant pairwise genetic differentiation between Jackson, Gros Ventre, and Pinedale (Figure 2), the genetic data also indicated that contemporary asymmetric gene flow exists between areas in northwest Wyoming with Gros Ventre possibly acting as a sink and Jackson and Pinedale as independent source populations with no gene flow occurring in opposite directions. Results from BAYESASS indicated a ~10% immigration rate from Jackson into the Gros Ventre population with a lesser degree of genetic contribution derived from Pinedale (~2%; Table 3). Other species such as pronghorn that also breed in Grand Teton National Park migrate south each year using the Gros Ventre River Drainage system as a corridor, thereby remaining connected to their wintering grounds in the Pinedale area (Sawyer et al. 2005). More work is needed to determine to what extent sage-grouse are currently using the Gros Ventre River Drainage for contemporary dispersal between areas and/or to determine factors that are limiting dispersal from Pinedale into Gros Ventre and Jackson using a similar route observed with pronghorn. These results do suggest that maintaining connectivity between the Gros Ventre and Jackson populations is supported and that the two areas should be managed as subpopulations (e.g., Waples and Gaggiotti 2006) with Gros Ventre dependent on dispersing individuals from Jackson.

However, it remains uncertain whether the Jackson and Gros Ventre populations were in fact connected to populations such as Pinedale for much longer periods of time prior to European settlement, similar to Gunnison sage-grouse (*C. minimus*; Young

et al. 2000). For example, Jackson is surrounded by high elevation forest, including multiple mountain ranges (i.e. Teton, Wyoming, Wind River, Gros Ventre ranges, Figure 1) that most likely limit sage-grouse dispersal. If this is the case, then management should focus more on maintaining adequate habitat required by the population for long-term sustainability (e.g., Johnson et al. 2009) as opposed to introgression of genes that may result in outbreeding depression (Frankham et al. 2011). Although no formal investigation has been conducted to determine whether sage-grouse in northwest Wyoming differ from other greater sage-grouse based on morphology or behavior, the population's geographic location and early historic records (Schroeder et al. 2004; Figure 1) suggest that the population may have been isolated prior to European settlement.

Unique habitat differences (i.e., elevation, annual precipitation) do exist between Jackson/Gros Ventre and to the other areas sampled for this study. If sufficient time has passed following isolation, habitat differences may then cause differences to develop among sage-grouse populations resulting in reproductive isolation (i.e., ecological speciation; Schluter 2009; Nosil 2012). The genetic differentiation observed with STRUCTURE (Figure 2) and BAPS corresponds to the level I ecoregion delineation for the state of Wyoming (see Commission for Environmental Cooperation Working Group, 1997; Olson et al. 2001; Figure 1). If ecological differences are sufficient, local adaptation may further limit contemporary gene flow, eventually resulting in separate species, similar as happened with Gunnison sage-grouse (Young 2000) and red crossbill (*Loxia curvirostra* complex; Benkman 2003; Smith and Benkman 2007; Smith et al. 2012). Some evidence suggests that the sage-grouse in Jackson utilize different habitats than other sage-grouse populations (Chong et al. 2011), concurrent with the theory of local differences arising as a result of different ecological pressures. Given that the differences in ecoregions corresponded to genetic differentiation among the sage-grouse populations in this study, further investigation is warranted to determine the role of different habitat characteristics influencing gene flow across the entire distribution of greater sage-grouse and whether unique adaptations exist within the Jackson and Gros Ventre populations that may suggest that they are diverging by ecological speciation from other sage-grouse populations.

In addition to being small and geographically and genetically isolated, both Jackson and Gros Ventre sage-grouse populations also possess significantly reduced levels of neutral genetic diversity compared to

the large core populations in Pinedale. Populations that are small and isolated are subject to exponential loss of genetic diversity over time through genetic drift at a rate that depends on their effective population size (N_e ; Frankham 1996; Frankham et al. 2009). Therefore, because Jackson and Gros Ventre sage-grouse populations possess small N_e , they are expected to lose more genetic diversity compared to larger populations over the same time period. Reduction in genetic diversity in small, isolated populations has been shown to negatively influence individual and population fitness due to increased inbreeding (Keller 1998; Daniels 2000; Liberg 2005; Blomqvist et al. 2010; also see Keller and Waller 2002). Inbreeding has resulted in decreased immunocompetence, reproductive success, and survival among multiple bird species (Charpentier et al. 2008; Frankham et al. 2009; Blomqvist et al. 2010; Hammerly et al. 2013). Thus, inbreeding depression presents a potential risk for small, isolated populations with reduced genetic diversity, such as the Jackson and Gros Ventre sage-grouse populations observed in this study.

◆ CONCLUSIONS

Identifying isolated populations of greater sage-grouse is a conservation priority given the extent of recent land use changes throughout the species' distribution. It has been shown that maintaining isolated peripheral populations is important for protecting unique genetic variability, which should prove useful for long-term persistence of a species (Channell and Lomolino 2000; Nielsen et al. 2001; Willi et al. 2006; Peterman et al. 2013). Thus, identifying and managing isolated populations in order to prevent their extinction should contribute to the long-term survival of a species.

While the present study identified Jackson and Gros Ventre as isolated sage-grouse populations, it is not known if isolation was caused primarily by recent human mediated changes to the landscape or more historic processes. Further work is currently underway to determine whether recent anthropogenic activities contributed to their isolation. Regardless of recent or historic processes, however, management priority should focus on preventing further reduction in current population size in an effort to minimize the rate of genetic diversity loss.

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SUMMARY OF AN ONGOING POPULATION STUDY OF *PARNASSIUS CLODIUS* BUTTERFLIES



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♦ ABSTRACT

Global and regional climate patterns suggest that future conditions in the western United States will be warmer and drier. Changing climatic conditions are predicted to impact ecosystems on many levels including at a population level. Decreases in population distribution and sizes have the potential to disrupt community and species diversity. Insects are particularly useful organisms to study because of their shorter life spans and sensitivity to changes environmental conditions. We expanded on previous population studies of a butterfly species, *Parnassius clodius*, located in Grand Teton National Park using mark-recapture techniques. We collected data to assess population size and sex ration on one particular population located in the park. Using mark-recapture techniques, we were able to collect data to assess population numbers, total number of males and females, sex rations and number of mated versus unmated females throughout the flight season. Here we compiled information about this population to provide benchmark information for this species and its population dynamics. The combined population data will be further used to study how changing climatic conditions have affected this population throughout the study years. The results will be valuable for understanding the population and also for understanding potential climate-related impacts on butterfly populations in other locations.

♦ INTRODUCTION

Global and regional climate patterns suggest that future conditions in the western U.S. will be warmer and drier, and ecosystems at higher altitudes

and latitudes may be subject to larger, more rapid changes (Harte and Shaw 1995; Thuiller et al. 2005). As a result of increasing temperatures and decreasing winter precipitation, it is predicted that the duration of snow cover will decrease (IPCC 2007). Such changes have the potential to impact the dynamic interactions among organisms and their habitat (Bradley *et al.* 1999; Folke et al. 2004). Climatic changes are predicted to alter species distributions, life histories, community composition, and ecosystem function that cascade through the ecosystem because of the complex interplay of organisms (i.e. Kudo 1992; Dunne *et al.* 2003; Parmesan and Yohe 2003; Inouye 2008). In particular, changes in population sizes, as a result of changing climate conditions, have the potential to decrease community and species diversity (Root et al. 2003). Evidence from various studies indicates that range shifting in response to climate warming may lead to population extinctions (i.e. Walther et al. 2002; Parmesan 2006). One particular group of organisms that serves as a useful indicator of climate change effects is insects because they are short-lived ectotherms with wide variation in population size over space and time (Bale et al. 2002; Maclean and Wilson 2010).

Insects have provided clear evidence for ecological responses to climate change. Examination of populations in Europe and North America reveal that butterfly distributions are shifting poleward (Parmesan and Yohe 2003; Parmesan 2006), and phenological events, such as emergence and spring activity, are advancing to earlier spring dates as a result of climate warming (Roy and Sparks 2000; Peñuelas *et al.* 2002; Stefanescu *et al.* 2003). Given the greater availability of both current and historical information on species distributions and population sizes,

Lepidoptera can play a key role in providing evidence and further understanding climate change.

Parnassius clodius is a common butterfly in the Greater Yellowstone Ecosystem. However, two related European species, *Parnassius mnemosyne* and *Parnassius apollo* are considered to be vulnerable throughout much of their European range as populations have undergone substantial decline and extinction due primarily to habitat change and climate change (Van Swaay and Warren, 1999; Bergström 2005; Descimon *et al.* 2005; Nakonieczny *et al.* 2007; Ashton *et al.* 2009; Gorbach and Kabanen 2010). Utilizing data obtained from population studies on a common species, we may be able to inform ecologists and land managers as to what factors play a role in population stability.

This study, begun in 2009, was established to provide more information on population dynamics of one of the largest populations of *Parnassius clodius* in Grand Teton National Park by expanding on previous studies from 1999-2001. We collected data using mark-recapture techniques to assess population dynamics, such as population size and sex ratio. Here we compile information obtained from population studies and observations of *P. clodius* from 2009-2012. Our goal is to provide a benchmark of information on this species and its population dynamics for future studies that may utilize the same sites.

◆ METHODS

Study Organism

P. clodius are moderately large in size (wingspan of 5 -7 centimeters), predominantly white butterflies found in western Canada and the western United States. Highest densities of *P. clodius* are typically found in dry, gravelly sagebrush meadows (Auckland *et al.* 2004). *P. clodius* adults have one flight per year from mid-June to mid-July. Adult females lay eggs on vegetation near the host plant species, *Dicentra uniflora*. *D. uniflora* is a spring ephemeral that is found growing near the edges of snowmelt (Craighead *et al.* 1998). *P. clodius* larvae feed on the host plant throughout the spring until pupation. Adults display virtually no evidence of courtship behavior. Rather, patrolling males grab females in flight and force them to the ground to copulate (McCorkle and Hammond 1985).

Study Sites

A mark-recapture-release (MRR) study of a

P. clodius population was conducted in a dry, sagebrush meadow with a relatively homogeneous topography at an elevation of ~2100 meters located within Grand Teton National Park, WY. The meadow is approximately 2 x 0.5 km in size (Auckland *et al.* 2004) and located along Pilgrim Creek Road, just south of the University of Wyoming-National Park Service Research Station. Based on previous studies, we concluded that the Pilgrim Creek population is one of the larger populations of *P. clodius* within the Greater Yellowstone Ecosystem. Thus there were sufficient numbers (e.g., hundreds) of butterflies present annually for a mark-recapture-release study (Auckland *et al.* 2004).

Mark-recapture-release (MRR) study

Adult population size was investigated during the annual flight period in summer months from 2009 – 2012. For each year, MRR studies were initiated immediately after adult emergence and were terminated when less than 5 butterflies were seen summed across all of the plots, signaling population decline. Daily surveys were limited to times between 10:00 and 17:00 hours, and when the temperature was above 21° C, wind was <16kmh⁻¹, and the sun was not obscured by clouds. When conditions did not meet the above requirements, MRR surveys were not performed. However, during all four summers, the majority of the days during the flight season were adequate for MRR. Using MRR technique, two investigators walked within 50 x 50 meters plots (located approximately 200 meters apart) for 20 minutes and captured any *P. clodius* individual within the boundary of the plot using a butterfly net. Individuals were then placed in glassine envelopes and held by the investigator in a small box attached to a belt until the end of the survey. At the end of the survey time, surveyors moved off of the plot to a shady location to process the butterflies caught and record data. All unmarked captured individuals were marked with unique numbers, indicating the plot in which they were caught, on the ventral side of each hindwing, using a felt-tip permanent marker. Information for previously marked individuals was recorded, including the plot number where the individual was captured. Males and females were identified based on external morphological differences. Female mating status was determined by the presence or absence of a spermatheca (a waxy structure deposited by the male during mating that prevents future matings). Wing wear of each captured butterfly was recorded for each butterfly. Wing wear classification was as follows: 1) good conditions, no visible damage, 2) slightly damaged wings, small tears, 3) heavily damaged wings or missing wings. Behavior at the time of

sighting (in flight, nectaring (and plant species upon which it was nectaring), or basking/resting (type of surface)) was also recorded. After all the information was recorded for the captured individuals within that plot (~30. min or less), butterflies were released from the center of the plot. It is also important to note that there were generally less than two mortalities per year of all butterflies captured as a result of capture and handling. We randomly surveyed the plots starting with a successive number the following day in order to sample at different times of day for each plot.

◆ RESULTS

Initially, six 50 x 50 plots (plots 1 – 6) were surveyed in 2009. Due to a separate but related experiment in the meadow, plot 4 was removed from surveys after the 2009 field season. The original five plots (1 – 3; 5 – 6) were surveyed in 2010. Plot 2 was not surveyed in 2011 due to bear presence. However, two additional plots (7a and 8) were added to the 2011 surveys. In 2012, the original plots (1 – 3; 5 – 6) were surveyed with an additional plot (7b). Table 1 lists the locations (UTM – zone 12N) for each of the plots surveyed and the years in which they were surveyed.

In all years, males were captured more frequently than females (Table 2). Based on the number of plots surveyed, the average number of males that were captured per plot ranged from 141 to 33 individuals, while the average number of females per plot ranged from 35 to 9. The capture sex ratio males/females also varied from year to year with the highest ratio occurring in 2009 with 4 males to 1 female. The lowest sex ratio of males/females occurred in 2012 with 2 males to 1 female.

Annual flight periods varied among years (Table 3). The earliest date of male emergence occurred in 2012 when males emerged on June 13th. In 2011, males were not seen until July 6th. In general, females emerged after males, ranging from 1 – 7 days after the first males were seen. This resulted in a later peak flight time for females when compared with males. Females also stayed on the wing slightly longer than males.

Average wing-wear condition showed a steady increase as the flight season progressed. Males showed slightly greater wing wear overall when compared with females. Also, as one might expect due to the forceful nature of copulation in this species, mated females had greater wing wear than unmated females.

Table 1. Summary of UTM coordinates for plots surveyed and years surveyed (UTM NAD 1983 zone 12N).

Plot #	Northeast Corner	Southeast Corner	Southwest Corner	Northwest Corner	Years Surveyed
1	E0534108 N4862885	E0534099 N4862833	E0534051 N4862845	E0534059 N4862886	2009 - 2012
2	E0533907 N4862808	E0533902 N4862755	E0533847 N4862765	E0533860 N4862808	2009 - 2010; 2012
3	E0533812 N4862642	E0533801 N4862579	E0533751 N4862602	E0533760 N4862649	2009 - 2012
4	E0533917 N4862535	E0533924 N4862525	E0533872 N4862471	E0533850 N4862503	2009
5	E0533717 N4862409	E0533750 N4862373	E0533704 N4862346	E0533678 N4862387	2009 - 2012
6	E0533629 N4862510	E 0533622 N4862458	E 0533573 N4862465	E05337578 N4862519	2009 - 2012
7a	E0533488 N4862389	E0533421 N4862369	E0533442 N4862415	E0533488 N4862389	2011
7b	E0533614 N4862181	E0533604 N4862131	E0533552 N4862140	E0533561 N4862192	2012
8	E0533582 N4862292	E0533622 N4862254	E0533581 N4862219	E0533547 N4862256	2011

Table 2. Summary of number of plots surveyed per year, average number of males and females per plot by year and ratio of males to females captured.

Year	# of plots surveyed	Ave. # males/plot	Ave. # females/plot	Ratio of male/female
2009	6	141.14	34.83	4.05
2010	5	45.80	12.80	3.58
2011	7	32.71	9.29	3.52
2012	6	56.00	27.00	2.07

Table 3. Summary of emergence dates for males and females by year and last date sampled by year.

Year	Male Emergence Date	Female Emergence Date	Last Date Sampled
2009	24-Jun	25-Jun	12-Jul
2010	4-Jul	6-Jul	15-Jul
2011	6-Jul	7-Jul	18-Jul
2012	13-Jun	20-Jun	3-Jul

◆ CONCLUSIONS

Our MRR study has resulted in a large dataset that contains a great deal of information on *Parnassius clodius* butterflies. Throughout the course of data collection, we were able to collect data on many variables that relate to population dynamics in *P. clodius*, such as emergence dates for males and females, peak flight dates for both sexes, wing wear throughout the season, and mating status. Each of these factors varied throughout the years the study was conducted. This report summarizes some of the information obtained from these studies. Future analyses will be performed to uncover potential reasons for variations in population sizes and emergence dates and to correlate these responses to annual weather patterns.

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YELLOWSTONE NATIONAL PARK



ASPEN, ELK AND WOLVES IN YELLOWSTONE: ARE ASPEN RECOVERING SINCE THE RETURN OF WOLVES?

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✦ ABSTRACT

We assessed aspen stand conditions in 2012 in 87 stands randomly located across the northern winter ungulate range of Yellowstone National Park (YNP), and compared these data to baseline conditions measured in 1997-98 shortly after wolves were reintroduced. In 1997-98, browsing rates (the percentage of leaders browsed annually) in aspen stands were consistently very high, averaging 88% of stems browsed; only 1% of young aspen in sample plots were taller than 100 cm and none were taller than 200 cm, the height at which aspen begin to escape from browsing by elk. Using the same methods in 2012, 17 years after wolf reintroduction, browsing rates were much lower averaging 44%, 34% of sampled young aspen were taller than 100 cm, and 5% taller than 200 cm. Mean heights of young aspen in 2012 were inversely correlated with browsing intensity ($R^2=0.64$, $p<0.001$), but heights were not associated with current annual growth in height (an index of site productivity; $R^2= 0.02$, $p=0.2$). Some stands were still heavily browsed in 2012 with wide spatial variation across the range and between stands, but on average, browsing declined after 2003 followed by a relatively rapid increase in height of the tallest saplings. The greatest change was on the eastern side of the northern ungulate winter range, corresponding with recent changes in elk population distribution. Recent growth of young aspen into tall saplings will likely result in the regeneration of overstory trees and the persistence of aspen stands into the future, though aspen recovery will take many years and some stands may continue to decline. These results support the

hypothesis that a trophic cascade following the return of wolves to Yellowstone has begun to reverse the decades-long trend of aspen decline on the northern range.

✦ INTRODUCTION

Aspen (*Populus tremuloides*) stands were unable to regenerate and declined in northern Yellowstone National Park (YNP) in the 20th century due to intensive browsing of young aspen by elk (*Cervus elaphus*) (Romme et al. 1995, NRC 2002, Barmore 2003). Through their effects on elk population densities and foraging behavior, wolves (*Canis lupus*) can play a role in the relationship between elk and aspen (White et al. 1998), and the reintroduction of wolves to YNP in 1995-96 (Smith and Bangs 2009) provided an opportunity to observe this interaction. Larsen and Ripple (2001, 2005), working on the Yellowstone northern ungulate winter range ("northern range") in 1997-98, found that about 90% of young aspen leaders were browsed annually, and most young aspen were kept shorter than 100 cm by repeated browsing, preventing stand regeneration. Through analysis of tree cores, they found that the historical decline of aspen tree recruitment (i.e., growth of young aspen into trees) roughly coincided with the time that wolves were eliminated in the park, supporting the idea that the decline of aspen was due to a trophic cascade following the loss of wolves (Larsen and Ripple 2003). Subsequent research by Ripple and Beschta (2007, 2012) in 2006 and 2010 supported the trophic cascade hypothesis, with

evidence that aspen were beginning to recover in the eastern part of the northern range following the return of wolves. However, Kauffman and others (2010) found no evidence in 2004-07 that aspen were recovering in northern Yellowstone, and concluded that elk herbivory was still intensive enough to suppress aspen regeneration. These studies used different methods (Beschta and Ripple 2011) and sampling was limited to either a small number of stands (Kauffman et al. 2010) or to one portion of the YNP northern range (Ripple and Beschta 2012). More research is needed to explore the developing relationship between aspen, elk and wolves in the northern Yellowstone ecosystem.

In the eastern portion of the YNP northern range elk densities have declined to relatively low levels in recent years (White et al. 2012), so changes in aspen are likely in at least some areas, but aspen stands did not recover in the 1950s and 1960s despite more than two decades of relatively low elk population densities when elk and bison (*Bison bison*) herds were annually culled (Yellowstone National Park 1997, Beschta and Ripple 2011). Trophic cascades from wolves to elk to aspen have been observed in other ecosystems (White et al. 2003, Hebblewhite et al. 2005, Beschta and Ripple 2007); these have varied in the strength of the cascade, and in the importance of other factors affecting aspen regeneration (Eisenberg et al. 2013). In northern Yellowstone, the history of exceptionally high elk population densities, complete absence of wolves, and nearly complete absence of aspen regeneration (Wagner 2006) makes the area exceptionally well-suited for a natural experiment to detect the influence of wolves on aspen.

The 1997-98 research of Larsen and Ripple (2003, 2005) provided a baseline for aspen conditions shortly after wolf reintroduction. In the summer of 2012, we used this baseline to assess changes in browsing rates and heights of young aspen over time in 87 stands randomly selected across the YNP northern range within the park boundary, compared to 79 of the same stands sampled by Larsen in 1997-98. The ability to compare aspen conditions over a 14-year span of time is a distinct advantage of this study. We collected additional data as well, for a more detailed analysis of aspen stand conditions in 2012, and to account for factors other than browsing that could affect aspen growth such as differences in stand productivity.

Larsen randomly located 93 aspen stands on the northern range to assess the age distribution of aspen trees, and collected data on young aspen in 79 of those stands. Between July 24 and September 1, 2012, we revisited 76 of these 79 stands (three did not have GPS locations), plus 11 more stands from the 1997-98 study for a total of 87 stands sampled in 2012. We excluded one stand on a steep scree slope, which previous research has shown to inhibit ungulate browsing as a partial exclosure (St. John 1995, Larsen and Ripple 2005). A stand was defined as a group of aspen separated from other aspen by >30m. We recorded the GPS location, slope, aspect, elevation, distance to roads, distance to conifer forest, plant community type (xeric, mesic, or wet), and topographic position (riparian or upland; see Ripple and Beschta 2007, 2012). Conifer cover in aspen stands was classified as 0 (none), 1 (few, little cover), 2 (<half covered), or 3 (>half covered). As an index to ungulate use of the area, ungulate fecal piles, including elk, bison, deer (*Odocoileus* spp.) and pronghorn (*Antilocapra americana*) were counted in four 2x50 m plots spaced 7 m apart, placed outside of the stand perimeter in the nearest open area used by ungulates accessing the stand. Sampling plots for fecal piles were not placed within aspen stands because many stands were wet with very dense vegetation, some with standing water for part of the spring and summer. Placing the scat plots outside of the stands resulted in a much more consistent probability of scat detection, and a useful index to relative ungulate densities across the landscape. A viewshed index was calculated from the average of the distance at which view was obstructed, (to 900 m, the limit of the laser rangefinder) in each of the four directional quadrants (Ripple and Beschta 2006), from the point of origin of the ungulate scat plots.

Most stands were relatively small and each stand was sampled with a 2x30 m plot (Kay 1990), beginning at the closest tree on the perimeter of the closest stand to the GPS location, and extending toward the centroid of the stand. Plots were not duplicates of the 1997-98 plots, but were in the same aspen stands. An aspen tree is defined as having a diameter-at-breast-height (dbh) >5 cm; aspen <5 cm dbh are called young aspen, and young aspen 200 cm tall or taller are saplings. In each sampling plot we recorded the dbh of all aspen trees and saplings, and all other species of trees taller than 200 cm. For young aspen in the sampling plot, we recorded the height and browsing status (browsed or not) of the tallest leader for fall 2012 (top height), spring 2012, and spring 2011, as indicated by bud scars and browsing scars (Keigley and Frisina 1998). If the righthand side of the

◆ METHODS

plot (1x30 m) had 25 or more aspen sprouts older than one year, sampling of young aspen was ended with this reduced plot. If the entire 2x30 m plot had less than 15 aspen sprouts, the plot was extended in increments of 30 m² to reach a count of at least 15. We also located the five tallest young aspen in the stand (within 60 m of the sampling plot) and used plant architecture to assess height and browsing status over all previous years for these five tallest young aspen (Ripple and Beschta 2012).

In the 1997-98 aspen data, the heights of young aspen in sampling plots were classified as taller than 100 cm or 200 cm. We compared between 1997-98 and 2012 the mean percentage of young aspen in these two height categories, and the mean percentage of stems browsed (browsing rate), using bootstrapping to test for differences and generate confidence intervals. Browsing rate calculations did not include aspen >200 cm tall, following Larsen (2001). Most browsing by elk occurs at heights below 200 cm, so taller shoots could bias the result if included. Values were first calculated within a plot, and then averaged across plots for a grand mean. Bootstrapping was used because the distribution of the data was not suitable for distributional analysis methods. A 95% confidence level was used to assess statistical significance for all tests.

Data collected in 2012 permitted a more detailed analysis of browsing intensity and young aspen height. The 1997-98 data did not identify sprouts new that summer that had not been exposed to winter browsing, so the browsing rate underestimated the true browsing rate in plots that contained new sprouts. For further analysis of 2012 data we calculated an adjusted browsing rate that did not include new sprouts, resulting in a slightly higher browsing rate in plots that had new sprouts than was used in the comparison with 1998. As an index of site productivity the mean leader length or current annual leader growth was calculated as the difference between spring height and fall height, averaged across the sampling plot. Confidence intervals and tests for differences for mean height, leader length, and browsing rates were calculated using t-statistics, as the 2012 data were approximately normally distributed and less skewed than the 1998 data. Multiple regression was used to test for the significance of leader length, browsing rate, and other site variables as explanatory variables for the average height of young aspen, with natural logarithm transformations where needed to meet the assumption of constant variance. Coefficients were tested for significance using extra-sums-of-squares F-tests. The fit of the models was also assessed using the coefficient of determination (R²).

◆ PRELIMINARY RESULTS

Compared to 1997-98, browsing rates of young aspen were significantly lower in 2012, the percentage taller than 100 cm or 200 cm was much greater, and both browsing and height had greater variation (Table 1). Recruitment of tall young aspen >100 cm and saplings >200 cm had increased compared to 1997-98, with a much higher of percentage of plots containing at least one young aspen in these height categories (Figure 1).

Table 1. Summary of young aspen browse rates and heights in 1997-98 and 2012, with 95% CI in parentheses.

Years	%Browsed	% \geq 100cm	% \geq 200cm	n
1997-98	88 (84, 91)	1 (0.5, 2)	0	79
2012	44 (39, 49)	34 (28, 40)	5 (3, 8)	87

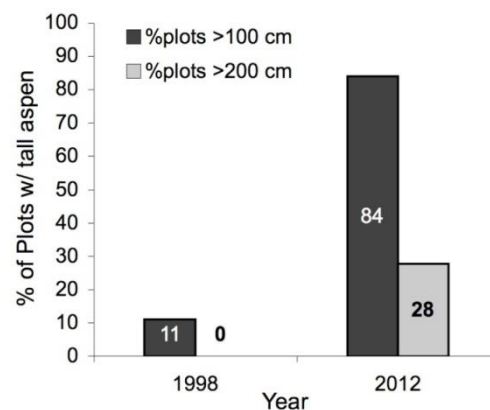


Figure 1. Percentage of samplings plots with at least one young aspen >100 cm or >200 cm tall or taller.

These results show that aspen have begun to recover in northern Yellowstone, but new saplings were small, most <3 cm dbh, and there were no trees in sampling plots smaller than 27 cm dbh indicating a large gap in recruitment. This gap is the legacy of past conditions, when there were no saplings (Figure 1) and no recruitment of aspen trees. Today, the new saplings are tall enough to escape from elk browsing and are likely to replace dying overstory trees, thus ensuring the persistence of northern range aspen stands into the future (Figure 2). This recovery is in an early stage, which may explain why Kauffman and others (2010) did not find recruiting saplings with limited sampling in 2004-7.

Ripple and Beschta (2007, 2012) used a method of measuring the five tallest saplings in a stands, a method more likely to detect the beginnings

of aspen recovery. We also measured the five tallest saplings in each stand and found that 46% of stands had one or more taller than 200 cm in the spring of 2012, and 25% of stands had five or more saplings taller than 200 cm, a strong indication that the stand will successfully regenerate by replacing overstory trees (Kay 2001). Most of these tall saplings originated after 2003, an indication that survival and heights of young aspen have recently increased, but this change would have been difficult to detect by random sampling when Kauffman and others did their research.



Figure 2. Aspen stand in northern Yellowstone showing overstory aspen trees and young saplings. Lack of intermediate ages and sizes classes is due to the legacy of lack of recruitment due to suppression by herbivory; young saplings in this stand are now taller than the normal browse level of elk and thus likely to grow into new trees.

Could the recent changes in aspen from decline toward recovery be the result of changes in climate? The long-term trend in the region has been toward milder, shorter winters with less snowpack, and dry hot summers (Wilmers and Getz 2005, McMenamin et al. 2008), conditions that would be likely to inhibit aspen recovery due to increased herbivory and drought stress (Brodie et al. 2011, Hanna and Kulakowski 2012). A longer growing season could cause greater annual height growth, contributing to recovery, but if that were the cause of aspen recovery we would expect to find an association between the average length of annual leader growth in a stand and the average height of young aspen. The relationship between leader length and height was very weak ($R^2=0.02$, $p=0.2$), but there was a strong inverse relationship between browsing rate (averaged over 2011-12) as an explanatory variable for height ($R^2=0.64$, $p<0.001$). Differences in height between stands appeared to be driven primarily by the amount of browsing, with differences in rates of growth coming into play only where browsing has been

reduced. None of the other site variables we collected were statistically significant as explanatory variables for stand browsing rates or heights of young aspen.

In 1997-98, young aspen in nearly all stands experienced high browsing rates and were relatively short, but this was not the case in 2012. After adjusting browsing rates by removing new sprouts from the analysis, in 2012 about 40% of stands had browsing rates greater than 60%, and remained short with little variation in height among stands, an indication of suppression of height by browsing. The remaining 60% of stands with browsing rates from 0-60% showed increasing variation in height, with the tallest heights and greatest variation associated with lower browsing intensity. Browsing rates were generally lower and heights taller on the eastern side of the northern range, which is consistent with recent trends in elk population distribution (White et al. 2012). On the eastern side of the range elk population densities have dropped considerably in recent years, with much less change on the western side of the range. Our scat counts showed the same trend, with an overall reduction compared to surveys done in 1999 (Ripple et al. 2001) when scat counts ranged about 20-40 piles/100m², and strong contrasts across the range in 2012 with the lowest elk scat densities in the eastern part of the range (Table 2). Our East, Central and West sectors follow the same divisions as the Upper, Middle and Lower Inside sectors of White and others (2012). Bison scat showed the opposite trend, with the greatest density in the eastern sector reflecting the large herds of bison that gather there in summer. Willow (*Salix* spp.) and cottonwood (*Populus angustifolia*, *P. trichocarpa*) are browsed by bison in the Lamar Valley area, compensating for some of the reduction in elk herbivory and weakening the effect of a trophic cascade from wolves to woody plants (Painter and Ripple 2012), and bison may have a similar effect on aspen.

Table 2. Mean elk and bison scat densities in sectors of the Yellowstone northern range in 2012, with (95% CI).

Sectors	Elk pellet piles/100m ²	Bison scat piles/100m ²
East	4 (3, 6)	11(9, 14)
Central	11 (7, 15)	7 (5, 9)
West	17 (11, 22)	0.7 (0.4, 1)

The spatial distribution of elk across the northern range (White et al. 2012), lower in the east and greater in the west (Table 2) appears to have been the most important factor influencing aspen herbivory, suggesting that changes in elk population density have

been driving aspen recovery. The fact that a general aspen recovery did not occur without substantial reductions in elk numbers, suggests that behavioral responses to predation alone were not enough to bring about aspen recovery at a landscape scale. However, predation risk responses such as changes in elk grouping dynamics (White et al. 2012) and habitat selection (Mao et al. 2005) may be driving some of the small-scale variation between stands in the same area, and predation risk may also be a factor in the large-scale redistribution of the elk herd (Proffitt et al. 2009). Elk numbers increased in the portion of the Yellowstone northern range outside of the park before the return of wolves, but this did not result in reduced elk densities or reduced herbivory inside park boundaries. The fact that aspen did not recover during a period of low elk population density in the 1950s and 1960s suggests that something more than a simple reduction in elk numbers was needed to reverse the aspen decline.

Our results update and expand knowledge of aspen stand conditions across Yellowstone's northern range. We found that aspen stands have begun to recover relative to conditions before wolf reintroduction, but this recovery is in an early stage and highly variable across the landscape. The reductions in browsing and associated height increases of young aspen were greatest in the eastern part of the range, but within each sector there also was wide local variation. The recent increase in recruitment of aspen saplings was associated with a reduction in browsing, linked most plausibly to the return of wolves and subsequent changes in elk numbers and distribution. The Yellowstone example suggests that wolves could play a role in support of aspen conservation through reduction of herbivory. The complex relationship of wolves, elk and aspen will continue to unfold, interacting with an increasing bison population, warming climate, changes in land use and hunting outside the park, and other facets of the Yellowstone ecosystem.

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COMPARING STREAM INVERTEBRATE ASSEMBLAGES BEFORE AND AFTER WILDFIRE IN YELLOWSTONE NATIONAL PARK

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✦ ABSTRACT

Warmer, dryer climate conditions during the past 3 decades are thought to have increased severe fires in the western United States. Severe fires may change food webs due to altered light levels, nutrient concentrations, and hydrology in streams. To measure how wildfire changes stream food webs, we collected aquatic invertebrates before and after a fire, and calculated their density and biomass. To investigate the effects of wildfire on streams, we collected aquatic invertebrates from Cub and Little Cub Creeks on the east side of Yellowstone Lake before and after the East Fire (Figure 1). The timing of our study was serendipitous with the fire burning after our first year of collecting samples. Therefore, we collected samples prior to the wildfire (2003), and 1 (2004), 2 (2005), and 9 years post fire (2012). The East Fire was a crown fire that set ablaze >17,000 acres and burned $\geq 95\%$ of the watersheds of these streams. Working in Yellowstone National Park was opportune, because few other perturbations existed and the effects of wildfire can be easily studied. We analyzed the samples to understand how wildfire altered stream invertebrates. Our specific questions were: 1.) What affect did wildfire have on the density and biomass of aquatic invertebrates? 2.) How did the composition of aquatic invertebrates change before and after wildfire? Results from our study will inform managers about how the food base for fish and many birds (i.e., aquatic invertebrates) changes after wildfire.



Figure 1. Cub Creek 9 years post wildfire.

✦ INTRODUCTION

Warmer, dryer climatic conditions during the past 30 years have been attributed to increases in severe, stand-replacing fires in the western US (Westerling et al. 2006). The 1988 fires in Yellowstone National Park are an example of large, severe, stand replacing fires. Severe fires continue to burn in Yellowstone National Park in recent years, where thousands of hectares of forest were consumed. These stand-replacing fires remove the forest canopy and begin new successional trajectories that persist for decades (Turner et al. 2003). In addition, a shift in the dominant terrestrial vegetation, along with the creation of abundant bare mineral soil can often increase the inputs of important nutrients such as nitrogen into adjacent streams and lakes (e.g., Gresswell 1999). The

effects of fire are similar to the response measured by Likens et al. (1970) who discovered large pulses of nutrients exported from watersheds after clear-cutting a forest. Turner et al. (2007) studied terrestrial N cycling in Yellowstone and Grand Teton National Parks after fire and noted that N uptake switch from microbes to plants as succession proceeded. Turner et al. (2007) and climate predictions have prompted us to further investigate how fire will alter aquatic invertebrates in burned watersheds.

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

To investigate the effects of wildfire on streams, we collected aquatic invertebrates from Cub and Little Cub Creeks on the east side of Yellowstone Lake before and after the East Fire. Many studies of wildfire compared a burned stream with a reference stream (Minshall et al. 2001b), because collecting samples prior to a wildfire is by chance. Thus, having samples before and after fire will improve our knowledge of the effects of wildfire on stream invertebrates. The timing of our study was serendipitous with the fire burning after our first year of collecting samples. Therefore, we collected data prior to the wildfire (2003), 1 year (2004), 2 years (2005), and 9 years after the fire (2012). Therefore, our study design is ideal to estimate the effects of wildfire on stream invertebrates. The East Fire was a crown fire that set ablaze >17,000 acres and burned $\geq 95\%$ of the watersheds of these streams. Working in Yellowstone National Park was opportune, because few other perturbations existed and the effects of wildfire could easily be studied. Our specific questions were: 1.) What affect did wildfire have on

the density and biomass of aquatic invertebrates? and 2.) How did the composition of aquatic invertebrates change before and after wildfire? Results from our study will inform managers about how the food base for fish (i.e., aquatic invertebrates) changes after wildfire.

◆ METHODS

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

To investigate changes in these streams due to wildfire, we collected aquatic invertebrate samples from Cub and Little Cub Creeks. Six Hess samples (0.086 m²) were collected in each stream every 2-4 weeks during the summers of 2003 to 2005, and in August 2012. We preserved samples in 70% ethanol and identified aquatic invertebrates using a dissecting microscope and available keys (Merritt et al. 2008, Thorp and Covich 2010). We calculated biomass by measuring the first 20 individuals of each taxon and converting lengths to biomass using published regressions (Benke et al. 1999).

◆ PRELIMINARY RESULTS

In Cub Creek, we collected 40 invertebrate taxa of which 37 were insects from 6 orders. Insects were far more abundant (99%) than non-insect invertebrates. Diptera were the most abundant order of insects in the stream (66%), followed by Ephemeroptera (20%) and Plecoptera (12%). In contrast, Ephemeroptera (52%) had the highest biomass, followed by Diptera (18%) and Plecoptera (23%). On average, we collected 13 (range 3-21) taxa in each sample. Average total invertebrate density was 6800 ind/m² and biomass was 767 mg/m².

Total invertebrate density in Cub Creek was similar the summer before (13,000 ind/m²) and 2 years after wildfire (7600 ind/m²), but total density was lower immediately after wildfire (2800 ind/m²). Total density was also low 9 years post wildfire (3800 ind/m²). In contrast, invertebrate biomass was similar before (580 mg/m²) and immediately after wildfire (600 mg/m²), but biomass was twice as high 2 years after wildfire (1100 mg/m²). Nine years after wildfire, biomass was intermediate between previous values (760 mg/m²).

Before the fire, the invertebrate assemblage was primarily composed of Diptera (83%), Ephemeroptera (9%), and Plecoptera (5%) numerically. However, the dominance of Diptera declined immediately after wildfire (54%), and the percent of Plecoptera (15%), and Ephemeroptera (30%) increased. Nine years post fire, the percent of Diptera continued to decline (41%), Plecoptera were similar (17%), and Ephemeroptera became more prominent (38%).

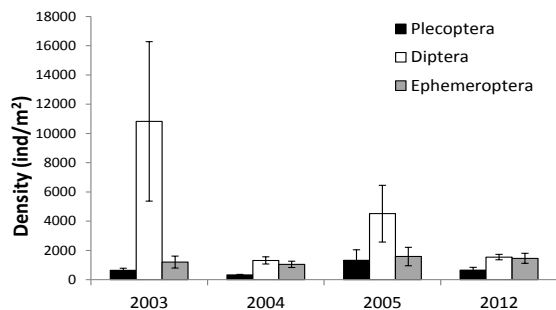


Figure 1. Density of insects in Cub Creek before and after wildfire. Bars are standard errors.

The biomass distribution of invertebrates in Cub Creek differed from the distribution based on density. Before fire, Plecoptera had the highest biomass (46%) followed by Ephemeroptera (28%), and Diptera (20%). Immediately after wildfire (2004), the percent of biomass from Plecoptera and Diptera both decreased to 9%, and Ephemeroptera increased (80%). In 2005, Ephemeroptera had the highest biomass (44%), followed by Diptera (29%), and Plecoptera (26%). Nine years after fire, Ephemeroptera continued to dominate (52%), and the percent of Diptera (18%) and Plecoptera (12%) both decreased.

The invertebrate assemblage of Cub Creek changed before versus after fire. For example, we only collected *Drumnella grandis* (Ephemerellidae) before wildfire. In contrast, we only observed *Podmasta* (Nemouridae), and leeches after wildfire. Still other taxa we only observed during a single year after the

fire (*Taenionema*, Taenioptergidae; *Claassenia*, Perlidae; *Cinygma*, Heptageniidae). Interestingly, two new taxa appeared 9 years post fire: *Paraleptophlebia*, Leptophlebiidae and *Pericoma/Telmatoscopus*, Psychodidae. Despite these changes, the average number of taxa collected in a sample was similar among years.

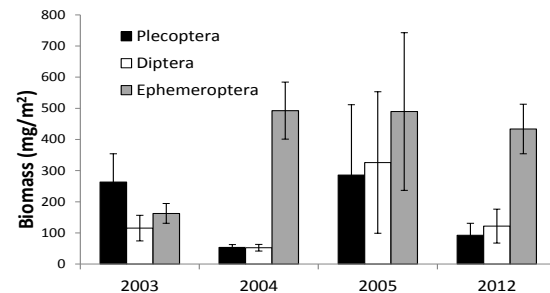


Figure 2. Biomass of insects in Cub Creek before and after wildfire. Bars are standard errors.

We collected 44 invertebrate taxa in Little Cub Creek of which 38 taxa were insects in 5 orders. The assemblage was dominated by insects (88%), but non-insect invertebrates composed 12% by abundance. Diptera were the most abundant order of insects (44%) followed by Ephemeroptera (21%) Coleoptera (15%), and Plecoptera (6%). According to biomass, Ephemeroptera (29%) and Diptera (29%) were the dominant insects, followed by Coleoptera (19%), and Plecoptera (12%). On average, we collected 13 taxa per sample (range 5-21). Overall, mean invertebrate density was 12,500 ind/m² and mean biomass was 1755 mg/m².

Total invertebrate density was lowest before wildfire (6000 ind/m²). Immediately after wildfire, densities increased to 11,000 ind/m². Nine years after wildfire, total density was even higher (21,600 ind/m²). Similarly, biomass also increased after wildfire. Insect biomass was similar before and immediately after wildfire (1000 ind/m²), but densities were >2 times higher in 2005 (2300 ind/m²) and 2012 (2600 mg/m²) in Little Cub Creek.

The composition of invertebrates by abundance changed through time. Before wildfire, Diptera (40%), Coleoptera (18%), Plecoptera (10%) and Ephemeroptera (6%) were the most abundant orders of insects in Little Cub Creek. Immediately after wildfire, Diptera were by far the most abundant order (63%), and Coleoptera (9%), Plecoptera (6%), and Ephemeroptera (5%) all had lower abundances. Nine years after wildfire, Ephemeroptera were the dominant order (41%). Additionally, the percent of

Diptera decreased (25%), Coleoptera increased (24%), and Plecoptera remained similar (6%).

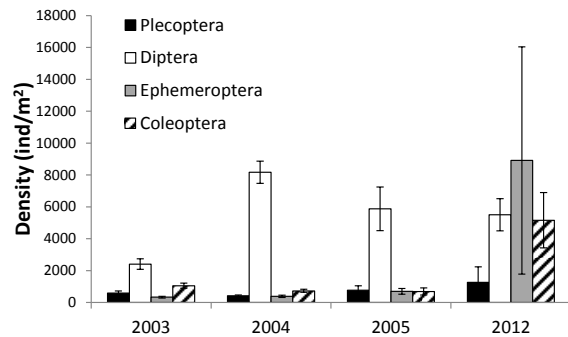


Figure 3. Density of insects in Little Cub Creek before and after wildfire. Bars are standard errors.

The distribution of invertebrates according to biomass in Little Cub Creek also varied through time. Before wildfire, Diptera (31%) were the dominant insect order, and Plecoptera (20%), Ephemeroptera (21%), and Coleoptera (22%) composed similar fractions. After wildfire, Diptera made up a greater percent of biomass (44%), Ephemeroptera remained similar (19%), and Coleoptera (11%) and Plecoptera (10%) decreased. Nine years after wildfire, Ephemeroptera (46%) were the dominant insect according to biomass and Coleoptera (28%) biomass was higher than previous estimates. The percent biomass of Diptera (9%) was much lower 9 years post fire, but the fraction of Plecoptera (11%) biomass remained similar.

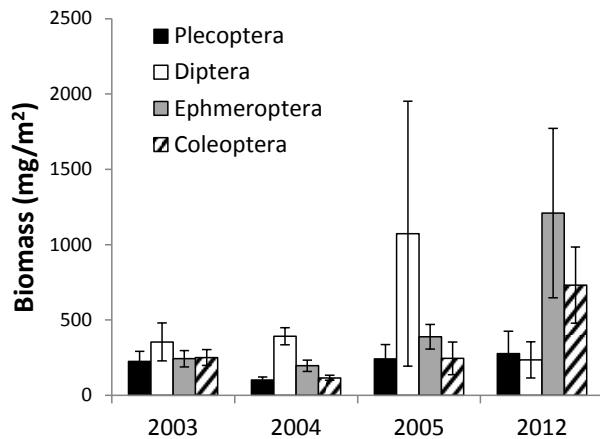


Figure 4. Biomass of insects in Little Cub Creek before and after wildfire. Bars are standard errors.

The invertebrates that composed the assemblage in Little Cub Creek changed through successional time. For example, we only observed *Acerpenna* (Baetidae) and leeches before wildfire. *Suwallia* (Chloroperlidae) and *Rithrogena* (Heptageniidae) were only present before and

immediately after wildfire, but we did not collect these taxa 2 years or 9 years post fire. In contrast, we only observed *Megarcys* (Perlodidae), *Podmasta* (Nemouridae), an unknown Leuctridae, Dolichopodidae, and *Epeorus* (Heptageniidae) after wildfire. Three new taxa appeared 9 years post wildfire; *Paraleptophlebia* (Leptophlebiidae), *Dicosmoecus* (Limnephilidae), and *Hydroptilla* (Hydroptilidae). Despite these changes, the average number of taxa collected in each samples was similar among years.

◆ MANAGEMENT IMPLICATIONS

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

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

Previous studies reported that aquatic invertebrate densities increased after wildfire (Albin 1979; Roby and Azuma 1995; Gresswell 1999). Similarly, invertebrate density in Little Cub Creek increase after wildfire. In fact, densities were nearly 4 times higher 9 years after wildfire. In contrast, invertebrate densities in Cub Creek were highest before wildfire. A flood in July 2004 greatly reduced the abundance of invertebrates in Cub Creek during that year. Minshall et al. (2001b) noted that density was lower in burned streams compared to reference streams in Idaho. In this stream, densities were likely

lower because of scouring and runoff in the stream channel, similar to what we observed in 2004.

We did not observe a change in taxa richness after wildfire in Cub or Little Cub Creeks. Invertebrate richness is generally thought to decrease in burned compared to reference streams (Gresswell 1999, Roby and Azuma 1995, Minshall et al. 2001b). Roby and Azuma (1995) found that invertebrate richness was lower in burned streams for the 11 years that they collected samples. In contrast, taxa richness was similar in burned and reference streams 10 years after fire in Idaho streams, which may have been caused by lower water levels during drought (Minshall et al. 2001b).

Wildfire can alter the composition of stream invertebrates. In burned Idaho streams, disturbance adapted insects, such as *Baetis* and Chironomidae, increased in abundance after wildfire (Minshall et al. 2001b). Similarly, Chironomidae density increased in Little Cub Creek after fire. Conversely, the density of more sensitive taxa can decrease after wildfire. For example, Ephemeroptera (Minshall et al. 2001a) and Trichoptera (Albin 1979) densities were lower in burned compared to unburned streams. The density of Ephemeroptera in Cub and Little Cub Creeks generally increased after wildfire. Ephemeroptera did particularly well after the 2004 flood in Cub Creek, where they were some of the few invertebrates that survived a scouring flood. In particular, the density of Ephemeroptera with flattened bodies (Heptageniidae) increased density after wildfire. The body form of these genera may have allowed them to persist through floods and other scouring events that occurred after the fire while other taxa were swept away. Similar to Albin (1979), Trichoptera densities in Cub and Little Cub Creeks decreased immediately after fire. These filter feeders may have been negatively affected by the initial increase in fine sediments that often occurs after wildfire (Minshall et al. 2001a). However, Trichoptera densities were highest 9 years after wildfire and we collected 2 new genera of Trichoptera in Little Cub Creek. The ability to withstand floods and increased fine sediments may have been at least partially responsible for the changes we observed immediately after fire.

Two opposite forces affect streams after wildfire. First, more nutrients and light typically increase primary production in streams. Increases in in-stream food resources may cause bottom-up effects that increase stream invertebrates and their consumers (e.g., fish). Second, the loss of vegetation and forest on the landscape can alter the hydrology of a watershed. The lack of terrestrial primary producers

can cause variable discharge, scours, and floods. In unburned watersheds, the primary producers slow the movement of water through the watershed creating a slow and decreased release of water through the growing season. In Cub Creek, hydrology controlled the invertebrate assemblage in 2004 by likely reducing biofilm and removing invertebrates. However, bottom-up effects dominated in 2005 when there were no major floods and invertebrate densities were higher.

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

◆ ACKNOWLEDGEMENTS

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INTERN REPORTS



ARCHITECTURAL PRESERVATION INTERNSHIP REPORT

GRAND TETON NATIONAL PARK



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♦ ABSTRACT

As an architectural preservation intern at the Grand Teton National Park, I worked on a number of projects over the summer of 2012. The primary research project that spanned the two months was an investigation into the history of the Upper Granite Patrol Cabin. Questions had been raised by my supervisors Katherine Longfield and Betsy Engel as to what purpose the original cabin had been built, with reason to believe it may have been built as a poacher's cabin. Using resources within the GTNP, the Jackson Hole Historical Society, and research on similar

building types, I determined that the cabin was not likely to be a poacher's cabin, but was most likely to be an early ranger's patrol cabin, built before the CCC and the standardization of park structures.

While the Upper Granite research project spanned the length of my internship, I worked on a number of shorter projects along the way. One of the most interesting projects was the week-long restoration of a cabin at the BarBC Ranch. Working with a group of volunteers from Wisconsin, I assisted Harrison with the direction of the project and helped the volunteers with preservation skills. The project was hands-on and many of the volunteers had never

worked on historic buildings, but they were all very passionate and willing to learn. It is amazing what can be accomplished with a group of volunteer labourers in the short span of a week. The dilapidated cabin was rebuilt in its original form from the ground up, reusing as much original material as possible. For another cabin at the Bar BC Ranch, I worked with Katherine to design a workable green roof plan that was both simple in construction and historically sensitive, and one that would hold up in a Wyoming winter. A volunteer group constructed the green roof a week or so after I left, so I will have to enquire on its condition next summer.

An ongoing project that I picked up once I arrived was the Grand Teton National Park smart phone app project. The app had been programmed by a graduate student in the preceding year, but the app was still missing data about historical sites within the park. Working my way along the roads throughout the park, I wrote concise histories of all the major historic sites that visitors may stop at. For Mormon Row, I wrote a walking guide for visitors to access, with numerous points to access the history about the place,

people and way of life as they walk along the road. In a similar fashion, I also wrote a walking tour for the historic sites around Menor's Ferry.

A number of sites within the Grand Teton National Park needed National Register Nominations prepared for them. I wasn't able to get through as many as I had hoped, but I did proofread and finish the nomination for the Jenny Lake Lodge, and I compiled and wrote the remaining portions for the Menor's Ferry and Colter Bay nominations. Some smaller projects included photographing all the structures on Mormon Row, and a few others throughout the park, and organising the photograph files within the system.

My time flew by while working with the Grand Teton National Park. I found the work both interesting, and challenging at times, but always enjoyable. It will be hard to find a better place of employment. I am extremely grateful for the opportunity.

CREATING COMMUNICATION CONDUITS: A GREATER YELLOWSTONE SCIENCE LEARNING CENTER INTERNSHIP



ELIZABETH E. PERRY
OREGON STATE UNIVERSITY ♦ CORVALLIS, OREGON



♦ ABSTRACT

Communicating scientific endeavors in a manner accessible to researchers, managers, and the public alike is an important, yet often neglected, aspect of conducting studies. For research carried out on America's public lands, including the National Park Service's, this communication is even more important, as we are all owners and stewards of these magnificent ecological and cultural landscapes. This summer, I worked with The Greater Yellowstone Science Learning Center, Grand Teton National Park, and researchers from across the country to augment and enhance the information about current park studies and resource status reports available to the Science Learning Center's website visitors. This addition of pertinent information to the website is of value to all those interested in the socio-ecological landscapes the National Park Service is tasked to conserve, scientific studies occurring in Grand Teton National Park, and potential implications of these studies and findings

beyond park boundaries. The additions not only reach those who are currently invested in stewardship of our national parks, but also potential stewards with whom we have the unique opportunity to communicate with digitally, vastly expanding science communication and involvement opportunities.

♦ INTERNSHIP SUMMARY

Communicating scientific studies and the status of park resources falls directly in line with the National Park Service's mission to conserve protected surroundings and provide for future generations' enjoyment. Without conducting inquiries as to the nature of the park's resources and visitors' experience, and relaying this information to a wide audience of stakeholders (i.e., the American public and park enthusiasts world-wide), we leave the mission unfulfilled. This summer, to better communicate the research in Grand Teton National Park (GRTE) and to support this mission, I spent 10 weeks assisting in

creating a fuller representation of the park's projects and resources on the Greater Yellowstone Science Learning Center (GYSLC) website.

Working with Sue Consolo-Murphy (Chief of Science and Resource Management) and Holly McKinney (primary content creator for GRTE on the website), I formed initial priorities for my summer's internship. Resource briefs are important components of the website and assist visitors in obtaining a detailed snapshot of a park resource's current status. I focused a portion of my internship on learning about mountain goats in the area and correspondingly conducting a major re-write of the current resource brief on this topic, with input from knowledgeable park staff and sources.

As Ms. McKinney focuses on resource briefs, and I have prior experience creating them, we determined the best use of my internship would be to focus on a complementary and equally important aspect of the site: the park projects, including the Boyd Evison Fellowship. This would help expand my skill set while providing GRTE with a relevant product. Therefore, I strived to update all the Fellowship recipients/projects pages and enter all of GRTE's 2012 permitted research projects onto the site. I successfully accomplished both, updating and expanding information on all of the Fellows' pages, increasing the number of projects on the site by 17%, and updating many ongoing projects, resulting in additions or edits to 25% of the projects linked to the GYSLC site (Table 1).

One of the main reasons I focused on projects (beyond it being a need and information gap for GRTE), is that I actively sought out communicating directly with researchers about their projects and soliciting further information for posting. I feel this was a great accomplishment of my time here, as I was able to contact many researchers and work with them to present their projects in a way that encompassed the park's commitment to resource protection and science, as well as the need for adequate and appropriate communication of these aspects with the public. Indeed, I contributed additional information or new profiles for 45 researchers, constituting 18% of the researchers currently listed for the entire site (Table 1). Through these communications, I gained access to images, reports, and multimedia presentations that invite site visitors to explore topics more in-depth. These communications led to edits of 3% of the overarching topic pages listed, a 6% increase in the number of products linked to the site (Table 1), and an undoubtedly larger percentage of products linked specifically to GRTE. Throughout this summer, I kept

careful track of my progress through file structure and digital spreadsheets, as sound data management is vital for park staff to continue efficiently with projects (such as with a short internship) and preserve the institutional memory of what has been accomplished.

Many times, researchers do a wonderful job of communicating within their community but a lesser job with engaging others in a dialog about scientific endeavors in protected areas. It was my intention this summer to learn more about how to foster and promote this communication among user groups and site visitors, as it is a career skills goal of mine. In working with different researchers and park staff, I feel that I learned a variety of avenues by which to approach scientific communications for both broad and specific audiences. All of these successes helped to raise the profile of GRTE on the website and to the visitors.

Numbers alone cannot capture what this internship personally meant for me. With a strong interest in science communication and increasing park relevancy to visitors, I was eager to explore this in a national park setting. In a park as iconic as GRTE, the opportunity to work with park researchers and staff, to make their scientific inquiries more accessible to their fellow researchers, management staff, and the public, was incredible. I developed skills this summer that will be useful not only for application to my M.S. thesis on public knowledge and perceptions of the newly established Oregon marine park system, but also in my career, hopefully in the capacity of a National Park Service science communications specialist or social scientist. As park stewards continuously access the Internet to a greater degree for information on their favorite parks, working with the GYSLC to relay information to this audience allowed me to gain experience in communicating via this influential and dominant medium.

Of course, spending the summer in a location such as GRTE was rewarding beyond the work day. I especially enjoyed living at the AMK Ranch and interacting with researchers there. I took full advantage of the location as well and hiked the majority of the park's main trails this summer, leaving no major area unexplored. Through the internship, these explorations, and conversations with staff and visitors, I came to profoundly appreciate all the park's resources and its place within the National Park Service system and mission. These explorations helped deepen my understanding of resource management complexity and diversity and the importance of effectively navigating the ecological-social nexus of protected areas. Combined with my work on the website, this experience at GRTE helped

to further my desire to build a career fostering an involvement in and attachment to protected areas, which are multifaceted and never consist of solely a natural or cultural fabric. These two interwoven components meld together in sites such as GRTE's, sharing narratives rooted in the ecological and social landscape. This landscape is expressed on the GYSLC site and I feel privileged to have had a role in expanding it through this internship.

Table 1. Greater Yellowstone Science Learning Center website content updated and created by Elizabeth E. Perry during summer 2012.

Entry Category	Content Category			
	Researchers	Projects	Products	Topics
Updated Entries	12	25	5	5
New Entries	33	33	26	0
Total Entries on Site	248	229	485	168
Percentage Added / Improved upon	18%	25%	6%	3%

www.greateryellowstonescience.org

CLASSES



FIELD RESEARCH AND CONSERVATION

INSTRUCTORS ✦ CHUCK COLLIS ✦ JENNIFER ADAMS
CLAYTON HIGH SCHOOL ✦ CLAYTON, MO



Students on the top of Grand View Overlook.

✦ CLASS OVERVIEW

Field Research & Conservation emphasizes long-term field research experiences, examines ecosystem processes, and explores the evolution of American perspectives about nature. This year we also served as research assistants to and participated in a research symposium with Dr. Scott Sakaluk and Dr. Chad Johnson.

Our primary fieldwork was a behavioral ecology study on a sagebrush cricket (*Cyphoderris strepitans*) population at the Bridger-Teton field site. Over several nights, we cleared male crickets from a delineated section of the site and processed them in the lab facilities at AMK Ranch. Each male was affixed with number and marked with a color of fluorescent paint that indicated his date of capture. Once the males were released to their capture locations, their mating status (females chew up male wings while copulating) was recorded on subsequent nights.



Students during night time collecting.

In the lab we cared for research subjects and scored video recordings to determine the influence of diet on mating behavior. Females and males were held on low-quality diets (apple only) or high quality diets (apple, pollen, and cat chow ad libitum) for two days and then placed in Plexiglas containers for filming of mating behavior. We scored how frequently males called, elapsed time between female mounts, and duration of each mount. Once we returned to St. Louis, students statistically analyzed the data and determined that while diet significantly influenced subject mass, mating behaviors were not significantly different. This is due, in part, to sample size. We would like to continue this research in future years to gather more data from females in particular.



Students in lab analyzing data.

Students read numerous articles from Behavioral Ecology, Animal Behavior, Physiological Zoology, and

others. After discussing articles in detail with their instructors (Collis and Adams), students participated in several research based conversations with the principal authors (Harlow, Sakaluk, and Johnson).



Students in discussion session.

Living within a community of research scientists had tremendous benefits to my students. On numerous occasions we conversed with researchers about their work and gained valuable insights concerning the design and implementation of scientific studies. More specifically, we discussed research involving restoration ecology, feeding dynamics of bees, and disease transmission in small mammals.

Aside from conducting research, we explored Grand Teton and Yellowstone National parks while learning about ecosystem dynamics, the role of disturbance and succession, local flora and fauna, and the influences of geologic process in shaping landscapes and the communities that occupy them.



Students on a hike during a day of work.

UNIVERSITY OF NEBRASKA-LINCOLN FUNDAMENTALS OF GEOSCIENCE IN THE FIELD AND METHODS IN GEOSCIENCE FIELD INSTRUCTION

INSTRUCTORS ✦ DAVID HARWOOD ✦ KYLE THOMPSON
DEPARTMENT OF EARTH AND ATMOSPHERIC SCIENCES
CENTER FOR MATH AND COMPUTER SCIENCE EDUCATION
UNIVERSITY OF NEBRASKA ✦ LINCOLN



Students with Mount Moran in the background.

✦ CLASS OVERVIEW

This field course offers in-service teachers and pre-service science education majors an opportunity to discover the geological history of the Rocky Mountains and experience inquiry-based geoscience education during a 2-week journey across Wyoming, South Dakota and Nebraska. In 2012 this course utilized the UW-NPS facilities for 3 days in mid-June. The group built upon their growing geological knowledge to investigate the geological evolution of the Teton Range. The 2012 course included six in-service teacher participants (all from Nebraska), two pre-service graduate education majors, and one Geoscience Education Research professor who observed the process. The staff included two

instructors and one geology undergraduate teaching assistant. This course is offered through the University of Nebraska-Lincoln's Nebraska Math and Science Summer Institute (NMSSI) Program. This course improves educators' ability to teach inquiry-based science, gain knowledge and understanding of geoscience, and to demonstrate effective teaching methods that can integrate geoscience into K-12 learning environments. The UW-NPS facilities provide an excellent opportunity for participants to discover the natural history of the Teton Range and catch up on fieldbook notes while sitting at a real table - - a welcome change from our normal campground setting.

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

✦ **CLASS OBJECTIVES**

Major goals of these courses are: (1) to enhance the 'geoscience experience' for pre-service and in-service science educators, (2) to teach inquiry concepts and skills that K-12 educators are expected to understand and teach (as outlined in national standards), (3) to engage science educators in field-based geoscience education and inspire them to use inquiry and geoscience as unifying themes in their classes/teaching activities, (4) to provide participants with an opportunity to pursue authentic geoscience fieldwork, and (5) to enhance pedagogical understanding and provide all participants with a 'tool-kit' of effective inquiry-based, and discovery-learning teaching practices.

NATIONAL PARK SERVICE OPERATIONAL LEADER AMK RANCH (UW-NPS RESEARCH CENTER)

CATHIE JEAN ♦ NATIONAL PARK SERVICE ♦ GREATER YELLOWSTONE NETWORK



National Park Service inventory and monitoring staff at AMK Ranch in Grand Teton National Park
(Photo credit: NPS Laura O'Gan).

♦ OPERATIONAL LEADERSHIP

On May 30 and 31, 2012, a group of 18 National Park Service employees convened at AMK Ranch to learn the principles of Operation Leadership. Operational Leadership, at its core, is a systematic process that assists individuals in making informed decisions to reduce and manage risk in the workplace. Operational leadership is about each employee becoming a leader within his or her own job, taking responsibility for his or her own safety and the safety of coworkers, and learning to work effectively in a team environment. It pertains to every job skill and empowers employees to be assertive about their safety and the safety of their team.

The two-day course was facilitated by Patrick Hattaway and Reggie Treese of Grand Teton National Park, both of whom did a fantastic job introducing the group to the seven critical skills necessary to reduce the probability of human error.

Operational Leadership skills include:

1. Leadership

Not in the traditional sense, leadership here refers to individual and team leadership qualities. In the workplace each of us must be a leader in order to create a safer environment.

2. Human Error and Accident Causation

In order to reduce the probability of human error, we must first understand how and why human error occurs, and how human error leads to accidents.

3. Mission Analysis

Everything we do in life is a “mission;” as leaders we must be able to analyze each mission, assess its risks, mitigate those risks, and plan and act accordingly.

4. Stress and Performance

Once we begin the mission analysis process, we must be able to continually monitor our situation and be flexible to changing conditions. In order to do this, we must understand how stress, fatigue, and morale affect our performance.

5. Situational Awareness

Meeting mission demands and monitoring our mission success requires constant awareness of our surroundings, and the ability to recognize potential hazards.

6. Decision Making

The backbone of Operational Leadership is good decision making, and the fortitude to make those decisions and stand behind those who make them.

7. Effective Communication and Assertiveness.

Each of the first six skills requires team members to communicate effectively, and to be assertive about their involvement in the risk management process. Each employee is responsible for speaking up about potential hazards to the team.

The two-day course was organized by the Greater Yellowstone Inventory and Monitoring Network. Participants included a diverse mix of employees, many of which work for the Greater Yellowstone and Rocky Mountain I&M networks. These networks conduct inventory and monitoring activities in national parks such as Glacier, Rocky Mountain, Great Sand Dunes, Yellowstone, and Grand Teton, as well as many smaller parks including Bighorn Canyon National Recreation Area, and Little Bighorn Battle and Florissant Fossil Beds National Monuments.



National Park Service employees at the Berol Lodge prepare for another lesson in Operational Leadership (Photo credit: NPS Laura O’Gan).

UNIVERSITY OF WYOMING OUTDOOR STUDIO ART CLASS



INSTRUCTOR ✦ PATRICK KIKUT ✦ UNIVERSITY OF WYOMING ✦ LARAMIE



Students and faculty of the UW Art Program.

✦ CLASS OVERVIEW

Since its inception as a Summer Innovative Course in 2000, the Department of Art Summer Outdoor Studio class has been exceptionally grateful for the opportunity to stay and work at the AMK Research Station as part of the three week summer intensive. For art students, the dramatic setting and accommodation are inspiring and it is a highlight of the experience. From the AMK Ranch, students have full access to the Teton NP, Yellowstone NP as well as the National Wildlife Museum in Jackson. Art students also appreciate the interaction with students

from different disciplines in the sciences and often those conversations have direct impact on the creative work student's produce during their stay. The AMK staff and in particular Professor Hank Harlow have offered us incredible hospitality and generosity. Professor Harlow's knowledge of the geology, biology, and history of Teton National Park is invaluable to this course. Also, his enthusiasm for art and scientific research is infectious. Our stay at the AMK always culminates in an exhibition of student and faculty creative work, hosted by Hank Harlow, UW NPS Research Station Director.



Views from the Boathouse and dock.



Students taking inspiration from the boat dock.



Students working from the Johnson Lodge porch.

LARAMIE COUNTY COMMUNITY COLLEGE

GEOLOGY OF YELLOWSTONE AND GRAND TETON NATIONAL PARKS

GEOL 1035-60 Summer 2012



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



Students entering Grand Teton National Park.



Students entering Yellowstone National Park.

♦ CLASS OVERVIEW

This is a 3 credit hour field course in geology offered through Laramie County Community College.

The title of the course is Geology of Yellowstone National Park (GEOL 1035-60).

♦ COURSE DESCRIPTION

A study of Yellowstone's and the Grand Teton's earth materials and processes including rocks, minerals, streams, glacial history, geologic structures, earthquakes, and plate tectonics. Students acquire

scientific knowledge about the formation of Yellowstone's landscape, geothermal features, soils, and geologic hazards. Students will record observations and take notes in a field book that will be assessed as part of their grade.

♦ COURSE OBJECTIVE

Students gain an understanding and appreciation of the geologic processes that form the Yellowstone and Teton landscapes. Participation in daily hikes, lectures, field note preparation and readings will allow students to comprehend the geology of the area.

- We had 12 students participate in the course this year. The maximum enrollment is 13.
- Students learn the basic geologic processes involved in the creation and continuous shaping of the Yellowstone and Grand Teton ecosystem. Participating students are to have had at least an introductory geology, physical geography or other Earth science class; or, have a specific interest in geosciences. Through the use of the text Windows into the Earth: The Geologic Story of Yellowstone and Grand Teton National Parks (Smith 2000); recording field notes and making sketches in their field books; and, by exploring and seeing geologic features and processes in the field during daily field trips, students get a front row seat to the show that *is* Earth in action (see attached course syllabus and schedule).

◆ **COURSE BACKGROUND**

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

◆ **GRAND TETON NATIONAL PARK**

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

WYOMING INBRE COMMUNITY COLLEGE NETWORK RETREAT AMK RANCH (UW-NPS RESEARCH CENTER)



R. SCOTT SEVILLE ✦ WYOMING INBRE PROGRAM COORDINATOR
UNIVERSITY OF WYOMING ✦ LARAMIE



Students and Faculty from across the state. (R.S. Seville, 2012).

✦ MEETING OVERVIEW

The Wyoming INBRE Community College network meets yearly to present research taking place throughout the state. The focus is on undergraduate research taking place at the community colleges throughout Wyoming. The students present on their individual projects and faculty present on their research and partnerships they have formed. This is also a time for students and faculty to collaborate on projects statewide.

✦ PROGRAM BACKGROUND

The University of Wyoming is one of 22 institutions funded by the National Institutes for Health IDeA Networks for Biomedical Research Excellence (INBRE) Program. INBRE funding is intended to enhance biomedical research capacity, expand and strengthen the research capabilities of biomedical faculty, and provide access to biomedical resources for promising undergraduate students throughout the eligible states.

The Wyoming IDeA Networks for Biomedical Research Excellence (INBRE) Program is

funded by the National Institutes for Health National Center for Research Resources (NCRR). The ultimate goal the INBRE program is to promote the development, coordination, and sharing of research resources and expertise that will expand research opportunities and increase the number of competitive investigators in IDeA-eligible states. INBRE programs are intended to enhance the caliber of scientific faculty at research institutions and undergraduate schools, thereby attracting more promising students to these organizations.

The goals of Wyoming INBRE are to:

1. Establish a multidisciplinary research network with scientific foci that will build and strengthen biomedical research at UW and its partner institutions (Wyoming Community Colleges);
2. Provide research support to faculty, postdoctoral fellows and graduate students;
3. Create a "pipeline" for undergraduate students at UW and Wyoming community colleges to foster advanced education and training in the biomedical sciences;
4. Provide outreach activities for UW and community college students that are part of the university's INBRE network;
5. Enhance science and technology knowledge of the state's workforce;
6. Expand Wyoming research opportunities across the region.

To accomplish these goals Wyoming INBRE has established a number of programs designed to provide support for activities at all levels of education that enhance biomedically related research, training, education, and recruitment. Support for research is targeted at projects and programs that address health issues important to Wyoming residents that range from benchtop research to clinical, translational, or community based investigations. Two current areas of particular research interest are cardiovascular health and Type 2 diabetes. Support is currently provided to selected junior investigators on the UW Laramie campus developing projects related to the two focal areas. Additional support is available for researchers through the annual INBRE Pilot Grant Program, INBRE Graduate Assistantship Program, INBRE Undergraduate Support Grant Program, and the INBRE UW- CC Collaborative Grant Program. Proposals for projects related to cardiovascular health and Type 2 diabetes are encouraged but projects

focused on other health related issues will be considered. In addition INBRE is interested in partnering with other UW units to provide faculty start-up support for biomedically targeted faculty hires by colleges and departments and for major equipment purchases that build UWs research infrastructure.

To support biomedically related education INBRE has several programs available to UW faculty in Laramie and at Wyoming Community Colleges. Support is provided to participating Wyoming Community College faculty to develop research projects on their campuses that can engage students in the process of science and potentially attract them into biomedically related degree programs. The Outreach Videoconference System was developed and is maintained in part with INBRE support and is available for use for courses, seminars, and meetings at no charge for INBRE and other biomedically related uses. Other programs focused on education and recruitment include: INBRE Transition Scholarship Program that supports outstanding community college students transferring to the University to pursue baccalaureate degrees; INBRE Transition Course Program that supports development of distance delivered upper division courses for students across Wyoming pursuing baccalaureate degrees in the life sciences; INBRE Bioinformatics Summer Institute for students interested in pursuing advanced education and training in bioinformatics; and the INBRE Community College Videoconference Seminar Series that provides monthly seminars to community college faculty and students from UW, Community College and visiting scientists. In addition INBRE is developing projects for K-12 faculty and students that will enhance their knowledge of educational and career opportunities in biomedicine. INBRE is also interested in partnering with other UW and Community College units to support projects focused on public health and health awareness.

Last, Wyoming INBRE is working with other western INBRE states to develop regional opportunities for research collaborations and educational opportunities for students and faculty. In the future support will be available for researchers pursuing collaborative projects and educational opportunities with colleagues from INBRE programs in Alaska, Idaho, Montana, Nevada, New Mexico, Montana and the University of Washington Institute for Translational Sciences (ITHS), University of New Mexico Clinical and Translational Sciences Program (CTSA), and the University of Colorado Medical Center CTSA. Wyoming INBRE is working with these programs to foster innovative new decentralized regional clinical and translational research programs that leverage and build on resources throughout the

Western region. To achieve this goal, Wyoming INBRE is interested in promoting research programs that are community based and/or patient-centered.

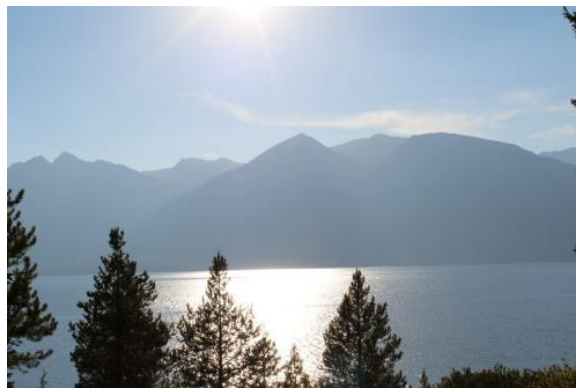
For questions or additional information contact Dr. Jun Ren (jren@uwyo.edu), INBRE Program Director or Scott Seville (sseville@uwyo.edu), INBRE Program Coordinator.



Delina Barbosa, student at University of Wyoming/Casper College Center, presents. (R.S. Seville, 2012).



Students enjoy some time exploring. (Barbosa, 2012).



View from AMK Ranch. (LCCC, 2012).



Students and faculty out on a hike. (LCCC, 2012).

This project was supported by grants from the National Center for Research Resources (5P20RR016474-12) and the National Institute of General Medical Sciences (8 P20 GM103432-12) from the National Institutes of Health.

SPECIAL TOPICS IN BIOLOGY: ECOLOGY OF GREATER YELLOWSTONE

INSTRUCTORS ✦ TONY STANCAMPIANO ✦ RICK JONES
OKLAHOMA CITY UNIVERSITY ✦ OKLAHOMA CITY



Students on Inspiration Point.

✦ CLASS OVERVIEW

Special Topics in Biology: Ecology of Greater Yellowstone is a freshman level, non-majors biology course emphasizing basic ecological principles with specific application to the ecosystems found in Grand Teton and Yellowstone National Parks. This course is offered during Maymester at Oklahoma City University. The field portion of the course took place from May 22-31, 2012.

This year 5 students participated in the course. After completing 4 units in the classroom, students embarked on a journey to the AMK Ranch with overnight camping stops in Bayfield, Colorado and Logan, Utah along the way. The 6 day stay at AMK allowed students to experience, in the field, all of the material they had learned in the previous 2 weeks in the on campus portion of the class. The on

campus learning consists of a series of lectures and associated exercises providing knowledge from multiple areas including:

- Physical ecology
- Basic geology
- Geology of Yellowstone and Grand Tetons
- Evolution and Natural Selection
- Systematics
- Field identification
- Journaling

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



College Van at Signal Mountain Lodge

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

Areas visited include, but are not limited to, the following:

- Lewis Falls
- Kepler Cascades
- Lonestar Geyser
- Old Faithful
- Upper Geyser Basin- Firehole River
- Midway Geyser Basin- Grand Prismatic Spring
- Lupine Meadows Trailhead
- LeHardys Rapids
- Hayden Valley
- Grand Canyon of the Yellowstone
- Lamar Valley
- Indian Pond
- Two Ocean Lake
- Miller Butte
- Jenny Lake Area
- Inspiration Point
- Moose Visitor Center and Moose-Wilson Road
- Laurence S. Rockefeller Preserve
- Willow Flats



Day Hikes.

The AMK ranch and the University of Wyoming make this unique opportunity possible for

students at OCU. Dr. Henry Harlow and his staff facilitate our housing and accommodations at the AMK. Upon our arrival, Dr. Harlow addresses the students to inform them of general information, current events, personal safety in the parks, bear biology, history of the AMK, and related ecology/biology topics.



Back Country Tracks.



Receiving background information from Park Naturalist

INTERNATIONAL COOPERATIVE TEAM STUDYING ICONIC NATIONAL PARKS

PATRICIA A. TAYLOR ✦ WYOMING SURVEY & ANALYSIS CENTER
BURKE D. GRANDJEAN ✦ DEPARTMENT OF STATISTICS
UNIVERSITY OF WYOMING ✦ LARAMIE



Team members setting out to check lake and stream levels in Grand Teton National Park (l-r: Wardell-Johnson, Peake, Herbst, Biggs, Taylor, photo by Bill Carter).

✦ MEETING OVERVIEW

In August 2012, six ecologists visiting the University of Wyoming from three continents joined with two University of Wyoming faculty researchers to continue a five-year project comparing changes in some of the world's most iconic national parks. Of particular interest to this group is the response of park managers to the potential effects of climate change on tourism.

There are seven natural protected areas included in the study so far, with an eighth site likely to be added. Presently the parks include Fraser Island and Great Barrier Reef in Australia; Grand Teton,

Yellowstone, and Glacier in the U.S.; Kruger in South Africa; and the Galapagos Marine Reserve in Ecuador. Efforts are under way to add a protected area in China or elsewhere in Asia to the project. The team members include: Duan Biggs, University of Queensland; Bill Carter, Sheila Peake, and Angela Wardell-Johnson, University of the Sunshine Coast; Burke Grandjean and Patricia Taylor, University of Wyoming; Marna Herbst, South African National Parks; and Diego Quiroga, University of San Francisco de Quito. Stephen Walsh of the University of North Carolina is also a key participant, but was unable to attend in August. Travel funds for the six international visitors came from their home institutions and from several departments and offices at the University of Wyoming.

Additional in-kind support (housing at AMK) was provided by the UW-NPS Research Station.

The team spent three days in Laramie for planning meetings and discussions before beginning their research travel north for site visits and interviewing at Grand Teton, Yellowstone, and Glacier. The time in Laramie also included a public presentation at the UW Union about the research. Using AMK as a base of operations in Grand Teton, the team conducted a series of meetings with park managers and rangers, interviews with concessionaires, observations comparing high-water marks along streams and lakes, and examination of the interpretive materials concerning climate change that are available at visitor centers. This process was repeated at both Yellowstone and Glacier.

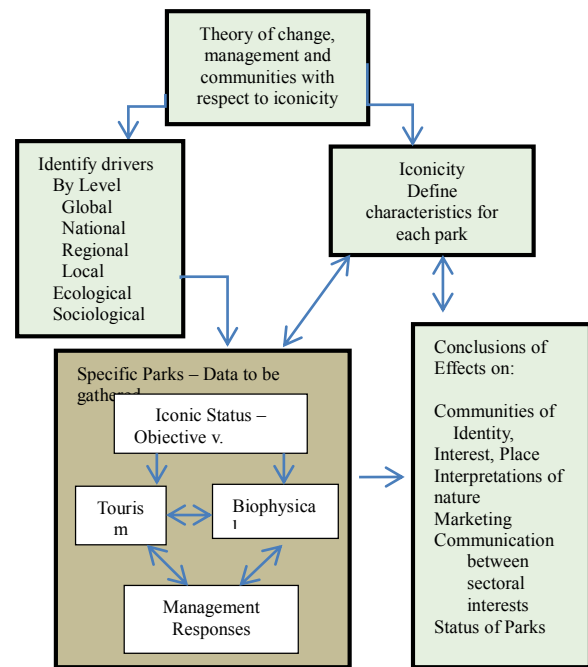


Group members examining interpretative materials .

The research team also held daily work sessions to compare observations on the parks and park visitors. As an immediate product, the meetings in August generated a detailed research plan for comparative case studies of the managerial planning process in three sites (Yellowstone, Kruger, and Galapagos), and one site report (on Galapagos) has been published with respect to tourist attitudes and climate change. More studies and comparisons are currently under way. The meetings also laid the groundwork for several grant proposals to fund similar studies at the other sites, and to integrate the results of the case studies into an overall comparative analysis.

Finally, the meetings gave us the time to consider differences in our own back-grounds, the

studies of protected areas in our own regions, and then how we would weave together the theories of change, management, and communities with our iconic national parks. By developing a theoretical outline that places the effects we wish to study with the data that need to be gathered, our work can run parallel even as we work at separate locations. This approach should help us to have data which are comparable from different iconic parks so that we may develop a comparative model of social, climate, and economic changes on parks, their management, and the tourism associated with the parks. The more people value the parks and return as tourists, the more likely the parks will be maintained into the next century.



UTAH STATE UNIVERSITY WATERSHED SCIENCES GRADUATE STUDENT INDUCTION COURSE



INSTRUCTORS ♦ JOSEPH M. WHEATON ♦ PATRICK BELMONT
UTAH STATE UNIVERSITY DEPARTMENT OF WATERSHED SCIENCES ♦ LOGAN



Student and faculty participants.

♦ CLASS OVERVIEW

Utah State University Department of Watershed Sciences runs an introductory course for all incoming graduate students (15 in Fall 2012) immediately prior to each Fall semester. The course is an intense, five day introduction to the fundamental concepts of Watershed Science, as well as the people

of the Department of Watershed Science and the techniques they use in research. The course begins with one day focused on water quality and wetlands at Cutler Reservoir in Logan, Utah, then one and a half

days focusing on collection of fish, remotely sensed data, and topographic surveys in the Logan River watershed, followed by one and a half days discussing landscape organization and evolution and making field observations in the Grand Teton region. We use AMK Ranch for lectures, discussions, group dinners, sleeping quarters, and as a central base for Teton area activities, including rafting on the Snake River (photos above).

♦ CLASS OBJECTIVES

The general objectives of the course are to help incoming graduate students get acquainted with the nearby landscape, the people in the Department of Watershed Sciences, some of the broader concepts and questions that define Watershed Science, and some of the techniques that USU faculty use to answer those questions.

A sampling of the techniques demonstrated: Terrestrial laser scanning, Real-time kinematic GPS, Collection of visible in IR aerial photography using drone aircraft, Field mapping, Soil evaluation, Collection and analysis of climate data, Fish and macroinvertebrate sampling, water quality monitoring.



Students running the river in rafts.



Students running paddle board and kayaks.