CHANGE IN DECIDUOUS WOODY VEGETATION, IMPLICATIONS OF

INCREASED WILLOW (*SALIX* SPP.) GROWTH FOR BIRD SPECIES DIVERSITY,

AND WILLOW SPECIES COMPOSITION IN AND AROUND YELLOWSTONE

NATIONAL PARK'S NORTHERN RANGE

by

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APPROVAL

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Lisa Marie Baril

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DEDICATION

I dedicate this thesis to my grandparents, Donald and Eileen Evans whose incredible strength, determination, and wonderful humor has and continues to inspire me in everything I do. I am a better person for having had you both in my life. Thank you.

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ABSTRACT

Deciduous woody vegetation (DWV) in Yellowstone's northern range is a rare, but important habitat type. Including willow, alder, aspen, and cottonwood, DWV was limited in height and areal extent since the early 1900s. Since the mid-1990s; however, DWV has increased in height and areal extent in some locations. Previous studies regarding DWV change have focused on quantifying change in vegetation growth in areas of limited extent and none have quantified increased DWV growth at the scale of the landscape. Furthermore, no studies have evaluated the implications for increased growth of DWV for wildlife in the region or how DWV species themselves may influence rates of growth. In this thesis I evaluate change in DWV within wetland and riparian areas using aerial photographs from 1991 and 2006. I also investigate how an increase in willow, the dominant component of DWV in the region, has likely influenced bird diversity. Finally, since willow species vary with respect to genetic limitations on growth and reproduction that in turn may influence observed patterns of growth; I examine willow species composition across the northern range. Results of the air photo interpretation revealed a 170% increase in DWV. Most plots that increased did so by recruitment rather than densification; however, DWV was difficult to detect below 100 cm indicating that the number of plots increasing by recruitment may have been overestimated. Bird community variables were examined in three willow growth conditions: height suppressed, recently released, and previously tall (tall prior to observed increase in growth). I found that willow structure generally increased in complexity from structurally simple height suppressed willows to structurally complex previously tall willows and that this allowed for greater bird richness, abundance, diversity, and the abundance of several willow dependent bird species. I also found that willow species composition was similar and diverse between the released and previously tall condition, but that the suppressed condition was dominated by a singe species. I conclude that increased DWV has allowed for greater bird diversity in the northern range and that increased willow growth in the suppressed condition may be influenced by species composition there.

CHAPTER 1.

INTRODUCTION TO THESIS

Deciduous woody vegetation (DWV) in Yellowstone National Park's northern range has been height suppressed since the early 1900s (NRC, 2002). DWV includes aspen (*Populus tremuloides*), cottonwood (*Populus* spp.), willow (*Salix* spp.), and alder (*Alnus* spp.) and occurs in wetland and riparian areas throughout the northern range (Chadde et al., 1988). The northern range is a low elevation region in northern Yellowstone where winter ungulate densities, in particular elk (*Cervus elaphus*) and bison (*Bison bison*), are high (Houston, 1982). In the middle to late 1990s DWV began to increase in height growth and areal extent in some locations across the northern range (e.g. Groshong, 2004; Beyer et al., 2007). Although DWV represents a small component of the region's vegetation, its' significance in maintaining several important ecological processes (e.g. minimizing stream erosion and aiding in nutrient cycling) and providing habitat to a variety of wildlife (e.g. birds, beaver, moose) is well known (Naiman and Décamps, 1997).

The recent increase in DWV is hypothesized to be the result of a trophic cascade whereby wolves (*Canis lupus*), reintroduced to Yellowstone in 1996, have altered the density and foraging behavior of elk resulting in increased growth of DWV (Ripple and Beschta, 2004). Alternatively, recent growth could be the result of climate change. Longer growing seasons resulting from warmer spring and fall temperatures have resulted in increased DWV productivity in the Rocky Mountain region (Cayan et al.,

2001, Myneni et al., 1997; Nemani et al., 2003). Additionally, warmer spring

temperatures have altered the timing (Stewart et al., 2005) and intensity (Lins and Slack,

1999) of peak river flows that may affect patterns of vegetation growth.

Studies concerning DWV change up to this point have largely focused on drivers

responsible for the observed increase in growth; however, several important aspects of

change in DWV across Yellowstone's northern range also merit study. This thesis

focuses on three of these aspects: 1) landscape level changes in DWV; 2) implications of

an increase in willow, the dominant component of DWV, for bird diversity in the region;

and 3) differences in willow species composition that may partially explain spatial

variation in the observed increase in willow growth in the northern range.

Specifically, in Chapter 2 I evaluate change in DWV across riparian and wetland

areas across the northern range using a set of aerial photographs from 1991 and 2006.

Although several studies have documented change in DWV for some locations, none

have evaluated change in this cover type at the scale of the landscape. Knowledge of

whether change in DWV is detectable at this scale and the extent of that change is an

important first step in evaluating hypotheses regarding change in growth for this cover

type in the region.

In Chapters 3 and 4 I take a narrower approach by focusing on willow, the

dominant component of DWV in the region and the genus thought to be experiencing the

greatest increase in growth in recent years. While willow has increased in growth in the

northern range, changes have not been uniform. Some willow stands remain height

suppressed while others have been released from height constraining factors. In Chapter

3 I investigate how birds have likely responded to increased willow growth by comparing the bird community present in each of three willow growth conditions: height suppressed, recently released, and previously tall or tall prior to 1998 when observations of willow release first occurred. Finally, in Chapter 4 I compare willow species composition among the three willow growth conditions. Differences in patterns of willow growth among growth conditions may be the result of species composition which could have implications for spatial variation in future rates of willow growth in the region.

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Literature Cited

Beyer, H.L., E.H. Merril, N. Varley and M.S. Boyce. 2007. Willow on Yellowstone's northern range: evidence for a trophic cascade? Ecological Applications 17: 1563-1571.

Cayan, D.R., S.A. Kammerdiener, M.D. Dettinger, J.M. Caprio, and D.H. Peterson. 2001. Changes in the onset of spring in the western United States. Bulletin of the American Meteorological Society 83: 399-415.

Chadde, S.W., P.L. Hansen, and R.D. Pfister. 1988. Wetland plant communities of the Northern Range, Yellowstone National Park. School of Forestry, University of Montana.

Groshong, L.C. 2004. Mapping riparian vegetation change in Yellowstone's Northern Range using high spatial resolution imagery. M.A. thesis, University of Oregon, Eugene, OR.

Houston, D.B. 1982. The northern Yellowstone elk: ecology and management. MacMillan Publishing Co., Inc., N.Y. 474 pp.

Lins, H.F. and J.R. Slack. 1999. Streamflow trends in the United States. Geophysical Research Letters 26: 227-230.

Myneni, R.B., C.D. Keeling, C.J. Tucker, G. Asrar and R.R. Nemani. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. Nature 386: 698-702.

Naiman, J.R. and H. Décamps. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology and Systematics 28: 621-658.

National Research Council. 2002. Ecological dynamics of Yellowstone's northern range. National Academy Press, Washington, D.C.

Nemani, R.R., C.D. Keeling, H. Hashimoto, W.M. Jolly, S.C. Piper, C.J. Tucker, R.B. Myneni, and S.W. Running. 2003. Climate-driven increases in global terrestrial net primary productivity form 1982 to 1999. Science 300: 1560-1563.

Ripple, W.J. and R.L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? Bioscience 54: 755-766.

Stewart, I.T., D.R. Cayan, and M.D. Dettinger. 2005. Changes toward earlier streamflow timing across western North America. Journal of Climate 18: 1136-1155.

CHAPTER 2.

CHANGE IN DECIDUOUS WOODY VEGETATION ACROSS YELLOWSTONE'S
NORTHERN RANGE FROM 1991 TO 2006

Introduction

Deciduous woody vegetation (DWV) in Yellowstone National Park's northern range is a historically rare cover type (NRC, 2002). Composed of willow (*Salix* spp.), narrow-leaf cottonwood (*Populus augustifolia*), black cottonwood (*Populus trichocarpa*), trembling aspen (*Populus tremuloides*), and alder (*Alnus* spp.), DWV occurs in wetland and riparian areas throughout the northern range (Chadde et al., 1988). The northern range is a low elevation region in the northern portion of Yellowstone where many ungulates, in particular elk (*Cervus elaphus*) and bison (*Bison bison*), reside during the winter months when deep snows limit movements and the availability of forage at higher elevations (Houston, 1982). Although DWV represents a minor cover type in the northern range, this habitat is one of the most highly productive, in terms of aboveground net primary productivity (Hansen et al., 2000), and species rich (Hansen et al., 2003; Finch and Ruggiero, 1993) environments in the arid west.

DWV provides habitat for as much as 80% of the local avian diversity in the region (Berger et al., 2001) as well as providing year-round habitat and forage for moose (Stevens, 1970; Dungan and Wright, 2005) and beaver (*Castor canadensis*) (Wolf et al., 2007). Although elk are primarily grazers, DWV provides important winter forage when deep snows limit access to preferred grasses and forbs (Christianson and Creel, 2007).

DWV also provides important ecosystem services by stabilizing banks, thus reducing soil inputs into aquatic environments, aiding in nutrient cycling between aquatic and terrestrial environments, modifying microclimate, and influencing stream channel morphology where DWV occurs along riparian zones (Naiman and Décamps, 1997).

Since the late 19th and early 20th centuries however, there has been documented loss of DWV across the northern range. Pollen records in lake sediments indicate a decline in willow since 1920 (Barnosky, 1988; Engstrom et al., 1991). Repeat photographs show complete loss of willow communities between 1871 and 1988 for 41 of 44 photosets for the northern range and considerably reduced stature for the remaining three photosets (Chadde and Kay, 1991). Recruitment of aspen into adult size age classes has been rare with the majority of the current tree-sized aspen originating prior to 1920 (Ripple and Larsen, 2000; Larsen and Ripple, 2003). Cottonwood establishment has also steadily declined since the early 1900s ceasing completely by the 1940s (Beschta, 2003). The loss and low stature of DWV has been attributed to factors including extensive browsing by elk*,* loss of beaver, fire suppression, drought, or an interaction among these factors (YNP, 1997).

Recently, YNP biologists have observed that DWV is expanding in height in some locations throughout the northern range (R. Renkin, personal communication, 2005). This is supported by a study of repeat photography showing an increase in cottonwood and willow height for 6 of 8 photosets from 1977 to 2002 (Ripple and Beschta, 2003). A study using high spatial resolution imagery found that riparian vegetation including willow, alder, and cottonwood, increased in areal extent by 279% in

a 4-km^2 region along the Lamar River-Soda Butte Creek confluence between 1995 and 1999 (Groshong, 2004). The recently documented "first significant growth in young aspen in the northern range for over half a century" (Ripple and Beschta, 2007) and a two-fold increase in willow stem growth ring areas also support observations of increased DWV growth (Beyer et al., 2007).

The recent growth of woody vegetation coincides with the reintroduction of wolves (*Canis lupus*) in 1995 and 1996, stimulating the hypothesis that the expansion of DWV may be the result of a trophic cascade between wolves, elk, and DWV (Ripple and Beschta, 2004). The trophic cascade hypothesis states that predation by wolves has altered the density and foraging habits of elk resulting in reduced browsing and increased growth of deciduous woody plants (Ripple and Beschta, 2004). This hypothesis has stimulated considerable interest and research in how top-level predators may drive top-down controls on ecosystem function and biodiversity (Berger et al., 2001; Ripple and Beschta; 2003; Fortin et al., 2005; Hebblewhite et al., 2005; Ripple and Beschta, 2006; Beyer et al., 2007).

While the trophic cascade hypothesis has received a great deal of attention in the literature, alternative mechanisms may also explain recent increases in DWV growth. Longer growing seasons resulting from warmer spring and fall temperatures have resulted in increased DWV productivity in the Rocky Mountain region (Cayan et al., 2001, Myneni et al., 1997; Nemani et al., 2003). Additionally, warmer spring temperatures have led to greater (Lins and Slack, 1999) and earlier (Regonda et al., 2005 and Stewart et al., 2005) peak stream flows that may affect patterns of vegetation

growth. Interestingly, increases in DWV height growth have not occurred uniformly across the northern range indicating that whether recent increases are the ultimate result of climate change and/or a trophic cascade, stand level biophysical characteristics such as soil texture, nutrient availability, slope, aspect, or other drivers may be important proximate factors in determining which stands of DWV are significantly increasing in height growth.

Although several studies have established change on a per species basis for aspen, willow, cottonwood, and alder over fine spatial scales, few have evaluated change in DWV at the scale of the landscape for the northern range (but see Savage and Lawrence, in press). Furthermore, the majority of these studies have established change in height as opposed to areal extent (but see Savage and Lawrence, in press; Groshong, 2004; McColley, 2007). Addressing hypotheses regarding the causes of DWV change in the northern range are beyond the scope of this study; however, this study does provide a necessary first step in evaluating hypotheses regarding causes of vegetation change in the northern range by establishing if change in areal extent (i.e. canopy cover) is detectable at the scale of the landscape and, if so, the extent of that change.

Medium and high-resolution aerial photography in conjunction with a geographic information system (GIS) can help resolve questions of landscape change and inform management decisions. Aerial photographs are best suited for analysis of change in DWV in the northern range for two reasons. First, aerial photos exist for the entire northern range since 1963 for multiple dates; and second, they are of a fine enough resolution to distinguish DWV from other vegetation types.

The objective of this study was to determine change in areal extent of DWV across Yellowstone's northern range between 1991 and 2006. We asked 3 questions for this study. First, was there a net positive gain in the areal extent of DWV in the northern range? Second, did plots containing DWV in 1991 increase in areal extent of DWV by 2006 (i.e. densification)? Densification is defined in this study as an increase in DWV for plots already containing DWV and can occur by an increase in crown cover for plants present or establishment of new plants. Third, did plots absent of DWV in 1991 gain in areal extent of DWV by 2006 (i.e. recruitment)? Hypotheses for each of these questions follow:

> Hypothesis 1: There was a net positive gain in areal extent of DWV in the northern range between 1991 and 2006.

> Hypothesis 2: Plots containing DWV in 1991 gained or expanded in areal extent of DWV in 2006 and will be referred to as densification.

> Hypothesis 3: Plots absent of DWV in 1991 gained in areal extent of DWV and will be referred to as recruitment.

Methods

Study Area

This study was conducted in Yellowstone's northern range defined as the region occupied by Yellowstone's northern wintering elk herd covering a 153,000 ha area in the Gardner, Lamar, and Yellowstone River watersheds (Figure 2.1) (Houston, 1982). Elevation varies from 1500 to 3209 m (Savage and Lawrence, in press). The majority of the northern range lies within Yellowstone National Park while the remainder lies within

the Gallatin National Forest and various private agricultural and ranch lands north of the

Yellowstone boundary (Houston, 1982). The semi-arid region receives approximately

260 mm of precipitation per year, most of which falls during the growing season

(Despain, 1987).

Relatively nutrient poor rhyolitic soils were deposited across the region two to

three million years ago during a period of intense volcanic activity while relatively rich

andesite soils found along valley bottoms were deposited approximately 12,000 to 14,000

years ago following the retreat of the Pinedale glacier (Christianson, 2001). Vegetation

in the study region is dominated by grasslands and sagebrush steppe in the lower

elevations while conifer forests predominate at higher elevations (Houston, 1982).

Deciduous woody vegetation (willow, aspen, cottonwood, and alder) occurs in the

lower elevation regions in four general landscape settings: "1) along stream and river

channels, in overflow channels, and on floodplains; 2) in depressions and around kettle

lakes formed by blocks of glacial ice; 3) adjacent to springs and seeps on lower mountain

slopes; and 4) in abandoned beaver channels and ponds" (Chadde et al., 1988). Willows

in particular can be found along portions of the Lamar River, Soda-Butte Creek, and

along lower order streams throughout the northern range, but also occur in small patches

in springs and seeps on toe slopes and particularly in flooded channels influenced by

beaver activity (Chadde et al., 1988). Understory vegetation within riparian areas are

dominated by various native sedges (*Carex* spp.), grasses, and forbs.

Imagery

To quantify change in DWV, we used a set of 1:24,000, true color aerial

photographs of the northern range from the 1991 growing season as the first date of

imagery (hereafter referred to as date 1). For the second date of imagery, we used a

digital ortho quarter-quadrangle (DOQQ) with 1-m ground sample distance rectified to

the National Mapping Standards at the 1:24,000 scale created by United States

Department of Agriculture's Aerial Photography Field Office (USDA-APFO). The

DOQQ is based on 7.5 x 15 or 7.5 x 11.25 minute quarter quadrangles. Quarter-quad

imagery was projected to the UTM coordinate system, NAD83 datum. The final image

was created by compressing quarter quadrangle tiles that cover the study region using

multi-resolution seamless image database (MrSID) compression with a ratio of 15:1 and

9 compression levels (hereafter referred to as date 2). All imagery and GIS layers were

obtained through the Yellowstone Center for Resources Spatial Analysis Center in

Mammoth, Wyoming.

Preprocessing

The area of change analysis included those portions of the northern range that

have the potential to support DWV. The DOQQ was subset using a wetlands layer and a

rivers and streams layer with a 60-m buffer on either side of the water body because this

is thought to include the entire width of the riparian zone in the region (personal

observation). Only those rivers and streams on less than 10% slope were included

because DWV generally cannot establish on steep gradients (Brichta, 1987). Within the
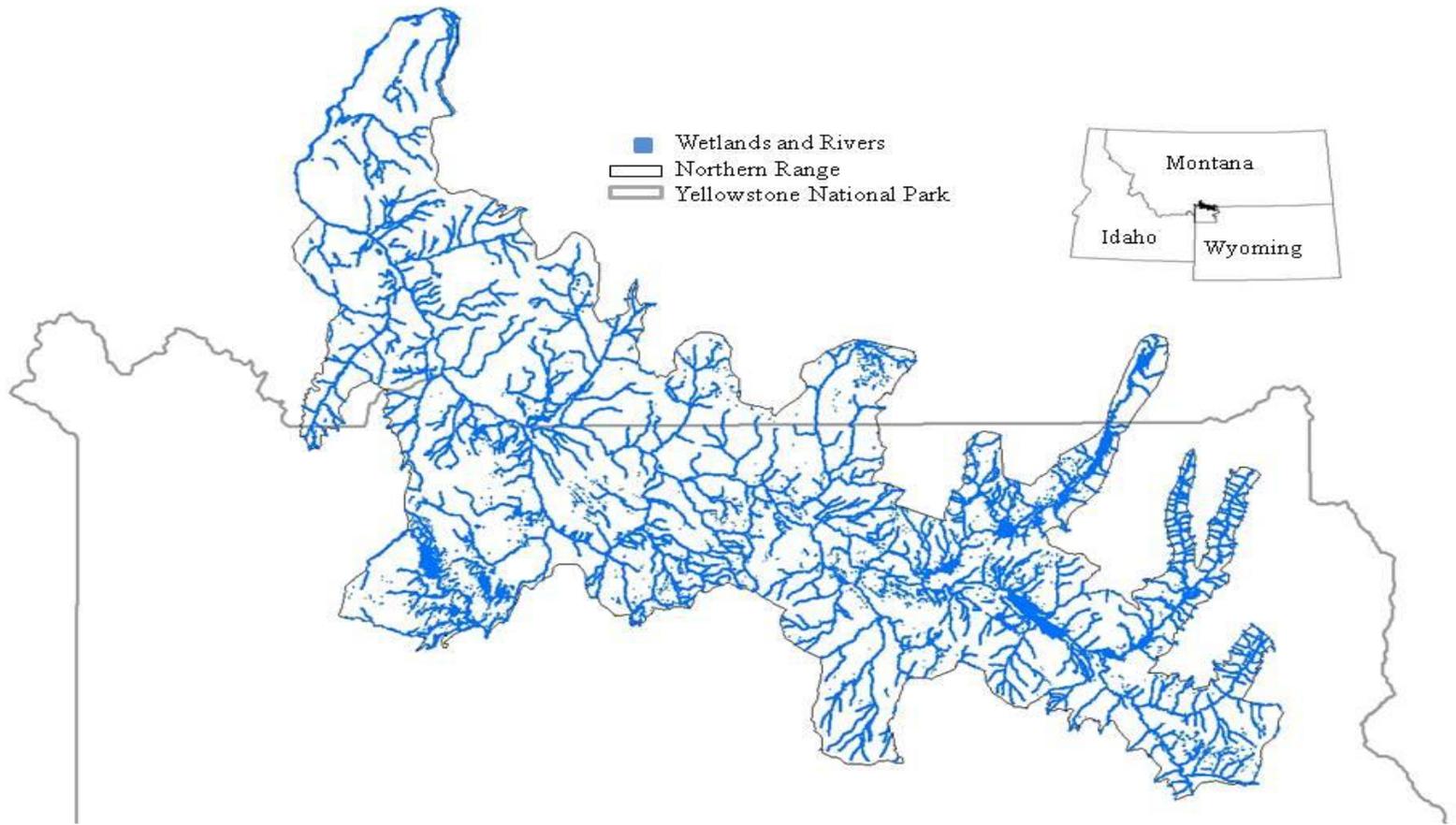
Figure 2.1. Map of the northern range study area.

subset area, a random sample of 1000, 0.81-ha plots were generated using Hawth's

Analysis Tools (Beyer, 2004). Plots of this size were chosen because it is the finest

resolution for which DWV areal cover could be accurately measured given the scale of

the aerial photographs. Plots were sampled if they contained less than 20% conifer and

were absent of manmade features (e.g. buildings, roads, agriculture). This resulted in 547

sample plots. Plots containing portions of a water body were moved the minimum

distance necessary to eliminate water from the sample plot. If the matched plot location

in date 1 imagery lied within a water body due to differences in channel morphology

between dates, the sample was removed from the analysis.

Change Detection and Analysis

Sample plots located in the DOQQ were then located in the 1991 photos by

matching landscape characteristics such as trees and roads occurring in both dates of

imagery. Both the 2006 DOQQ and the 1991 hard copy air photos were sampled with a

10-dot grid of equidistant spaced points. Each point center on the grid covering DWV

was considered a "hit". The percent DWV cover in each sample was calculated by

summing the number of "hits" in the sample at 10% increments. The data were

summarized by the percent DWV cover found in 1991 and 2006 and the percent of plots

that increased, decreased, and remained stable.

Although the paired differences do not meet the assumption of normality, the

sample size is large enough that the central limit theorem allows for use of parametric

statistics (Devore and Peck, 2005). Hypothesis 1 was evaluated using a two-sided paired

t-test of the full data set to determine the trajectory of DWV change. Hypothesis 2 was

evaluated by conducting a two-sided paired t-test using only those plots containing at least 10% DWV in 1991. Hypothesis 3 was evaluated by conducting two-sided paired t-test using only those plots that did not contain DWV in 1991. Data were analyzed using R Statistical Data software (R, 2007).

Accuracy Assessment

We used existing field data to qualitatively assess the accuracy of the air photo classification because field data were not collected at a resolution compatible to that of the air photo sampling, rendering a traditional quantitative accuracy assessment impossible. Field data consisted of two types: line transects and circular plots of willow stands located throughout the northern range. For assessing the air photo interpretation, willow is an adequate proxy for all DWV because of the similarity in color, texture, and crown shape at the scale of the imagery used.

Information on willow height was collected along 15 line transects during the summers of 1990 and 2006 by USGS biologists L. Zeigenfuss and F. Singer. These data were used to assess the minimum height detectable on the imagery and to determine the trajectory of willow change with respect to height growth, which is related to areal cover. The number of plants measured along transects varied from 2 to 12 across both years with 108 and 117 plants total measured in 1990 and 2006 respectively. Circular plot measurements of willow presence/absence and willow height if present were taken at 16 locations in each of 66, 5024-m^2 circular plots during the growing seasons of 2006 and 2007 (Baril, L. M., and A.J. Hansen, unpublished data). The 16 points were arranged as 4 points spaced 10 m apart in each of the cardinal directions. Each point where willow

was present was considered a "hit" and the percent cover for the plot was calculated by summing the number of hits in the sample at 6.25% increments. These data were used to assess the accuracy of the date 2 classification.

There are two sources of potential error in this study: imagery differences between the two dates and between-class confusion within imagery. To address imagery differences we attempted to assess the minimum DWV height detectable in date 1 and date 2 imagery. Similarity in minimum height detectable between imagery will support the assumption that image differences were negligible and that the results we observed in the change classification were genuine and not an artifact of imagery differences. Each species of DWV can occur at heights as low as a few cm. To determine the minimum DWV height detectable on air photos we sampled line transects of known willow height for each transect where all plants measured were marked with a GPS. For date 1 imagery this resulted in 11 transects where between 2 and 10 plants were measured per transect in 1990. For the 2006 DOQQ comparison this resulted in 13 transects where between 2 and 11 plants were measured per transect. Due to close proximity, 4 transects were combined in both dates resulting in 8 and 10 transects for 1990 and 2006 respectively. We then evaluated the transect for willow presence using a binary presence/absence response and compared this to the mean, minimum, maximum, and variation in willow height in that transect to estimate minimum vegetation height detectable in both images.

Although sufficient field data to assess the accuracy of date 1 classification do not exist, we were able to assess the accuracy of date 2 imagery using the circular plot data of percent willow cover thereby addressing between class confusion in date 2 imagery. We

created a shape file in Arc 9.2 of 0.50 ha circular plots matching the field sampling locations and then calculated percent willow cover for each sampling plot in the DOQQ. Using the results of field data and DOQQ observations we conducted a regression analysis to determine the relationship between the two methods. A slope of 1 and a y-intercept of 0 would indicate complete agreement between the two methods. To examine if there was a systematic bias between methods we plotted field measurements against the differences between measurements and tested for a linear relationship between the two. A slope of 0 would indicate non-systematic bias.

Since data used to determine the minimum height detectable in the imagery were limited we conducted another regression using only those data on plant height from each plot above the determined threshold to test the accuracy of our determination. An improvement in regression coefficients on the subset data compared to regression coefficients resulting when all data are used will support our determination of the minimum height detectable at least for the 2006 imagery.

Finally, using line transects we conducted a paired t-test on mean plant height per transect where at least five plants were measured per transect in each date to determine the trajectory of change in field measurements. The results of this analysis were compared to the trajectory of change in the change detection. This resulted in 9 transects measuring 75 and 78 plants in 1990 and 2006 respectively. Because the effective sample size for the paired t-test was only 9, we also conducted an unpaired t-test using individual plants, thereby increasing the sample size to 84 and 97 for 1990 and 2006 respectively.

This analysis included all plants regardless of the number of plants measured per transect. We expected the trajectory of change for the field data to match the trajectory of change in the change detection classification thereby providing evidence that what we observed in the imagery classification was accurate.

<div align="center">Results</div>

Accuracy Assessment

In 1990, mean height among transects ranged from 47 to 200 cm (Table 2.1). Willow was observed in all transects on the air photos except 2 where willow heights ranged from 34 to 74 cm. Willow was observed in the remaining 6 transects where heights ranged from 51 to 290 cm. In 2006 mean height ranged from 25 to 305 cm. Willow was detected in all transects except one where willow heights ranged from 24 to 32 cm. Willow was observed in the remaining 10 transects where heights ranged from 36 to 360 cm. With overlap in height ranges between transects, determining minimum height detectable on the imagery is impossible. Instead, we used the lowest mean for the transect where willow was observed as a threshold. In 1990, the minimum mean height where willow was observed was 106 cm and in 2006 it was 95 cm, therefore we concluded that willow and other DWV must be approximately 100 cm tall to be consistently classified as DWV.

Field measurements of percent willow cover as measured in the field correlated relatively well with percent willow cover as measured in the DOQQ ($R^2 = 0.69$, F = 142, $P < 0.0001$; Figure 2.2, panel A). The slope of 0.78 indicates that in general we

underestimated willow cover in the DOQQ. Approximately 61% of the DOQQ plots

underestimated willow cover, 19% overestimated willow cover, and 20% exhibited

complete agreement with the field data. All errors were within 43.75 percentage points;

however, the majority of errors (88%) were within 25 percentage points. The mean of

the differences was approximately 8%; however underestimates tended to be greater for

larger values of percent willow cover (Figure 2.2, panel B). We found a weak but

significant linear relationship between the differences between methods and the percent

cover recorded in the field ($R^2 = 0.15$, F = 11.16, P < 0.0001).

Table 2.1. Willow observed by transect in 1991 and 2006 air photos
for 1990 and 2006 field data. Height per transect is arranged in order
of mean height (cm).

Transect	Willow observed in photos	n	mean	min	max	range	std.dev
1990							
JBWB	No	6	47	34	74	40	14.35
MS4	No	2	51	43	59	16	11.31
BT	Yes	7	106	51	132	81	27.19
SB1-4	Yes	22	152	81	273	192	43.99
LL3	Yes	7	162	117	187	70	25.69
LS1	Yes	4	169	72	282	210	92.32
LS2	Yes	5	178	84	240	156	65.96
LL1	Yes	8	200	108	290	182	68.39
2006							
JBWB	No	6	25	14	32	18	6.86
MS2	Yes	5	95	79	135	56	23.04
SB1-4	Yes	22	122	90	200	110	33.89
MS4	Yes	2	135	120	150	30	21.21
LS1	Yes	4	168	80	220	140	63.96
LL1	Yes	8	198	36	330	294	104.79
BT	Yes	7	204	165	235	70	26.57
LL3	Yes	7	246	100	360	260	89.43
LS2	Yes	5	270	180	340	160	62.44
MS1	Yes	2	305	290	320	30	21.21
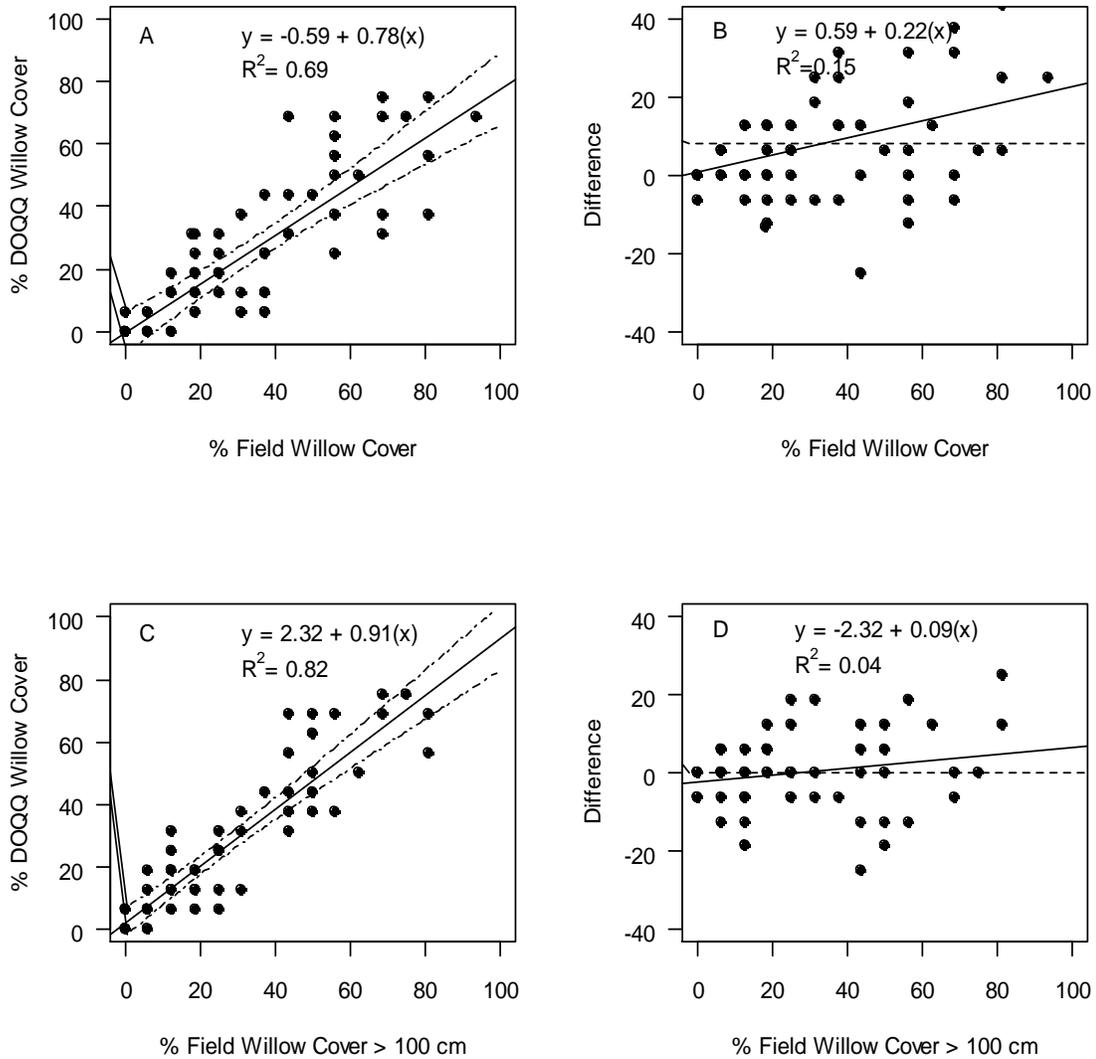
Figure 2.2. Correlation between % willow cover in field sampling plots and % willow cover in the DOQQ. Panel A shows the correlation between true % willow cover as measured in the field against the DOQQ measurements with a 95% confidence band around the regression line. Panel B shows % willow cover measured in the field correlated to differences between methods (difference = field measurements – DOQQ measurements). Panel C shows the correlation between % willow cover in the field excluding willows < 100 cm against DOQQ measurements with a 95% confidence band around the regression line. Panel D shows the % willow cover > 100 cm measured in the field correlated to differences between methods (difference = field measurements > 100 cm – DOQQ measurements). The dashed line in panels B and D represent the mean difference and the solid line represents the correlation between differences and percent field willow cover.

Since the minimum vegetation height detectable with the imagery was estimated at 100 cm, we excluded all willow points with willow less than this height from field measurements for comparison with the DOQQ classification, which improved the model fit ($R^2 = 0.82$, F = 294, P < 0.0001, Figure 2.2, panel C). The slope increased to 0.91 indicating stronger agreement between methods. The improved relationship also supports our finding that plants below 100 cm are likely not detectable. The percent of the DOQQ plots that agreed and overestimated percent cover increased to 36% and 33% respectively while plots that underestimated willow decreased to 31% providing evidence that there was no systematic bias. In addition all errors were within 25 percentage points of the DOQQ classification and 54% of the plots were within 6.25 percentage points of the DOQQ classification. The mean difference between methods was 0% and there appears to be no systematic relationship between the subset of percent willow cover and the DOQQ (Figure 2.2, panel D). There was not a significant relationship between the differences and percent willow cover over 100 cm ($R^2 = 0.05$, F = 2.91, P = 0.069).

The results of the paired t-test using line transect data were not significant (n = 9, t = -1.8881, P = 0.096) indicating there has been no significant change in willow height growth from 1990 to 2006. Mean willow height in 1990 was 141 cm, but was 188 cm in 2006. The data used in this analysis were limited to only 9 transects, which was likely not a large enough sample size to make inferences. When transects were not used as replicates and instead individual plants were used as samples the sample size increased to 84 and 97 plants for 1990 and 2006 respectively. The 2006 data were square root transformed to meet the assumptions of normality. The results of the unpaired t-test were

significant ($n_{date1} = 84$, $n_{date2} = 97$, t = ⁻19.16, P < 0.0001) indicating there has been an increase in willow height over the study period. Mean willow height in 1991 was 138 cm and was 176 cm in 2006 — a 12% increase in height.

Change Detection and Analysis

Of the 1,000 plots generated, 547 met the sampling criteria. The major areas sampled included the Gardner River, Lamar River, Soda Butte Creek, Slough Creek, and areas around Swan Lake (91%) with the remaining 9% of plots located in scattered wetland areas and low order creeks throughout the northern range.

Of the plots sampled 13% (n = 70) contained at least 10% DWV in 1991, but 29% (n = 157) of plots sampled contained at least 10% DWV in 2006. None of the plots contained more than 60% cover in 1991 and no more than 80% cover in 2006 (Figure 2.3). The majority of plots sampled did not contain DWV in either date indicating that although DWV appears to have increased it continues to be a rare cover type.
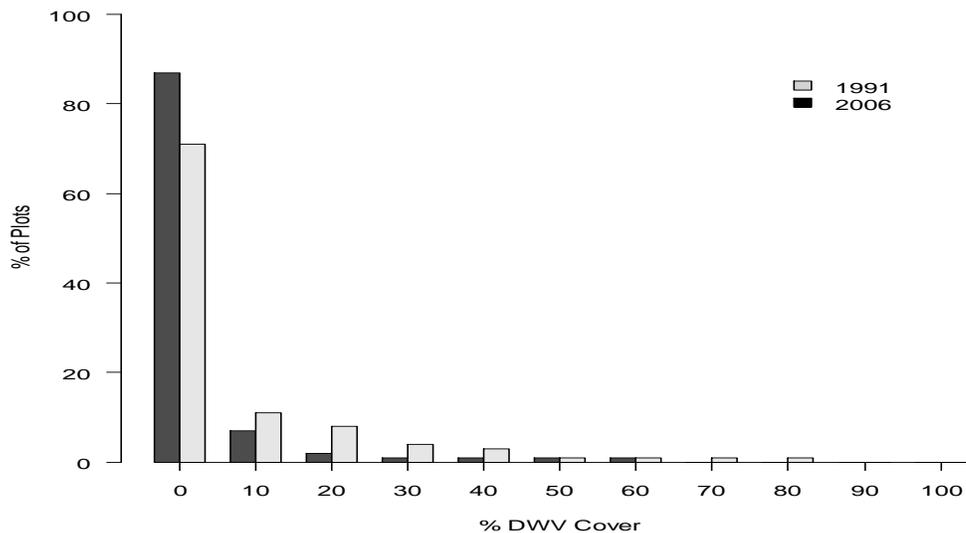
Figure 2.3. Distribution of % DWV cover for 1991 and 2006.

Most (68%, n = 371) plots did not change in DWV cover while 7% (n = 39) of plots decreased and 25% (n = 137) increased in DWV cover over the 15-year period (Figure 2.4). Of the plots that did not change 97% (n = 361) showed no DWV in either date. Of the samples that increased, 70% (n = 97) did so between 10 and 20 percentage points indicating there were relatively few large changes in DWV cover for any given plot (Figure 2.5).

Average DWV per plot changed from 3% in 1991 to 7% in 2006, a 170% increase. The paired t test on the full data set revealed a significant increase in DWV since 1991 (n = 547, t = 7.4, P < 0.0001). This finding fails to reject the null hypothesis of no change in DWV and therefore I conclude the alternative for hypothesis 1 for which we predicted a significant increase in DWV across the northern range over the 15-year period.
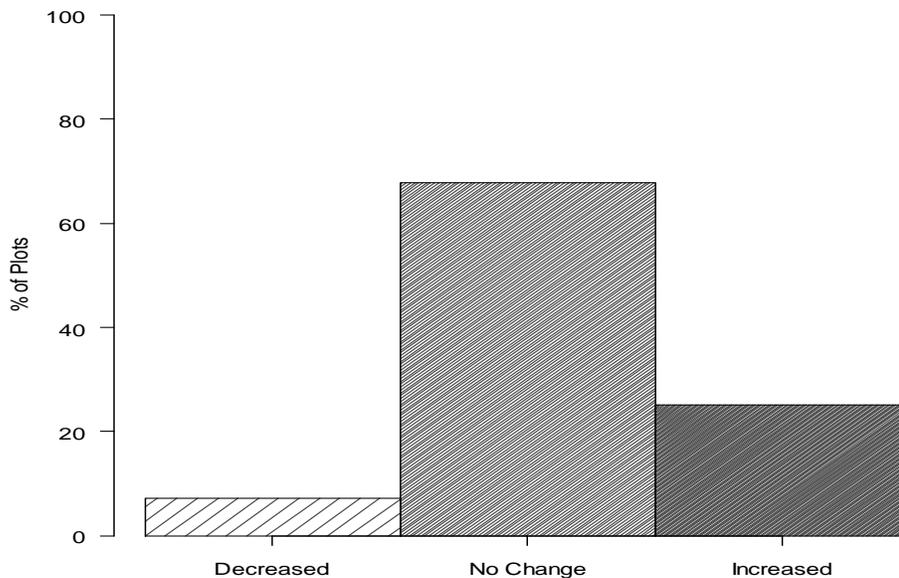
Figure 2.4. Overall distribution of change in DWV cover.
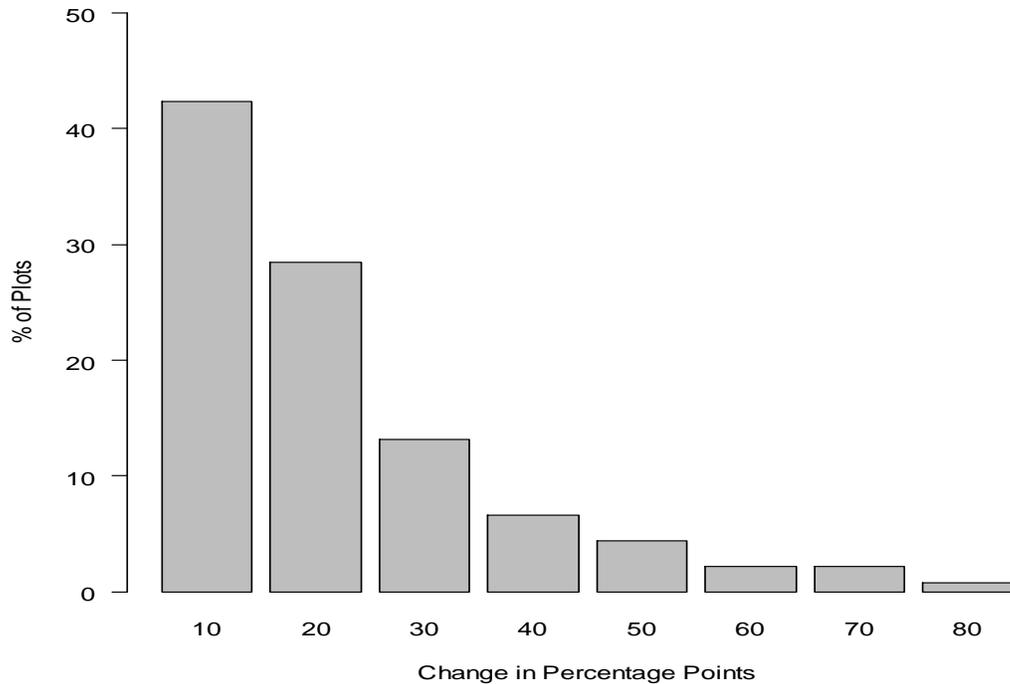
Figure 2.5. Change in percentage points for plots that increased in DWV.

Of the sample plots exhibiting positive change 85% (n = 116) were due to new recruitment while 15% (n = 21) were the result of densification (Figure 2.6). A paired t-test using only those plots containing at least 10% DWV in 1991 revealed that plots did not significantly increase or densify in DWV (n = 70, t = 0.65, P = 0.52); however, recruitment of DWV over the study period was statistically significant (n = 477, t = 9.6, P < 0.0001). These results indicate that there is not enough evidence to reject the null and conclude the alternative for hypothesis 2 for which we predicted significant densification of DWV. There is however, evidence to reject the null hypothesis and conclude the alternative for hypothesis 3 for which we predicted significant recruitment in DWV.
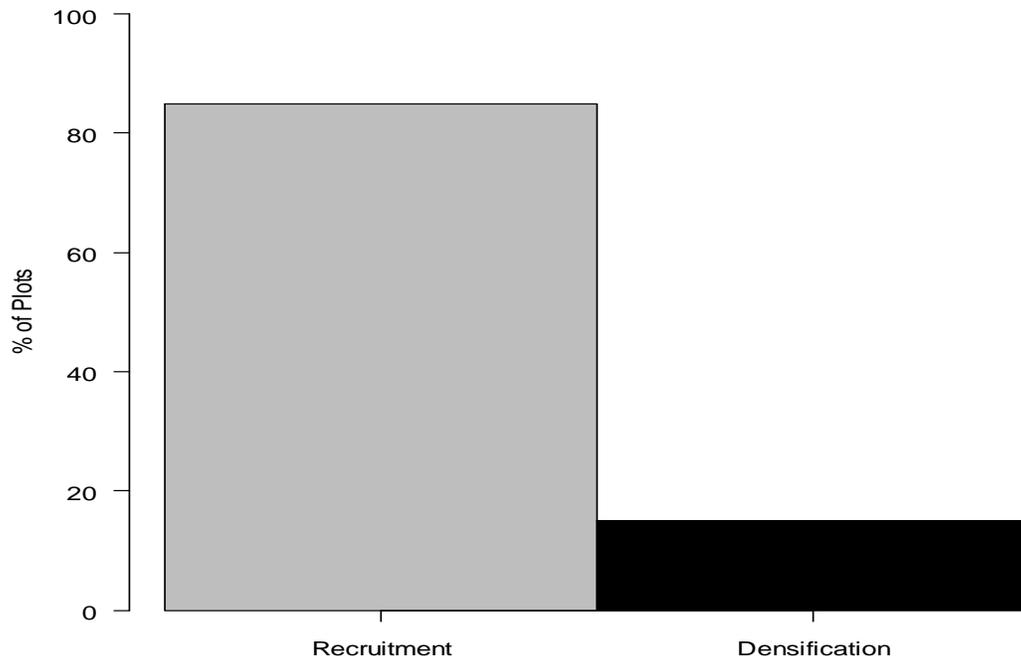
Figure 2.6. Percent of samples that increased by recruitment or densification.

Discussion

DWV appears to have more than doubled in areal extent (170% increase) across the northern range during the 15-year period. Results of the unpaired t-test of willow heights along line transects supports this finding with regard to the trajectory of change and is consistent with the results of other studies (Ripple and Beschta, 2003 and 2007; Groshong, 2004; Beyer et al., 2007). Despite this increase, DWV was absent in the majority of plots in both dates indicating that tall aspen, alder, willow, and cottonwood continue to be rare even within their habitat across the northern range.

The threshold of willow height detectable in 1991 and 2006 photos was estimated at 100 cm, indicating that differences between imagery were negligible and minimally affected the overall results. This is supported by the improved coefficient of determination (0.69 vs. 0.82) and slope (0.78 vs. 0.91) between percent willow cover measured in field sampling plots when excluding plants shorter than 100 cm. This also suggests that the results of significant DWV recruitment, but lack of densification, may be spurious. Plants shorter than the 100 cm threshold were likely present in at least some of the plots appearing to recruit vegetation, but were too short to observe at the scale of the imagery used. Because plants shorter than 100 cm are not detectable in the imagery, recruitment and densification cannot be adequately separated.

The majority of field studies in the region attribute recent changes in DWV to height increases for existing plants rather than to recruitment of new plants. For example, willow establishment has declined significantly since 1940, with older plants dominating the population of willow and young plants highly under-represented than what was predicted under a modeled stable age distribution (Wolf et al., 2007). Cottonwood establishment has declined since the early 1900s and has been virtually absent since the 1960s (Beschta, 2003) and aspen recruitment was less than 5% since 1920 (Ripple and Larsen, 2000). In contrast, willow growth ring area, which is related to height growth, increased since 1995 (Beyer et al., 2007); cottonwood and willows increased in height growth in 6 of 8 photosets (Beschta, 2003); and aspen have begun to show height increases in some locations (Ripple and Beschta, 2007).

When not accounting for willow height, the DOQQ interpretation underestimated percent DWV, especially for plots exhibiting high cover. Short willows in plots exhibiting high percent cover are dominated by wolf willow (*S. wolfii)*, a species rarely exceeding 100 cm in the northern range due to genetic constraints on height growth (Singer et al., 1994; Dorn, 1997). Wolf willow forms dense matt-like stands covering large areas that can appear similar to grasses and sedges in aerial photos. In low cover willow stands, wolf willow is rare and in addition, short willows in these stands are often single shrubs with a more distinct canopy that is more easily detected by the contrast in crown shape with the surrounding cover. When accounting for height, confusion was greatly reduced and errors were similar across the range of percent willow cover.

Altering the timing of imagery acquisition would reduce confusion between a grass-sedge class and a DWV class. A previous study found that riparian shrubs were more easily separated from the grass-sedge class when imagery was collected in September, a period when grasses and sedges had already senesced, but riparian shrubs were still green thus enhancing the spectral separability between the two classes (Groshong, 2004). Unfortunately, when conducting a change detection study, the researcher is limited by the data available and for this study September imagery at an appropriate spatial resolution was not available for the time periods under consideration.

There are three other remote sensing change detection studies of DWV conducted in the northern range within the time frame under consideration for which to compare this study. A study using 1:15,000 scale aerial photographs found that aspen canopy cover declined by 40%, but that willow and alder increased by 40% and 3% respectively along

Eagle Creek in the Gallatin National Forest portion of the northern range between 1990 and 2005 (McColley, 2007). The decrease in aspen was attributed to beaver utilization for dam building materials, which then raised the local water tables providing favorable growth conditions for willow and alder. Aspen and cottonwood increased slightly (0.21 and 0.01% respectively), but willow declined by 0.02% from 1985 to 1999 using Landsat satellite imagery (Savage and Lawrence, in press). Cottonwood, aspen, and willow were estimated to have increased in areal extent by 279% from 1995 to 1999 for the Lamar-Soda Butte confluence using high-resolution digital airborne photographs (Groshong, 2004).

The former study suggests that overall DWV cover was stable for Eagle Creek, but that the relative proportions of each changed over time. The latter study found an overall increase, but gave no indication of which DWV components increased, remained stable, or even decreased primarily because classification accuracies were poor when DWV was separated into individual classes (Groshong, 2004). However, reasonably good accuracies were achieved with Landsat satellite imagery when classifying change in aspen, willow and cottonwood (Savage and Lawrence, in press), but the scale of the imagery only allows for detection of changes in relatively large patches of vegetation. Addressing spatially explicit trajectories of change on a per species basis will be an important question for further studies of DWV change in Yellowstone's northern range and one we were unable to address given the sampling frame, scale of the imagery and large extent of the study area.

So why has DWV increased across the northern range? One explanation is climate change. A warmer and drier climate during the 20th century has led to increased fire frequency (Balling et al., 1992). The largest cohort of aspen and willow establishment occurred one year after the 1988 fires as a result of reduced competition and improved soil substrate conditions (Romme et al., 2005; Wolf et al., 2007). Hydrological shifts in response to climate change may also be responsible for changes in DWV. The 1990s were the wettest decade in the last 300 years with 100-year flood events occurring in both 1996 and 1997 (Graumlich et al., 2003), at about the time DWV began increasing in height growth. However, these are isolated incidents and while they may produce episodic increases in height growth and/or new recruitment opportunities, long-term changes in the population of these species may not occur based on these infrequent events. Climate warming has also led to earlier (Regonda et al., 2005 and Stewart et al., 2005) and greater (Lins and Slack, 1999) peak stream flows in the Rocky Mountain region. While this could result in increased growth of DWV, the benefit may be short-lived as climate is also expected to become drier consequently reducing winter precipitation and snowmelt runoff responsible for increased streamflow (Lapp et al., 2005).

An alternative is the trophic cascade hypothesis. Evidence suggests that landscape-scale characteristics have altered elk behavior in some riparian areas. Cottonwood stands in areas with low viewshed and ability to detect predators showed little browsing and increased height growth, while stands in broad floodplains with a large viewshed exhibited high browsing and low stature (Ripple and Beschta, 2003). In

low wolf-use areas, elk preferred aspen stands over other habitats, but when wolf presence increased, elk habitat preference shifted to conifer forests for the added protection against predation dense vegetation provides (Fortin et al., 2005). However, Creel and Christianson (2009) found that elk actually consumed more willow and aspen in the presence of wolves in the Gallatin River drainage adjacent to the northern range, a finding that contradicts the trophic cascade hypothesis suggesting that other mechanisms may be responsible for increased growth of deciduous woody plants.

The trophic cascade hypothesis has received more support in the literature than the climate change hypothesis when both are investigated together (Beyer et al., 2007, Wolf et al., 2007), although the climate change hypothesis has not been thoroughly examined in most studies. In the latter study, the authors suggest that competitive exclusion of beaver by elk under the absence of wolf predation caused declines in willow establishment, but that recent changes in browsing may not be sufficient to completely restore willow due to changes in stream geomorphology in the absence of beaver. This study suggests that while cascading effects of wolves in the northern range have resulted in taller deciduous woody vegetation, the relative importance of other potential influences on DWV growth and recruitment merit further study.

Beaver and DWV, particularly aspen and willow, are mutualists in the region. Aspen and *w*illow provide forage, dam, and lodge building materials for beaver whose activities promote the growth and establishment of woody riparian vegetation by raising local water tables and creating favorable conditions for growth and germination (Wolf et al., 2007; Bilyeu et al., 2008). After a prolonged absence on the majority of streams in

the northern range beaver are beginning to recolonize riparian areas with adequate aspen

and willow to sustain active colonies. Recolonization of northern range streams was

undoubtedly aided by the release of 129 beavers in the Gallatin National Forest portion of

the northern range over a 6-year period beginning in 1985. Although it wasn't until the

late 1990s, coincident with observations of increased DWV, that beaver colonies

expanded across the northern range and began establishing permanent colonies rather

than occupying sites ephemerally (Smith and Tyers, 2008). The presence of beaver in

response to increased DWV may have a rippling effect throughout the ecosystem through

the creation of habitat that will likely attract songbirds, waterfowl, herpetofauna, and

other species dependent on this habitat type.

The increase in DWV extent, a highly productive habitat in the region in terms of

aboveground net primary productivity, will likely have beneficial affects on bird

diversity. An increase in DWV patch area may reduce edge effects and increase the

number of interior patch specialists (Saab, 1999). Evidence suggests that willow stands

gaining in height growth since 1991 have been recolonized by several willow-riparian

dependent bird species such as willow flycatcher (*Empidonax traillii*), warbling vireo

(*Vireo gilvus*), and yellow warbler (*Dendroica petechia*) (see Chapter 3) and mature

stands of cottonwood and aspen will likely attract cavity-nesting birds such as red-naped

sapsucker (*Sphyrapicus nuchalis*) and American kestrel (*Falco sparverius*) (Sedgwick

and Knopf, 1990; Hollenbeck and Ripple, 2007).

Conclusions

The results of this study provide the first estimate of change in DWV for the

northern range since observations of increases began in 1998. Results indicate that DWV

increased in areal extent by 170% from 1991 to 2006, a 15-year period. Regardless of

whether changes in areal extent of DWV are the result of a trophic cascade, climate

change, fires, or other factors the increase in areal extent will likely benefit multiple

species.

The extent and physical condition of DWV in the northern range has been a

controversial issue stimulating considerable debate regarding management decisions

since the park's establishment in 1872 (NRC, 2002). As a result there will be a continued

need to evaluate change in DWV across the landscape. Careful consideration should be

given to study design so that appropriate field data can be collected for use as validation

data in future remote sensing studies. Because satellite imagery is becoming less

expensive, is available at fine spatial scales, and classification is automated, space-borne

imagery would likely be more effective for detecting DWV change at least at the scale of

the northern range.

An important question requiring further study is the relative contribution of each

species to the overall increase in DWV across the northern range and where these

changes are occurring; however, this would require extremely fine-scale resolution

imagery better than 1 m to accurately map these cover types separately, and would

require several hundred images to cover the extent of the study area (Groshong, 2004).

The number of scenes required and processing time would likely be extensive; however,

the effort may be warranted given the interest in DWV in the northern range.

Literature Cited

Balling, R. C. Jr., G. A. Meyer, and S. G. Wells. 1992. Climate change in Yellowstone National Park: is the drought-related risk of wildfires increasing? Climate Change 22: 35-45.

Barnosky, C.W. 1988. The relationship of climate to sedimentation rates in lakes and ponds. Page 4 in F. Singer, ed. First annual meeting of research and monitoring on Yellowstone's northern range. USDI, Nat. Park Ser., Yellowstone National Park.

Beschta, R. 2003. Cottonwoods, elk, and wolves in the Lamar Valley of Yellowstone National Park. Ecological Applications 13: 1295-1309.

Berger, J., P.B. Stacey, L. Bellis and M.P. Johnson. 2001. A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. Ecological Applications 11: 947-960.

Beyer, H.L. 2004. Hawth's Analysis Tools for ArcGIS. Available http://www.spatialecology.com/htools.

Beyer, H.L., E.H. Merril, N. Varley and M.S. Boyce. 2007. Willow on Yellowstone's northern range: evidence for a trophic cascade? Ecological Applications 17: 1563-1571.

Bilyeu, D. M., D. J. Cooper and M. T. Hobbs. 2008. Water tables constrain height recovery of willow on Yellowstone's northern range. Ecological Applications 18: 80-92.

Britchta, 1987. Environmental relationships among wetland community types of the northern range, Yellowstone National Park. M.S. thesis, University of Montana, Missoula, MT.

Cayan, D.R., S.A. Kammerdiener, M.D. Dettinger, J.M. Caprio and D.H. Peterson. 2001. Changes in the onset of spring in the western United States. Bulletin of the American Meteorological Society 83: 399-415.

Chadde, S.W., P.L. Hansen, and R.D. Pfister. 1988. Wetland Plant Communities of the Northern Range, Yellowstone National Park. School of Forestry, University of Montana.

Chadde, S.W. and C.E. Kay. 1991. Tall-willow communities on Yellowstone's northern range: a test of the "natural-regulation" paradigm. In R.B. Keiter and M.S. Boyce (Eds), *The Greater Yellowstone Ecosystem*. Yale University Press.

Creel, S. and D. Christianson. 2009. Wolf presence and increased willow consumption by Yellowstone elk: implications for trophic cascades. Ecology 90: 2454-2466.

Christiansen, R.L., 2001, The Quaternary and Pliocene Yellowstone Plateau volcanic field of Wyoming, Idaho, and Montana: U.S. Geological Survey Professional Paper: 729-G, 145 p., 3 plates, scale 1:125,000.

Christianson, D. and S. Creel. 2007. A review of environmental factors affecting elk winter diets. Journal of Wildlife Management 71: 164-176.

Despain, D.G. 1987. The two climates of Yellowstone National Park. Proceedings of the Montana Academy of Science 47: 11-20.

Devore, J.L. and R. Peck. 2004. Statistics: The exploration and analysis of data (5th edition). Duxbury Press.

Dungan J.D. and R.G. Wright. 2005. Summer diet composition of moose in Rocky Mountain National Park, Colorado. Alces 41: 139-146.

Engstrom, D.R., C. Whitlock, S.C. Fritz and H.E. Wright, Jr. 1991. Recent environmental changes inferred from the sediments of small lakes in Yellowstone's northern range. Journal of Paleolimnology 5: 139-174.

Finch, D.M. and L.F. Ruggiero. 1993. Wildlife habitats and biological diversity in the Rocky Mountains and northern Great Plains. Natural Areas Journal 13: 191-203.

Fortin, D., H.L. Beyer, M.S. Boyce, D.W. Smith, T. Duchesne, J.S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86: 1320-1330.

Graumlich, L. J., M. F. J. Pisaric, L. A. Waggoner, J. S. Littell, and J. C. King. 2003. Upper Yellowstone River flow and teleconnections with Pacific basin climate variability during the past three centuries. Climate Change 53: 245-262.

Groshong, L.C. 2004. Mapping riparian vegetation change in Yellowstone's Northern Range using high spatial resolution imagery. M.A. thesis, University of Oregon, Eugene, OR.

Hansen A.J., J.J. Rotella, M.P.V. Kraska and D. Brown. 2000. Spatial patterns of primary productivity in the Greater Yellowstone Ecosystem. Landscape 15: 505-522.

Hansen, A., T. Rotella, L. Klaas, D. Gryskiewicz. 2003. Riparian habitat dynamics and wildlife along the upper Yellowstone River. Technical Report. Landscape Biodiversity Lab, Montana State University.

Hebblewhite, M., C. A. White, C. G. Nietvelt, J. A. McKenzie, T. E. Hurd, J. M. Fryxell, S. E. Bayley, and P. C. Paquet. Ecology 86: 2135-2144.

Hollenbeck, J. P. and W. J. Ripple. 2007. Aspen patch and migratory bird relationships in the northern Yellowstone ecosystem. Landscape Ecology 22: 1411-1425.

Houston, D.B. 1982. The northern Yellowstone elk: ecology and management. MacMillan Publishing Co., Inc., N.Y. 474 pp.

Lapp, S. J. Byrne, I. Townshend, and S. Kienzle. 2005. Climate warming impacts on snowpack accumulation in an alpine watershed. International Journal of Climatology 25: 251-536.

Larsen, E.J. and W.J. Ripple. 2003. Aspen age structure in the northern Yellowstone ecosystem: USA. Forest Ecology and Management 179: 469-482.

Lins, H.F. and J.R. Slack. 1999. Streamflow trends in the United States. Geophysical Research Letters 26: 227-230.

McColley, S. M. 2007. Restoring aspen riparian stands with beaver on the northern Yellowstone winter range. M.S. thesis, Montana State University, Bozeman, MT.

Myneni, R.B., C.D. Keeling, C.J. Tucker, G. Asrar and R.R. Nemani. 1997. Increased Plant growth in the northern high latitudes from 1981 to 1991. Nature 386: 698-702.

Naiman, J.R. and H. Décamps. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology and Systematics 28: 621-658.

National Research Council. 2002. Ecological dynamics of Yellowstone's northern range. National Academy Press, Washington, D.C.

Nemani, R.R., C.D. Keeling, H. Hashimoto, W.M. Jolly, S.C. Piper, C.J. Tucker, R.B. Myneni, and S.W. Running. 2003. Climate-driven increases in global terrestrial net primary productivity form 1982 to 1999. Science 300: 1560-1563.

R Development Core Team. 2007. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Regonda, S.K., B. Rajagopalan, M. Clark, and J. Pitlick. 2005. Seasonal cycle shifts in hydroclimatology over the western United States. Journal of Climate 18: 372-384.

Ripple, W.J. and Larsen, E.J. 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. Biological Conservation 95: 361-370.

Ripple, W.J. and R. L. Beschta. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. Forest Ecology and Management 184: 299-313.

Ripple, W.J. and R.L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems. Bioscience 54: 755-766.

Ripple, W.J. and R.L. Beschta. 2006. Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. Forest Ecology and Management 230: 96-106.

Ripple, W.J. and R. L. Beschta. 2007. Restoring Yellowstone's aspen with wolves. Biological Conservation 138: 514-519.

Romme, W. H., M. G. Turner, G. A. Tuskan and R. A. Reed. 2005. Establishment, persistence, and growth of aspen (*Populus tremuloides*) seedlings in Yellowstone National Park. Ecology 86: 404-414.

Saab, V. 1999. The importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. Ecological Applications 9: 135-151.

Savage, S. L. and R. Lawrence. In press. Vegetation dynamics in Yellowstone's northern range: 1985-1999. Photogrammetric Engineering and Remote Sensing.

Sedgwick, J. A. and F. L. Knopf. 1990. Habitat relationships and nest site characteristics of cavity-nesting birds in cottonwood floodplains. Journal of Wildlife Management 54: 112-124.

Smith, D. W. and D. B. Tyers. 2008. The beavers of Yellowstone. Yellowstone Science 16: 4-15.

Stevens, D.R. 1970. Winter ecology of moose in the Gallatin mountains, Montana. Journal of Wildlife Management 34: 37-46.

Stewart, I. T., D. R. Cayan, and M. D. Dettinger. 2005. Changes toward earlier streamflow timing across western North America. Journal of Climate 18: 1136-1155.

Wolf, E.C., D.J. Cooper, and N.T. Hobbs. 2007. Hydrologic regime and herbivory stabilize an alternative sate in Yellowstone National Park 17: 1572-1587.

Yellowstone National Park. 1997. Yellowstone's northern range: complexity and change in a wildland ecosystem. National Park Service, Mammoth Hot Springs, Wyoming.

CHAPTER 3.

HAS THE POLICY OF NATURAL REGULATION INCREASED BIRD DIVERSITY IN WILLOW (*SALIX* SPP.) COMMUNITIES IN YELLOWSTONE'S NORTHERN RANGE?

Introduction

Willow (*Salix* spp.) is the dominant woody plant in many riparian zones across the northern Rocky Mountains; however, willow communities are rare, typically comprising less than 1% of northern Rocky Mountain landscape (Skagen et al., 1998). Embedded within a matrix of arid grasslands, shrublands, and upland coniferous forests, riparian willows represent one of the few deciduous wetland habitat types in the region. Disproportionate to the limited distribution of willow, biodiversity in this habitat type is considerably higher than in adjacent uplands, particularly with respect to birds (Finch and Ruggiero, 1993). As much as 80% of the local avifauna breeds in riparian willow habitat (Berger et al., 2001) and during spring and fall migration, bird species richness is 10-14 times that of upland environments (Stevens et al., 1977).

Many bird species dependent on riparian willows however, are declining across the northern Rocky Mountains, largely because of anthropogenic influence within and adjacent to riparian areas (Saab, 1999; Scott et al., 2003; Smith and Wachob, 2006; Fletcher and Hutto, 2008), especially those at lower elevations (Hansen and Rotella, 2002). As riparian willow habitat is increasingly influenced through river damming, agriculture, grazing, urban development, and human recreation, riparian willow habitat within protected areas such as parks and refuges becomes increasingly important for

maintaining viable populations of riparian and willow dependent bird species in the region. At acres 800,000 square kilometers, Yellowstone National Park is the largest protected area in the western United States, with many of its riparian areas dominated by willows (NRC, 2002).

Despite this protection, willow communities in Yellowstone National Park's northern range have been height suppressed since the early 1900s (NRC, 2002). The northern range is a lower elevation region in and adjacent to northern Yellowstone where high densities of ungulates, in particular elk (*Cervus elaphus*) and bison (*Bison bison*), reside in winter when deep snows limit movements and the availability of forage at higher elevations (NRC, 2002). Pollen records in lake sediments indicate a decline in willow since 1920 (Barnosky, 1988; Engstrom et al., 1991) and repeat photographs show complete loss of willow communities between 1871 and 1988 for 41 of 44 photosets and considerably reduced stature for the remaining three photosets (Chadde and Kay, 1991).

Since vegetation structure significantly influences habitat selection by birds (Hutto, 1981; Berger et al., 2001; Anderson, 2007; Olechnowski and Debinski, 2008) the reduced distribution and simplified willow structure representative of the northern range throughout much of the 20th century likely limited populations of riparian and willow dependent bird species there. A 1989-1990 study of willow-bird relationships in the northern range indicated that willow specialist species such as willow flycatchers (*Empidonax traillii*) and Wilson's warblers (*Wilsonia pusilla*) were either extremely rare or absent from the majority of willow stands sampled and that this was primarily the

result of low willow stature and simplified willow structure observed in the region (Jackson, 1992).

High elk densities, widely believed to be in excess of carrying capacity, were blamed for declining willow communities (Boyce, 1991); however, declines were also associated with drought, reduced fire frequency, and loss of beaver (YNP, 1997). Perceptions of over-browsing led to a culling program where over 24,000 elk were removed from Yellowstone's northern range from 1923 to 1968. Intense public protest over culling practices in the late 1960s led directly to the implementation of the natural regulation policy or policy of ecosystem process management in 1968 (Boyce, 1991).

The natural regulation policy is based on the contention that the elk population is limited primarily by density dependent factors such as competition for forage, rendering culling unnecessary (Boyce, 1991). However, willows and other woody vegetation continued to be height suppressed during the 1970s and 1980s, calling into question the hypotheses underlying this policy (Chadde and Kay, 1991). Biologists argued that a valid test of natural regulation could not be realized until wolves were restored to the landscape, and so in 1995-1996 wolves were reintroduced to Yellowstone in an effort to restore more natural ecosystem processes to the region (YNP, 1997).

In 1998, park biologists observed an increase in woody vegetation in some locations throughout the northern range; an observation subsequently supported by several studies. Beyer et al. (2007) found a two-fold increase in willow stem growth ring area since 1995. Photo comparisons revealed an increase in willow and cottonwood height for six of eight photosets from 1977 to 2002 (Ripple and Beschta, 2003). High

spatial resolution imagery indicated that riparian vegetation including willow, alder

(*Alnus incana*), and cottonwood (*Populus* spp.) increased in areal extent by 279% within

a 4 km^2 area along the Lamar River-Soda Butte Creek confluence between 1995 and

1999 (Groshong, 2004). Most recently, we (see Chapter 2) found from aerial photo

comparisons an overall net gain in areal extent of 170% in willow, alder, cottonwood,

and aspen (*Populus tremuloides*) across riparian and wetland areas throughout the

northern range between 1992 and 2006.

These observations of increases in willow height and areal extent stimulated the

hypothesis that the release of willow and other woody vegetation may be the result of a

trophic cascade where predation by wolves has lowered the density and altered the

foraging habits of elk, resulting in reduced browsing and increased growth of deciduous

woody plants (Ripple and Beschta, 2004). In Banff National Park, an apparent trophic

cascade has resulted in reduced herbivory, increased growth of willows, and greater bird

diversity (Hebblewhite et al., 2005). However, the recent willow release also coincides

with change in climate. Longer growing seasons, resulting from warmer spring and fall

temperatures have lead to increased productivity of deciduous woody vegetation in the

Rocky Mountains (Cayan et al., 2001, Myneni et al., 1997; Nemani et al., 2003) and

warmer spring temperatures have led to greater (Lins and Slack, 1999) and earlier peak

stream flows (Regonda et al., 2005 and Stewart et al., 2005) that may affect patterns of

vegetation growth. While the effects of growing season length on willow growth have

not been tested in the northern range, Beyer et al. (2007) found that winter severity and

elevation were included with wolf presence in the best model of stem growth ring area

for two common willow species and that precipitation was also included for one of the species suggesting that climatic factors are at least partially responsible for changes in willow growth.

While drivers behind willow height release have been the subject of intense interest in recent years, no studies have yet evaluated the significance of willow height release for birds associated with this habitat type, an important step in evaluating natural ecosystem process management in the northern range. Although a number of willow stands have increased in height and areal extent across the region, changes in growth have not been uniform (R. Renkin, personal communication, 2005). Some willows remain height suppressed while others have been released from height constraining factors. Although the release of willows is limited, those stands that have released could lead to an increase in bird diversity and provide important habitat that is declining elsewhere in the northern Rocky Mountains.

Our objectives for this study were to: 1) quantify willow structure in each of three willow growth conditions (height suppressed, recently released, and previously tall, or tall prior to 1998 when increases in willow growth were first observed); 2) examine differences in bird community variables (i.e. richness, abundance, and diversity) between the three willow growth conditions; 3) examine differences in the abundance of seven focal species known to be associated with willows in the region: common yellowthroat (*Geothlypis trichas*), Lincoln's sparrow (*Melospiza lincolnii*), yellow warbler (*Dendroica petechia*), song sparrow (*Melospiza melodii*), warbling vireo (*Vireo gilvus*), Wilson's warbler, and willow flycatcher; and 4) identify the willow structural characteristics that

best explain differences in bird community variables across the three willow growth

conditions by evaluating a set of *a priori* models based on prior knowledge of habitat

selection by birds. We tested the following hypotheses to address these objectives:

1) Willow structure would become increasingly complex along a gradient from
   suppressed (least complex) to previously tall (most complex) as measured by
   vertical (i.e. density, height, coefficient of variation in height, and foliage
   height diversity) and horizontal (i.e. patch size, horizontal cover, and
   frequency) structural characteristics.

2) Bird community variables (richness, abundance, and diversity) would increase
   along a gradient from lowest in suppressed to highest in previously tall
   willows. Each variable was tested as a separate hypothesis.

3) Common yellowthroat and Lincoln's sparrows (willow generalist species in
   the region) would be present in all three willow growth conditions, but would
   increase in abundance along a gradient from lowest in suppressed to highest in
   previously tall. Yellow warbler, song sparrow, and warbling vireo (willow
   associates) would be absent from suppressed willows, but would be present in
   released and previously tall willows although at a lower abundance in the
   former. Wilson's warbler and willow flycatcher (willow specialists) would be
   absent from both suppressed and released willows, but present in previously
   tall willows.

Methods

Study Area

This study was conducted in and around Yellowstone's northern range defined as the region occupied by Yellowstone's northern wintering elk herd covering a 153,000 ha area in the Gardner, Lamar, and Yellowstone River watersheds (Figure 3.1) (Houston, 1982). Elevation varies from 1500 to 3209 m (Savage and Lawrence, in press). The majority of the northern range lies within Yellowstone National Park while the remainder lies within the Gallatin National Forest and various private agricultural and ranch lands north of the Yellowstone boundary (Houston, 1982). The semi-arid region receives approximately 260 mm of precipitation per year, most of which falls during the growing season (Despain, 1987).

Relatively nutrient poor rhyolitic soils were deposited across the region two to three million years ago during a period of intense volcanic activity while relatively rich andesite soils found along valley bottoms were deposited approximately 12,000 to 14,000 years ago following the retreat of the Pinedale glacier (Christianson, 2001). Vegetation in the study region is dominated by grasslands and sagebrush steppe in the lower elevations while conifer forests predominate at higher elevations (Houston, 1982).

Deciduous woody vegetation (willow, aspen, cottonwood, and alder) occurs in the lower elevation regions in four general landscape settings: "1) along stream and river channels, in overflow channels, and on floodplains; 2) in depressions and around kettle lakes formed by blocks of glacial ice; 3) adjacent to springs and seeps on lower mountain slopes; and 4) in abandoned beaver channels and ponds" (Chadde et al., 1988). Willows

in particular can be found along portions of the Lamar River, Soda-Butte Creek, and along lower order streams throughout the northern range, but also occur in small patches in springs and seeps on toe slopes and especially in flooded channels influenced by beaver activity (Chadde et al., 1988). Understory vegetation within riparian areas are dominated by various native sedges (*Carex* spp.), grasses, and forbs.

Study Design Overview

We surveyed the bird community associated with three willow growth conditions in and around Yellowstone's northern range: suppressed, released, and previously tall — following the willow growth classification scheme of Singer et al. 2004 as described below. Willows in the suppressed condition were generally < 80 cm tall and showed evidence of browsing; released condition willows were formerly height suppressed in part by browsing, but have exhibited substantial height gain and reduced browsing since 1998; previously tall condition willows were generally 150 – 200 cm tall prior to 1998 and also showed little evidence of browsing. Willow sites were classified into one of the three growth conditions by Singer et al., 2004 or confirmed by park staff biologists knowledgeable of willow growth in the region. We then confirmed the classification of willow into the three willow growth conditions by comparing aerial photographs from 1991 to 2006.

For each willow growth condition, we sampled the vertical and horizontal structure of willow and the birds associated with each condition. Differences in willow structure and bird community variables were analyzed with one-way analysis of variance
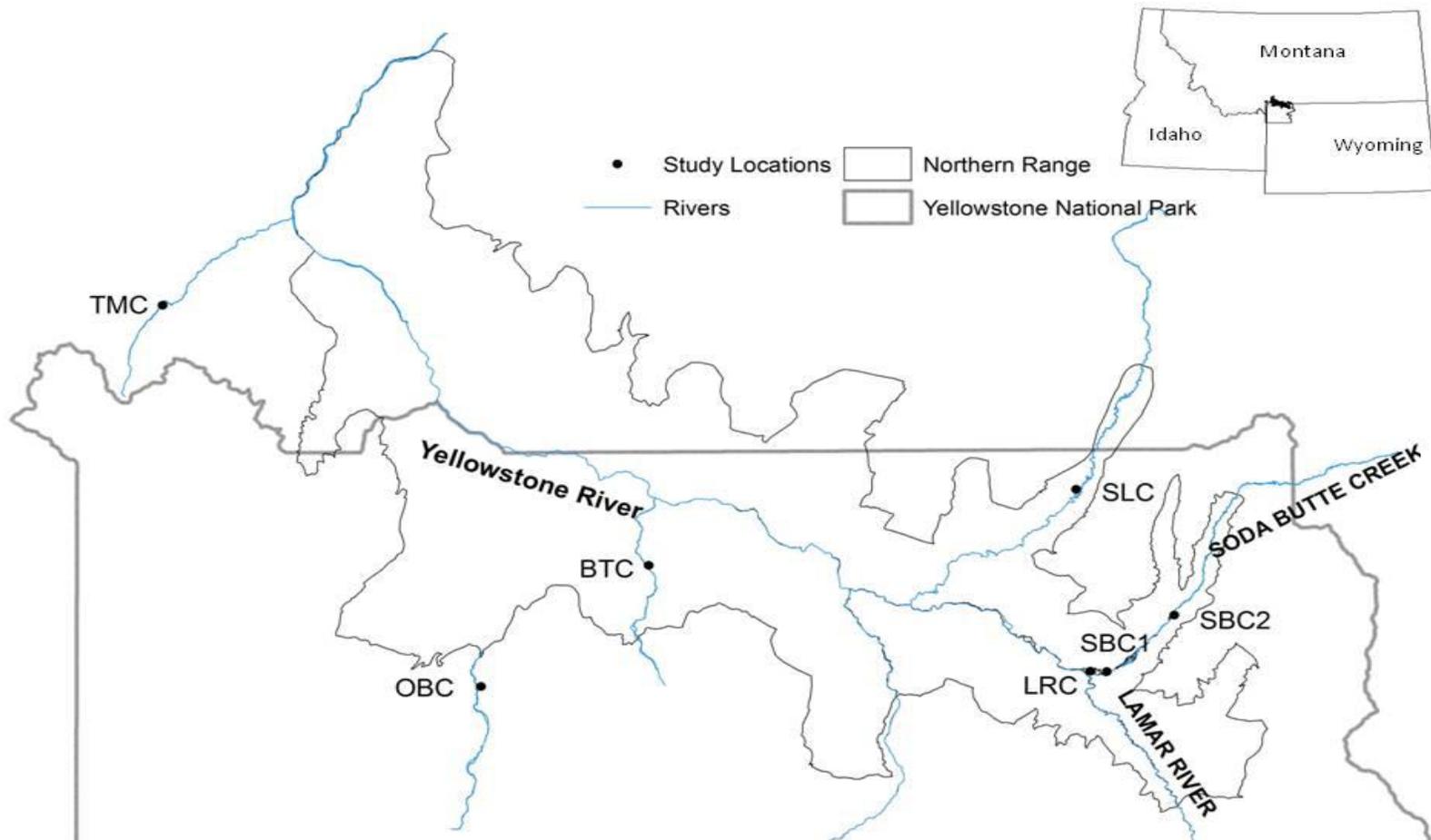
Figure 3.1. Map of the northern range study area and survey locations. Previously tall = TMC (Tom Miner Creek) and OBC (Obsidian Creek); released = BTC (Blacktail Deer Creek), LRC (Lamar River confluence), and SLC (Slough Creek); suppressed = SBC1 (Soda Butte Creek 1) and SBC2 (Soda Butte Creek 2).

(ANOVA). Using generalized least squares (GLS) we compared a suite of *a priori* models for which there was reasonable justification to determine the willow structural characteristics that best explain bird community variables across the three willow growth conditions. We modeled and controlled for spatial autocorrelation for both ANOVA and GLS models (specific details are provided in the statistical analyses section below). Statistical analyses were executed using R statistical software (R, 2007).

Study Sites

Potential samples in each growth condition were identified based on local expert knowledge of site location for each willow condition and long-term studies of willow growth in the region (Singer et al, 2004). Candidate sites meeting the initial willow growth condition criteria described above were considered for sampling if willow patches were at least 400 x 100 m in area and were within 15 km of a road for relative ease of access. We selected two to three willow sites in each growth condition based on observations of long-term willow growth in the region by YNP staff biologists (R. Renkin, personal communication, 2005) and long-term studies of willow growth in the region (Singer et al., 1994; Singer et al., 2004). Within each site we surveyed between four and sixteen 40-m radius sample plots depending on the size of the willow patch placed at least 100 m apart. Sample plots were placed systematically within a site by orienting parallel to the stream at the approximate center of the perpendicular edge of the willow patch. Using a compass and handheld Garmin GPS unit we walked in an approximate straight line and placed the center of the plot at 100 m intervals.

The two previously tall sites were located along Obsidian Creek (n = 16 sample plots) in Yellowstone National Park just south of the northern range and along Tom Miner Creek (n = 7 sample plots) in Tom Miner Basin west of the northern range for a total of 23 sample plots across the two previously tall sites (Fig 3.1). The two previously tall sites were located just outside of the northern range because willow sites meeting the previously tall growth condition criteria were absent in the northern range.

Released sites were located along upper Slough Creek (n = 9 sample plots), Blacktail Deer Creek (n = 8 sample plots), and along the Lamar River-Soda Butte Creek confluence (n = 4 sample plots) for a total of 21 sample plots across the three released sites. Suppressed sites were situated in two locations along Soda Butte Creek, SBC1 (n = 13 sample plots) and SBC2 (n = 10 sample plots), for a total of 23 sample plots across the two suppressed sites. In total, we sampled 67 plots stratified across the three willow growth conditions.

Confirming the Designation of Study
Sites into the Three Growth Conditions

To confirm the designation of sites into the previously tall, released, and suppressed willow conditions we compared two dates of aerial photography from 1991 and 2006. We used a set of 1:24,000 true color aerial photographs from the 1991 growing season as the first date of imagery. For the second date of imagery, we used a 2006 digital ortho quarter-quadrangle (DOQQ) with 1-m ground sample distance rectified to the National Mapping Standards at the 1:24,000 scale created by United States Department of Agriculture's Aerial Photography Field Office (USDA-APFO). All

imagery was obtained through the Yellowstone Center for Resources Spatial Analysis

Center in Mammoth, Wyoming.

We centered 0.81 ha squares over each of the 67 sample plots and recorded

willow cover at each of the two time periods. Air photo sample plots were larger than

field sample plots because this is the finest unit of analysis possible given the scale of the

imagery from 1991. Within each air photo sample plot we placed a 10-dot grid of

equidistant spaced points. Each point center on the grid covering willow was considered

a "hit". The percent willow cover in each sample was calculated by summing the number

of "hits" in the sample at 10% increments. Data were analyzed by willow condition

using a paired t-test to test for significant differences in willow cover between the two

dates of imagery.

We expected little change between imagery dates in both the previously tall and

suppressed willow conditions and a significant increase in the released willow condition.

We also expected the suppressed willow condition to reveal low percent willow cover in

both dates of imagery while the previously tall willow condition should reveal relatively

high percent willow cover in both dates of imagery. These results would be consistent

with the classification of willow sites into released, suppressed, and previously tall

growth conditions.

Field Vegetation Sampling

Willow structural characteristics were determined using a modified Robel pole

(Robel et al., 1970) and the line-intercept method (Canfield, 1941) in all 67, 40-m radius

sample plots (Figure 3.2). The Robel pole method was used to assess vertical vegetation

structure or density while the line-intercept method was used to assess horizontal vegetation cover and height. These methods allowed for a three dimensional evaluation of willow structure at each sampling plot. All willows were identified to species; however, since birds respond primarily to vegetation structure rather than to species composition we excluded composition variables from this analysis. Potential differences in willow species among growth conditions were analyzed in Baril et al. in prep (see Chapter 4).

Robel Pole Measurements: At the center of each sample plot four, 40-m transects were aligned north, south, east, and west. The Robel pole was divided into 0.50-m height classes and measurements were collected at 10-m intervals along each of the four transects for a total of sixteen sample points per sample plot. At each sample point an observer walked 1 m in a random direction from the Robel pole and recorded the cover type (other or willow) and the percent of the Robel pole obscured by that cover type in each height class up to the maximum height of the cover type present. The following cover classes were used to record the percent cover in each height class: 0 (0-1%); 1 (2-5%); 2 (6-25%); 3 (26-50%); 4 (51-75%) and 5 (76-100%).

Line Intercept Measurements: Line intercept measurements were collected along one transect that originated at the plot center and extended 40 m in a randomly selected cardinal direction. The transect was divided into 1 m intervals along which an observer recorded length and height of willow where it intersected with the meter tape at 1-m intervals.
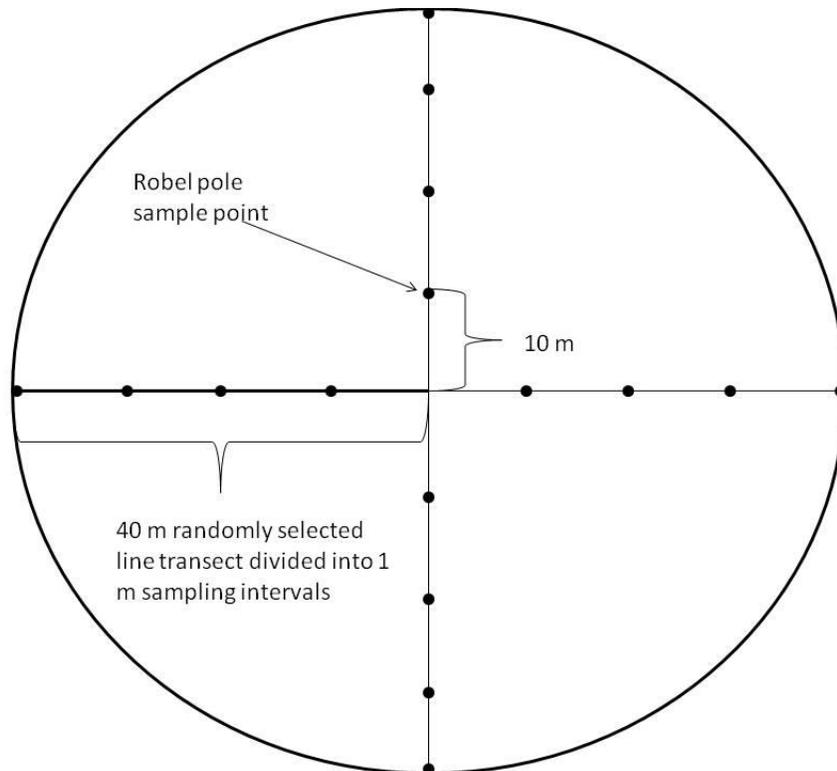
Figure 3.2. Plot configuration used to sample vegetation in the 67, 40-m radius circular sample plots.

Generation of Vegetation Predictors: A total of ten habitat variables were

generated from Robel pole and line intercept data (Table 3.1). Five of the ten variables

were generated from Robel pole measurements: vertical vegetation density in each of

four height classes and foliage height diversity, a measure of overall vertical structural

complexity. Vertical vegetation density in each height class was obtained by averaging

the % cover values across each height class strata per sample plot. Low vertical

vegetation cover or density values indicate more open spaces in the vertical structure of

willows while high values indicate dense willow cover and fewer open spaces. Foliage

height diversity was calculated using the Shannon-Wiener formula, which takes into

account both the number of vegetation layers and the density of vegetation in each layer,

as follows (MacArthur and MacArthur, 1961):

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

H'= index of diversity
S = # height classes where willow is represented
p_i = proportion of total willow cover belonging to the ith
       height class
ln= natural log

Five of the ten habitat variables were generated from line intercept measurements:

% horizontal cover, height, % frequency, coefficient of variation in willow height, and a

measure of willow patchiness calculated by the mean length of all willow patches divided

by the total number of willow patches. Lower values were indicative of willows with

fewer open spaces between patches while higher values were indicative of a more

clumped willow distribution.

Table 3.1. Summary of habitat variables measured and method used.

Description of habitat measurements	Units	Abbreviation	Method	Used in models
Average willow height	cm	HT	Line intercept	Yes
Coefficient of variation in willow height	cm	HT.cv	Line intercept	Yes
Frequency of willow	%	FREQ	Line intercept	Yes
Horizontal willow cover or extent	%	HZ	Line intercept	Yes
Index of willow patchiness	NA	PATCH	Line intercept	Yes
Foliage height diversity	NA	FHD	Robel pole	Yes
Willow density from 0 – 50 cm	%	VERT1	Robel pole	No
Willow density from 51 – 100 cm	%	VERT2	Robel pole	No
Willow density from 101 – 150 cm	%	VERT3	Robel pole	No
Willow density from 151 – 200 cm	%	VERT4	Robel pole	No

Bird Sampling

Birds were sampled in each of the 67, 40-m radius sample plots using standard point count techniques (Hutto et al., 1986). Birds were sampled in all 67 plots in 2006 and 2007, but only 30 of the plots were sampled during the pilot study season in 2005. Three rounds of point counts separated by at least 10 days were conducted for each sample plot surveyed in June and July of 2005 through 2007 except for five plots in 2005 and three plots in 2006, which were only sampled twice due to time and weather constraints. Bird community variables were corrected for the number of visits by averaging over two visits rather than three for those that were only sampled twice during a season. One-way ANOVA of bird community variables between years indicated that although the sample size was lower in 2005 than in 2006 and 2007 trends were similar across years thus data were pooled to simplify analyses.

Each count lasted 10 minutes during which time birds observed were identified to species and information on distance from the observer, time observed, sex, and behavior (e.g. singing, carrying food or nesting material) were recorded. Surveys were conducted from one half hour before sunrise until no later than 0930. The survey order and observers were varied throughout the season to avoid associated biases.

Generation of Bird Variables: We calculated bird richness, overall abundance, abundance for each of the seven focal species, and the Shannon-Weiner diversity index for each sample plot. Bird richness was calculated by summing the number of species detected per visit per year then averaging over the visits and then over years. We considered correcting abundance estimates using distance estimation techniques which

accounts for imperfect detection (Buckland et al. 2001). However, the relatively open

and short nature of willow in Yellowstone, the relatively short distance (40 m) within

which we sampled birds, and the high degree of vocalization among species commonly

found in willows allowed for high visual and auditory detection across species (Jackson,

1992). Therefore, the biases and assumptions associated with distance estimation

techniques may outweigh those associated with imperfect detectability for this study

(Alldredge et al. 2008; Johnson, 2008; Bachler and Liechti, 2007), thus we chose to

assume perfect detection and use uncorrected estimates of abundance.

The Shannon-Weiner diversity index, which takes into account both richness and

evenness, was calculated with the formula given above except that here S = # of species

and p_i = proportion of species belonging to the ith species. Finally, we calculated the

Renkonen index of community similarity between each pair of willow growth conditions

as defined by the following formula (Nur et al., 1999):

$$P = \sum_{i=1}^{i=s} \text{minimum } (p^A_i, p^B_i)$$

P = Percentage Similarity
p_iA = percentage of species i in sample A
$_{pi}$B = percentage of species i in sample B
S = the number of species found in either sample

Flyovers, waterfowl, marshbirds, and shorebirds were excluded from analyses

because point counts are not designed to adequately survey these species (Ralph et al.,

1995).

Statistical Analyses

Modeling Spatial Autocorrelation: Spatial autocorrelation was expected such that sample plots near each other were more likely to have similar values. Such correlation among samples is expected to inflate the degrees of freedom resulting in potentially inappropriately small p-values (Kutner et al., 2004). Thus, we controlled for spatial autocorrelation using GLS by modeling the spatial dependence present in the data (Crawley, 2007). For each variable examined we compared the relative support for four models that included spatial structure plus a GLS model without spatial structure which yields ordinary least squares (OLS) estimates using Akaike's Information Criterion (AIC_c) corrected for small sample sizes (Burnham and Anderson, 2002; Zuur et al., 2009; Crawley, 2007). The four models of spatial structure compared were: exponential, Gaussian, rational quadratic, and spherical. Although there are five models of spatial structure, the linear spatial model did not converge for any of the variables tested and so was dropped from all comparisons (Zuur et al., 2009).

We considered all models with ΔAIC_c of ≤ 2 to have received substantial support while those models with ΔAIC_c of ≥ 4 to have received substantially less support (Burnham and Anderson, 2002). For the selected model we examined the corresponding semivariogram to ensure that the spatial structure incorporated into the model was adequate in accounting for the spatial autocorrelation or to confirm that spatial autocorrelation was not an issue when the non-spatial model was selected as the best model.

Objectives 1, 2 & 3: Comparison of Vegetation
and Bird Variables Among Willow Growth Conditions: Differences in vegetation

variables among the three willow conditions were tested with one-way ANOVA within a

GLS framework. We examined diagnostic plots for normality of residuals and constant

variance and either square root or log transformed the response to meet the assumptions

of ANOVA; however, we report untransformed means and standard errors. Multiple

comparisons between willow conditions were made using the Bonferroni method.

Objective 4: Model Development and Evaluation: The relationship between bird

response variables (species richness, abundance, and diversity) and willow structural

characteristics were quantified using GLS regression. We used AIC_c to evaluate a set of

a priori models (Table 3.2). We considered all univariate models, a global model with all

covariates, and a suite of additive and multiplicative models for which there was

reasonable justification. We excluded vertical vegetation density stratified by height

class from model development since these measures are accounted for by foliage height

diversity.

We checked for correlation among covariates using Pearson's correlation

coefficients. No variables that were strongly correlated ($R \geq 0.70$) were included in the

same model except in the global model (Neter et al., 1996). We assessed multi-

collinearity between covariates with variance inflation factors (VIF). VIF values of ≥ 10

are considered to be correlated with one or more variables and were not used in the same

model except in the global model (Robinson-Cox, personal communication). We

assessed the fit of the global model by examining diagnostic plots for normality of

residuals and constant variance.

Table 3.2. Suite of *a priori* models evaluated for bird species richness, abundance, and diversity. The number of main effects in each model is indicated by 'k'.

Model Structure	Ecological Reasoning	k
HT	Taller willows provide greater structure for resource partitioning in the vertical dimension	1
HT.cv	Greater willow height heterogeneity is preferential to some species and increases the number of available niches	1
HZ	Greater willow extent provides greater structure for resource partitioning in the horizontal dimension	1
FHD	Greater vertical structural complexity (ie. tall and dense willows) may provide better concealment against predators and/or attract more prey species (e.g. insects) resulting in greater resources than tall willows alone	1
FREQ	Greater willow frequency results in more patches for resource partitioning (e.g. nesting and foraging)	1
PATCH	Few large patches provide more interior and less edge habitat than several small patches	1
HT + HT.cv	After willow height, height heterogeneity provides increased spatial resources for partitioning	2
HT + HZ	After willow height, larger extent of willow provides more resources in the horizontal dimension	2
HT + FREQ	After willow height, an increase in the frequency of willow results in more patches for resource partitioning	2
HT + PATCH	After willow height, fewer and larger patches provide more interior than edge habitat	2
FHD + HZ	After foliage height diversity, larger extent of willow provides more resources in the horizontal dimension	2
FHD + FREQ	After foliage height diversity, an increase in the frequency of willow results in more patches for resource partitioning	2
FHD + PATCH	After foliage height diversity, fewer and larger patches will provides more interior and less edge habitat	2
PATCH + FREQ	After willow patchiness, an increase in the frequency of willow results in more patches for resource partitioning	2

Table 3.2 Continued

HT + HZ + HT.cv	Two strong factors of height and extent of willow will largely explain measures of bird diversity, however height heterogeneity will also be important	3
HT + HT.cv + PATCH	Two strong factors of height and height heterogeneity will largely explain measurers of bird diversity, however patchiness will also be important	3
HT + HZ +HT:HZ	Two strong measures of height and willow extent will largely explain variation in bird diversity measures, however an interaction between height and extent will also be important	3
HT + HT.cv + HZ + HT:HZ	After willow height, height heterogeneity and horizontal cover will interact to determine measures of bird diversity	4
HT + HT.cv + HZ + HT:HZ + FHD + FREQ + PATCH	Global model is always considered	7

Results

Confirming the Designation of Willow
Sites into the Three Growth Conditions

The change detection results support the classification of sites into suppressed, released, and previously tall growth conditions (Figure 3.3). Willows across the previously tall condition did not change significantly between the two dates of imagery (n = 23, t = 0.68, P = 0.50). Mean willow cover in 1991 was 59% versus 60% in 2006. However, mean willow cover across the suppressed condition increased significantly from 5% in 1991 to 11% in 2006 (n = 23, t = 3.0, P = 0.007). Although suppressed willows appeared to increase in cover over the 15-year period, willow cover was low in both dates supporting the initial classification into the suppressed growth condition. The released willow condition contained an average of 4% willow in 1991, but increased to 35% willow cover in 2006, a substantial increase in cover over the 15 year period (n = 21, t = 7.94, P < 0.0001). The similar percent cover values in both the suppressed and

released condition in 1991 provide evidence that they were similar in height growth and areal extent during this time.
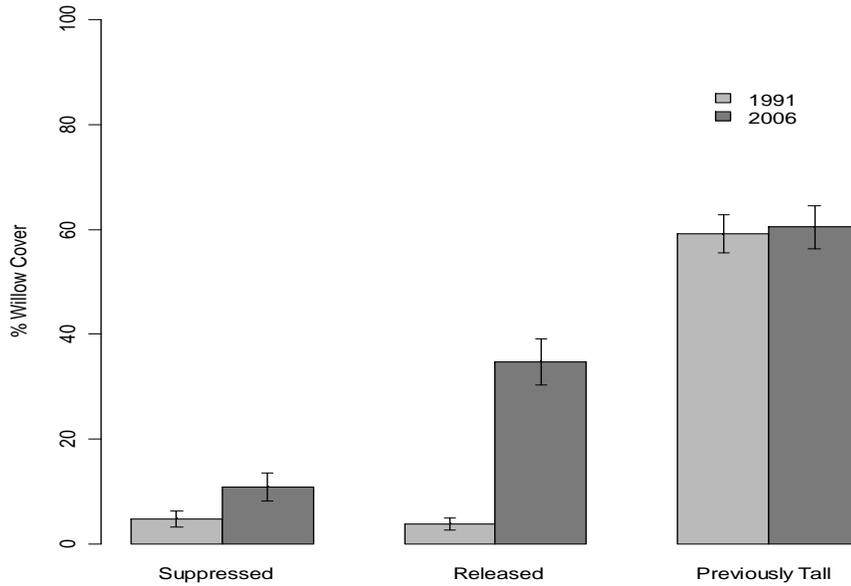
Figure 3. 3. Mean percent willow cover in 1991 and 2006 by willow growth condition as measured from aerial photographs.

The classification accuracy of willow was assessed with field data of willow height at known locations for both 1991 and 2006 (see Chapter 2 for complete methods and results). Accuracy in the classification of willow was generally consistent and reliable especially when willow was taller than 100 cm. Below this threshold willow was more difficult to detect in the air photos indicating that we likely underestimated willow cover classified into the suppressed condition in both dates. However, this provides further evidence that we correctly classified willow into the suppressed growth condition since even if willow was underestimated, it was because it was less than 100 cm, slightly above our threshold for inclusion of willows into the suppressed condition.

It is probable that we overestimated change for willows in the released condition since there was almost certainly greater willow cover in 1991 than we were able to detect. Nevertheless, the fact that willow cover was low in 1991 provides additional evidence that the majority of willow in released sites was < 100 cm tall at that time, a criterion for inclusion in the released willow condition. Furthermore, the high willow cover (35%) in 2006 relative to 1991 indicate that at least approximately 35% of the willows were greater than 100 cm tall signifies increased growth over the two time periods.

Modeling Spatial Autocorrelation

The inclusion of a spatial autocorrelation structure was a significant improvement for nearly half of the ANOVA models (Appendix A). The exponential spatial structure resulted in the lowest AIC_c score for HT and FHD; however, there was some similarity among models including spatial structure. For all other willow structure variables, none of the four models of spatial structure was an improvement over the model without spatial structure and so was excluded for those variables. For richness, abundance, diversity, and the abundance of the seven focal species, inclusion of the exponential spatial structural term or rational quadratic term was a significant improvement over models without a spatial structural term.

For the global GLS models, the exponential spatial structure was selected as the best model and so was incorporated into the suite of *a priori* models described in table 3.2 (Appendix B). Semivariograms indicated that the selected models adequately accounted for spatial autocorrelation or confirmed that spatial autocorrelation was not an issue for those models where we did not include a spatial autocorrelation term for both

the ANOVA (Appendix C) and GLS analyses (Appendix D).

Objective 1: Comparison of Willow
Structure Across Willow Growth Conditions

Previously tall willows averaged 180 cm in HT and tended to be relatively dense in all vegetation height classes; however, VERT tended to decrease with increasing height (Table 3.3). The height and density of previously tall willows resulted in relatively high FHD revealing structurally complex willows. Previously tall willows also occurred with high FREQ (73%) and represented 60% of the total HZ. The relatively high PATCH index indicates a few, large willow patches rather than several small willow patches as was found in the suppressed willow condition. The suppressed condition contained significantly lower FREQ (27 %), HT (62 cm), and FHD of willows compared with previously tall willows. Willow represented only 10% HZ in the suppressed condition, $1/6^{th}$ of that found in the previously tall condition. Previously tall and suppressed willows represent the two extremes of willow growth in the region, differing significantly from one another in all willow variables measured except for VERT1 and HT.cv.

Released willows were intermediate between suppressed and previously tall willows sharing structural attributes representative of each. Released willows were not significantly different from previously tall willows in HT, FHD, VERT1, VERT2, and VERT4, which are all measures of vertical distribution; however, released willows were significantly lower in HZ, FREQ, and PATCH than for previously tall willows, which are all measures of horizontal willow distribution. Willow HT.cv, FREQ, PATCH, and VERT1 were not significantly different between released and suppressed willows;

however, HT, HZ, FHD, and VERT2 in the released condition were more than twice that

found in the suppressed condition. In general, our hypothesis that willow structure would

increase along a gradient from least complex in the suppressed condition to most

complex in the previously tall condition was supported.

Table 3.3. ANOVA results for willow structural characteristics among suppressed, released, and previously tall willow growth conditions. Under "Differences" spaces between letters indicate significant differences. Growth conditions are indicated by first letter.

	Suppressed (n = 23) x $\pm$ SE	Released (n = 21) x $\pm$ SE	Previously tall (n = 23) x $\pm$ SE	F	P	Differences
HT (cm)	61.55 $\pm$ 19.03	143.08 $\pm$ 18.34	179.71 $\pm$ 19.91	15.08	< 0.0001	P,R S
HT.cv (cm)	0.37 + 0.04	0.39 + 0.04	0.39 + 0.04	0.11	0.8952	P,R,S
HZ (%)	9.61 $\pm$ 3.15	21.42 $\pm$ 3.29	60.39 $\pm$ 3.15	76.75	< 0.0001	P R S
FREQ (%)	26.53 $\pm$ 3.95	30.48 $\pm$ 4.13	73.48 $\pm$ 3.95	31.34	< 0.0001	P R,S
FHD	0.45 $\pm$ 0.12	1.39 $\pm$ 0.12	1.69 $\pm$ 0.13	29.37	< 0.0001	P,R S
PATCH	1.05 $\pm$ 2.06	2.95 $\pm$ 2.15	12.49 $\pm$ 2.05	11.31	0.0012	P R,S
Vert1 (%)	59.74 $\pm$ 3.65	69.20 $\pm$ 3.81	68.42 $\pm$ 3.65	14.33	0.2460	P,R,S
Vert2 (%)	20.29 $\pm$ 3.83	53.16 $\pm$ 4.01	63.85 $\pm$ 3.83	34.91	< 0.0001	P,R S
Vert3 (%)	NA	36.59 $\pm$ 4.90	51.16 $\pm$ 4.69	4.61	0.0375	P R
Vert4 (%)	NA	24.88 $\pm$ 5.05	34.98 $\pm$ 4.83	3.92	0.0544	P,R

Objective 2: Comparison of Richness,
Abundance, and Diversity Across Willow Growth Conditions

We observed 2,724 individuals from 33 species across all three willow conditions

over the three years of surveys (flyovers, marshbirds, and shorebirds not included in

totals). Observers recorded 1,012 individuals belonging to 25 species in previously tall

sites; 1,042 individuals belonging to 23 species in released sites; and 670 individuals

belonging to 16 species in suppressed sites (see Appendix E for a complete list of species

by growth condition).

Previously tall sites were significantly greater in species richness, abundance, and diversity than suppressed sites (Table 3.4). Not only were there fewer species and individuals of those species, but the relatively low Shannon-Weiner diversity index indicates that suppressed sites were dominated by a few abundant species. The Renkonen community similarity index indicates only 34% overlap between the previously tall and suppressed willow conditions revealing little similarity in their respective bird communities.

In contrast, the released willow condition was intermediate in richness between the previously tall and suppressed condition, but were similar to the previously tall condition in abundance and diversity. The Renkonen index indicates 66% community similarity between released and previously tall conditions and 59% similarity between released and suppressed conditions. Our hypothesis that richness would increase along a gradient from suppressed to previously tall was supported; however, hypotheses regarding abundance and diversity were not supported. Although abundance and diversity was significantly lower in the suppressed willow condition neither were significantly different between the released and previously tall condition.

Table 3.4. Bird species richness, abundance, and diversity among suppressed, released, and previously tall willow growth conditions. Under "Differences" spaces between letters indicate significant differences. Growth conditions are indicated by first letter.

	Suppressed (n = 23) $\bar{x} \pm SE$	Released (n = 21) $\bar{x} \pm SE$	Previously tall (n = 23) $\bar{x} \pm SE$	F	P	Differences
Richness	2.93 ± 0.34	5.72 ± 0.33	7.52 ± 0.34	48.04	< 0.0001	P R S
Relative Abundance	3.85 ± 0.39	5.98 ± 0.37	6.46 ± 0.41	14.64	< 0.0001	P,R S
Shannon-Weiner Diversity	0.76 ± 0.06	1.51 ± 0.06	1.78 ± 0.07	62.46	< 0.0001	P,R S

Objective 3: Comparison of Focal Species
Abundance Across Willow Growth Conditions

Five of the seven focal species were completely absent from suppressed willows, while previously tall willows contained all seven focal species. Only the common yellowthroat and Lincoln's sparrow occurred in all three growth conditions. Common yellowthroat abundance was significantly greater in released than in either previously tall or suppressed willows ($F = 14.01$, $P < 0.0001$; Figure 3.4). Lincoln's sparrow abundance was similar between previously tall and released willows, but both were significantly greater than abundance in suppressed willows ($F = 3.56$, $P < 0.0342$). Although both species were present in all three growth conditions, our prediction of increasing abundance from suppressed to previously tall was not supported for either species.

All three willow associates were absent from suppressed willows, but were present in both released and previously tall willows. However, only the warbling vireo was found to be significantly greater in previously tall than in released willows ($F = 4.91$, $P = 0.0322$) supporting our hypothesis for this species. Neither yellow warbler ($F = 2.11$, $P = 0.1532$) nor song sparrow ($F = 3.99$, $P = 0.0524$) abundance was significantly different between released and previously tall willows therefore we reject our hypothesis for these species that abundance would be greater in previously tall willows. As predicted Wilson's warblers were found exclusively in previously tall willows, but contrary to predictions willow flycatchers were found in both released and previously tall willows. However, differences were not significant ($F = 1.09$, $P = 0.3021$).
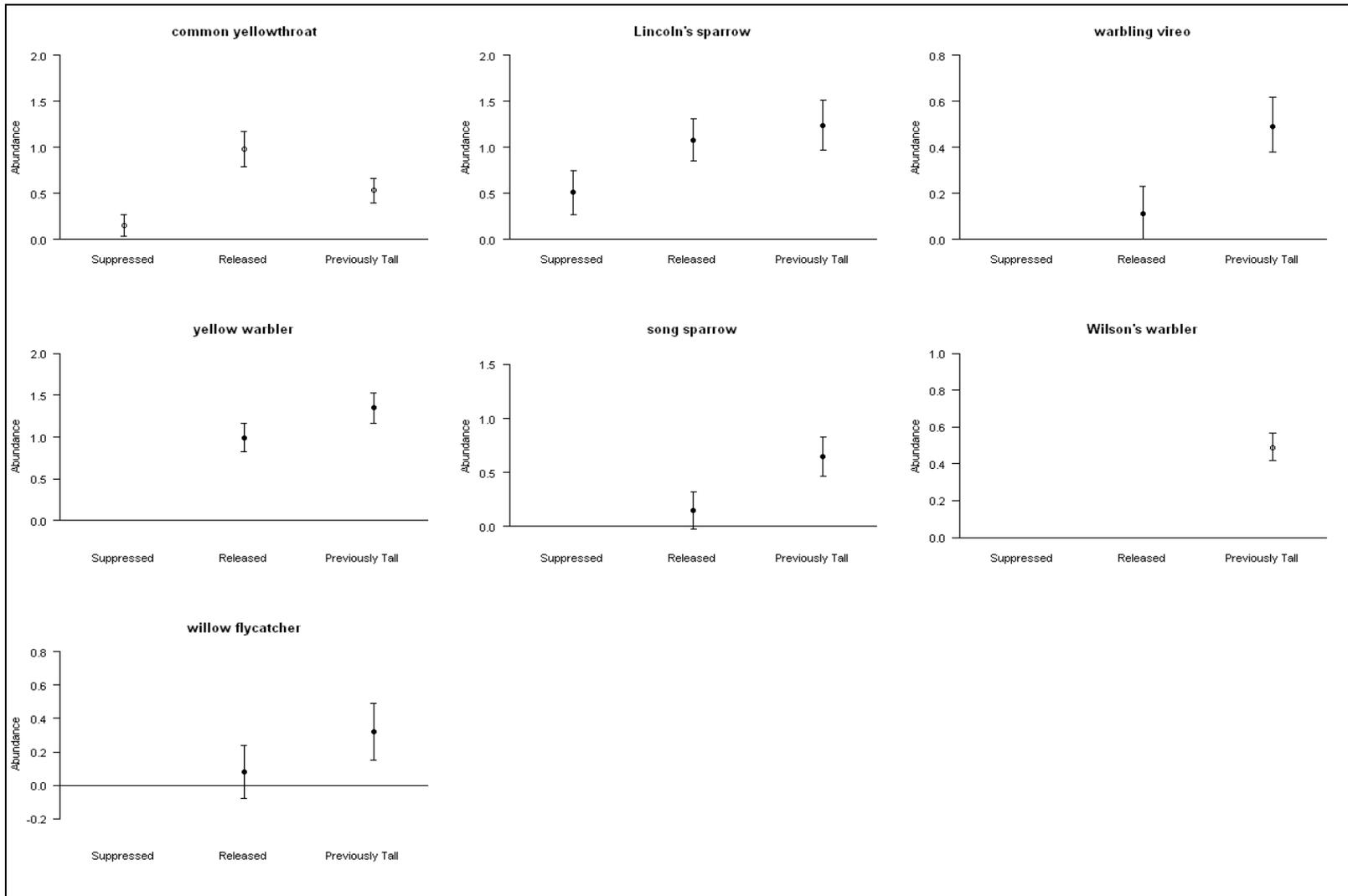
Figure 3.4. Comparison of abundance for the seven focal species across suppressed, released, and previously tall willow growth conditions in Yellowstone National Park's northern range. Note the difference in scale between panels.

Objective 4: Model Evaluation for
<u>Richness, Abundance, and Diversity</u>

Three pairs of variables were highly correlated (Table 3.5). FHD was correlated

with HT (R = 0.73), HZ was correlated with FREQ (R = 0.92), and PATCH was

correlated with HZ (R = 0.72). VIF values for HZ and FREQ were greater than the

threshold ($\geq$ 10) that would indicate multicollinearity. Highly correlated variables were

not used in the same model except for the global model. By examining diagnostic plots

for normality of residuals and constant variance for all global models we concluded that

each was a good fit to the data.

Table 3.5. Absolute value of the Pearson correlation coefficient among covariates used in
models. No covariate with a coefficient $\geq$ 0.70 were used in the same model.

Covariate*	HT	HT.cv	FHD	HZ	FREQ	PATCH
HT	1.00	0.11	0.73	0.41	0.28	0.21
HT.cv		1.00	0.01	0.05	0.20	0.16
FHD			1.00	0.47	0.38	0.19
HZ				1.00	0.92	0.72
FREQ					1.00	0.59
PATCH						1.00

The best model within our suite of models for richness (Table 3.6), abundance

(Table 3.7), and diversity (Table 3.8) contained FHD only, supporting our hypothesis that

greater vertical structural complexity provides better concealment against predators

and/or attracts more prey species resulting in more resources that can be partitioned

among multiple species. No model was within 2 ΔAIC_c units of the best model and all

were > 4 ΔAIC_c units of the best model indicating clear support for the FHD only model.

Table 3.6. Model selection results for competing *a priori* models for species richness. The letter 'k' indicates the number of estimated main effects. AIC$_c$ adjusted for sample size was used to select the best models. The weight of evidence for each model given the other models in the suite is indicated by w_i.

Model Structure	AIC$_c$	ΔAIC$_c$	w_i	k
FHD	25.22	0.00	0.96	1
HT.cv	32.56	7.34	0.02	1
FHD + PATCH	35.93	10.71	0.00	2
FHD + HZ	37.21	11.98	0.00	2
FHD + FREQ	38.35	13.13	0.00	2
PATCH	39.04	13.82	0.00	1
HZ	40.34	15.12	0.00	1
FREQ	40.91	15.69	0.00	1
HT	40.97	15.75	0.00	1
HT + HT.cv	44.37	19.15	0.00	2
HT + PATCH	49.37	24.15	0.00	2
PATCH + FREQ	49.60	24.38	0.00	2
HT + HT.cv + PATCH	53.19	27.97	0.00	3
HT + HZ	53.66	28.44	0.00	2
HT + FREQ	54.02	28.80	0.00	2
HT + HZ + HT.cv	57.17	31.95	0.00	3
HT + HZ +HT:HZ	73.16	47.94	0.00	3
HT + HT.cv + HZ + HT:HZ	77.00	51.78	0.00	4
HT + HT.cv + HZ + HT:HZ + FHD + FREQ + PATCH	89.51	64.29	0.00	7

Table 3.7. Model selection results for competing *a priori* models for species abundance. The letter 'k' indicates the number of estimated main effects. AIC$_c$ adjusted for sample size was used to select the best models. The weight of evidence for each model given the other models in the suite is indicated by w_i.

Model Structure	AIC$_c$	ΔAIC$_c$	w_i	k
FHD	-0.4	0	0.95	1
HT.cv	5.95	6.35	0.04	1
FHD + PATCH	10.03	10.43	0.01	2
FHD + HZ	12.73	13.13	0.00	2
FHD + FREQ	12.73	13.13	0.00	2
PATCH	13.25	13.65	0.00	1
FREQ	14.06	14.45	0.00	1
HZ	14.89	15.29	0.00	1
HT	15.88	16.28	0.00	1
HT + HT.cv	17.96	18.35	0.00	2
PATCH + FREQ	21.33	21.73	0.00	2
HT + PATCH	24.43	24.82	0.00	2
HT + HT.cv + PATCH	27.16	27.56	0.00	3
HT + FREQ	28.32	28.72	0.00	2
HT + HZ	28.88	29.28	0.00	2
HT + HZ + HT.cv	31.15	31.55	0.00	3
HT + HZ +HT:HZ	46.81	47.21	0.00	3
HT + HT.cv + HZ + HT:HZ	49.72	50.11	0.00	4
HT + HT.cv + HZ + HT:HZ + FHD + FREQ + PATCH	69.71	70.11	0.00	7

Table 3.8. Model selection results for competing *a priori* models for species diversity. The letter 'k' indicates the number of estimated main parameters and β_0. AIC_c adjusted for sample size was used to select the best models. The weight of evidence for each model given the other models in the suite is indicated by w_i.

Model Structure	AIC_c	ΔAIC_c	w_i	k
FHD	-78.40	0.00	0.97	1
HT.cv	-71.51	6.89	0.03	1
FHD + PATCH	-64.89	13.52	0.00	2
FHD + HZ	-64.48	13.92	0.00	2
FHD + FREQ	-63.62	14.78	0.00	2
HZ	-63.21	15.19	0.00	1
PATCH	-62.95	15.45	0.00	1
FREQ	-62.59	15.81	0.00	1
HT	-61.91	16.49	0.00	1
HT + HT.cv	-58.14	20.26	0.00	2
PATCH + FREQ	-50.21	28.19	0.00	2
HT + PATCH	-49.55	28.85	0.00	2
HT + HZ	-47.77	30.64	0.00	2
HT + FREQ	-47.40	31.00	0.00	2
HT + HT.cv + PATCH	-45.42	32.98	0.00	3
HT + HZ + HT.cv	-43.74	34.66	0.00	3
HT + HZ +HT:HZ	-27.26	51.14	0.00	3
HT + HT.cv + HZ + HT:HZ	-22.72	55.68	0.00	4
HT + HT.cv + HZ + HT:HZ + FHD + FREQ + PATCH	-2.71	75.69	0.00	7

Discussion

In this paper we examined bird response to recent increases in willow growth in and around Yellowstone's northern range by comparing bird community composition in recently released willows to that found in highly suppressed and previously tall willows. Overall, we found that willow structure generally increased in complexity from structurally simple height suppressed willows to structurally complex previously tall willows and that this variation in structural complexity influenced bird community variables and the abundance of riparian and willow dependent bird species. These results provide the first examination of the significance of an increase in a rare, but important habitat type for birds in the region.

While released willows have attained similar height and vertical structural complexity as previously tall willows, horizontal cover is still limited in the released growth condition, but is twice that observed in the suppressed condition. Although released willows exhibited significantly greater horizontal cover than suppressed willows, frequency was similar between the two, suggesting that successful recruitment of new willow plants is limited and that differences in horizontal cover are the result of existing willows getting larger and increasing in crown cover. This speculation is supported by a recent study, which showed that willow establishment has significantly declined in the northern range throughout the 20th century (Wolf et al., 2007). Declines in willow recruitment were attributed to prolonged absence of beaver from most streams in the

region during this time leading to increased stream incision and lowered water tables resulting in reduced recruitment opportunities for willow (Wolf et al., 2007).

Despite the lack of apparent establishment of new willow plants and significantly lower horizontal cover in the released condition than in the previously tall condition, bird abundance and diversity were similar between the two, suggesting that measures of vertical structural complexity are more important than horizontal structure in influencing bird community variables in our study and is supported by the results of others. Willow height significantly influenced songbird richness and abundance, whereas patch size did not in a study of willow-bird relationship in the greater Yellowstone ecosystem (Olechnowski and Debinski, 2008) and bird richness, abundance, and diversity were reduced in areas where ungulate browsing limited the height growth and density of willows (Berger et al., 2001; Anderson, 2007). Complex vertical vegetation structure (i.e. tall, dense willows) provides a greater variety of resources that can be partitioned among a greater number of individuals and species and thus accounts for higher diversity associated with complex vegetation (MacArthur and MacArthur, 1961); however, individual species respond differentially to specific aspects of vegetation structure reflecting niche associations (MacArthur, 1958; Finch, 1989).

Common yellowthroats and Lincoln's sparrows were found in all three willow growth conditions supporting our hypothesis that both species are generalists within the range of willow growth sampled; however, our predictions of increasing abundance along the gradient of willow growth was not supported by the data for either species. Lincoln's sparrow abundance was lowest in suppressed willows, but was similar between released

and previously tall willows, whereas common yellowthroat abundance was higher in released willows than in either suppressed or previously tall willows.

Both species nest and forage near to the ground in dense, shrubby vegetation (Ammon, 1995; Guzy and Ritchison, 1999), a feature found in all three willow growth conditions. However, the low horizontal willow cover and small patch size characteristic of the suppressed willow condition effectively lowered foraging and nesting opportunities, consequently limiting abundance there. Although Lincoln's sparrows nest and forage in low vegetation, they generally select tall willows for singing (Ammon, 1995). While willow height was similar between released and previously tall willows, tall willows were more abundant in the previously tall condition as indicated by the 3-fold increase in horizontal cover from released to previously tall, yet Lincoln's sparrow abundance increased only slightly. This suggests that other factors such as competition for additional limiting resources (e.g. food) or density dependent factors likely influenced abundance between these two willow conditions for this species.

The higher abundance of common yellowthroats in released willows than in previously tall willows may be partially the result of interference competition by Wilson's warblers. In a study of foraging heights among several warbler species associated with willows in Wyoming, common yellowthroats typically foraged in the lowest willow layer (< 0.6 m) in the presence of Wilson's warblers; however, when Wilson's warblers departed willow stands in late summer, common yellowthroats shifted their foraging height to the tallest willow strata (Hutto, 1981). The absence of Wilson's warblers from released willows in our study may account for the higher abundance of common yellowthroats observed there and suggests that if willows in released sites

eventually become suitable for Wilson's warbler occupation, common yellowthroat

abundance may decrease in these areas. The increased foraging height was also

coincidental with the departure of MacGillivray's (*Oporornis tolmiei*) and yellow

warblers (Hutto, 1981); however, MacGillivray's warblers were rare in our study area

and yellow warblers were present in equal abundance in both the released and previously

tall willow conditions and likely had little influence on common yellowthroat abundance.

As predicted, all willow associates (yellow warbler, song sparrow, and warbling

vireo) were absent from the suppressed willow condition, but present in both the released

and the previously tall willow conditions; however, only warbling vireo abundance was

significantly greater in the latter. This suggests that all three species require relatively

tall willows, but tolerate a wide breadth of horizontal vegetation cover and patchiness at

least over the range of willows measured in this study. Warbling vireos preferentially

nest and forage in tall vegetation and the greater horizontal cover in the previously tall

condition provided a greater amount of tall willows, which may account for higher

abundance there.

Both willow specialist species (willow flycatcher and Wilson's warbler) were

observed in the previously tall condition; however, the willow flycatcher was also present

in the released condition, although differences were not significant. Previous studies

indicate that willow flycatchers prefer a clumped willow distribution (Knopf et al., 1988)

with high vertical vegetation cover, especially in the 1-2 m height category (Anderson,

2007). Our results indicate that willow flycatchers can tolerate horizontal cover as low as

20% and a wide range of willow density (25% - 50%) in the 1-2 m height class.

Although willow flycatchers were in both willow conditions, abundance in both of these

was low indicating that this species is relatively rare in the northern range, but evidence suggests that it is more abundant than in 1989-1991 before willow height release when willow flycatchers were detected in only one site surveyed outside of the northern range (Jackson, 1992).

Wilson's warblers are typically associated with tall willows (Hutto, 1981; Douglas et al., 1992; Berger et al., 2001), yet despite no significant difference in willow height between released and previously tall willow conditions they were absent from released willows. This suggests that measures of willow distribution such as horizontal cover, frequency, and/or patch size are important for Wilson's warbler colonization and is supported by other studies demonstrating that abundance was positively correlated with increasing shrub cover (Finch, 1989; Donnelly and Marzluff, 2006). Because Wilson's warblers require specific structural requirements, are restricted to montane willow communities (Finch, 1989; Ammon and Gilbert, 1999), and are declining across the region (Ruth and Stanley, 2002), relatively high elevation willow stands, such as those found in Yellowstone, are important for the persistence of this species in the region.

Although vegetation height is often used to explain differences in bird community variables, our model selection results indicate that foliage height diversity exhibits better explanatory power than height alone; and confirms our speculation that measures of vertical structural complexity were responsible for differences in bird community variables between growth conditions. Foliage height diversity recognizes the importance of both the number and evenness of canopy layers and has been shown to be a significant factor in explaining patterns of species diversity (MacArthur and MacArthur, 1961; Finch, 1989; Douglas et al; 1992). The way species are organized in space is a function

of patterns of resource distribution and competition for those resources. High foliage height diversity provides a greater variety of foraging and nesting opportunities that in turn provides a broader resource base that can be partitioned among more species and individuals and therefore may reduce competition and potential competitive exclusion.

Willow structure in the northern range is in part modified by browsing. Suppressed willows in our study exhibited moderate to heavy browsing while released and previously tall willows showed little to no browsing, although this is a qualitative observation since this was not measured in our study. While low levels of browsing can be beneficial to bird diversity by promoting branching of willow stems, resulting in greater structural complexity, there is a threshold above which browsing simplifies vegetation structure thus reducing bird diversity (Jackson, 1992; Berger et al., 2001; Hebblewhite et al., 2005) and nest success (Ammon and Stacey, 1997; Berger et al., 2001; Heltzel and Earnst, 2006).

While heavy browsing was prevalent in the majority willow stands throughout the northern range during most of the 20th century (Chadde and Kay, 1991; Singer et al., 1994; Singer et al., 1998) several studies have reported decreased browsing of willows since wolf reintroductions (Ripple and Beschta, 2006; Beschta and Ripple, 2007) resulting in increased growth (Beyer et al., 2007) that could account for differences in willow structure across our study sites. Increased willow growth has been largely attributed to a behaviorally modified trophic cascade whereby wolf presence influences foraging patterns of elk (Ripple and Beschta, 2004); however, wolf presence has been

shown to actually increase consumption of willow by elk in the adjacent Gallatin River drainage (Creel and Christianson, 2009).

Although modification of willows by browsing is well established as a proximal factor influencing willow growth in the northern range, changes in the hydrologic regime could mediate the effects of browsing, leading to the observed increase in willow growth since 1998. Willow growth and establishment is dependent on the availability of an adequate and consistent water source (Cary, 2005). The 1990s were the wettest decade in the last 300 years with 100-year flood events occurring in both 1996 and 1997 (Graumlich et al., 2003), at about the time the willows began increasing in height growth. Furthermore, warmer spring temperatures have led to earlier (Stewart et al., 2005) and greater peak stream flows (Lins and Slack, 1999) that could provide a consistent, at least in the short term, water source for increased willow growth; however, the benefits may be short-lived as climate warming is expected to continue thereby reducing alpine snowpack responsible for increased flows (IPPC, 2007).

The hydrologic regime could also be modified through beaver manipulation of riparian areas. Willows gained significantly more height growth under an experimentally elevated water table designed to simulate beaver damming than willows under the ambient water table condition even under intense browsing (Bilyeu et al., 2008). After a prolonged absence of beaver on most northern range streams during the 20th century, stream channels became incised, thereby lowering local groundwater levels and reducing willow recruitment and growth opportunities (Wolf et al., 2007). The recent increase in beaver occupation of some northern range streams over the last decade will likely influence local willow growth (Smith and Tyers, 2008), although the extent to which

beaver activity has historically modified northern range stream flow and sedimentation is limited primarily because of the high velocity of many northern range streams preventing the construction of dams and subsequent modification of river flows (Persico and Meyer, 2009).

Conclusions

We have demonstrated that willows have increased in some locations in the northern range and that this increase in willow growth has resulted in a greater amount of structurally complex willow habitat. Increased structural complexity since 1992 has in turn likely allowed for greater bird richness, abundance, diversity, and abundance of six of the seven focal species studied. If the reintroduction of wolves has triggered a trophic cascade in the northern range, as is suggested by several studies (Beschta and Ripple, 2007; Beyer et al., 2007; Ripple and Beschta, 2006), then our study provides evidence that the progression towards natural regulation has been at least partially effective in restoring ecosystem function, and suggests that top predators should be reintroduced to other areas where they were extirpated to reestablish natural ecosystem processes. However, the amount of variation that is explained by wolves, beaver, and climatic variables remains unknown. Additional, research is needed to determine the relative roles of factors influencing willow growth in the northern range.

Literature Cited

Alldredge, M.W., T.R. Simons, & K.H. Pollock. 2008. A field evaluation of distance measurement error in auditory avian point count surveys. Journal of Wildlife Management 71:2759-2766.

Ammon, Elisabeth M. 1995. Lincoln's Sparrow (*Melospiza lincolnii*), *In* The Birds of North America Online, No. 191 (A. Poole, Ed.). The Birds of North America, Inc., Philadelphia, PA.

Ammon, Elisabeth M. and William M. Gilbert. 1999. Wilson's Warbler (*Wilsonia pusilla*), *In* The Birds of North America, No. 478 (A. Poole, Ed.). The Birds of North America, Inc., Philadelphia, PA.

Ammon, E.M. and P.B. Stacey. 1997. Avian nest success in relation to past grazing regimes in a montane riparian system. The Condor 99: 7-13.

Anderson, E.M. 2007. Changes in bird communites and willow habitats associated with fed elk. The Wilson Journal of Ornithology 119: 400-409.

Bachler, E. & F. Liechti. 2007. On the importance of g(0) for estimating bird population densities with standard distance-sampling: implications from a telemetry study and a literature review. Ibis 149:693-700.

Barnosky, C.W. 1988. The relationship of climate to sedimentation rates in lakes and ponds. Page 4 in F. Singer, ed. First annual meeting of research and monitoring on Yellowstone's northern range. USDI, Nat. Park Ser., Yellowstone National Park.

Berger, J., P.B. Stacey, L. Bellis and M.P. Johnson. 2001. A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. Ecological Applications 11: 947-960.

Beschta, R.L. and W.J. Ripple. 2007. Increased willow heights along northern Yellowstone's Blacktail Deer Creek following wolf reintroduction. 67: 613-617.

Beyer, H.L., E.H. Merril, N. Varley and M.S. Boyce. 2007. Willow on Yellowstone's northern range: evidence for a trophic cascade? Ecological Applications 17: 1563-1571.

Bilyeu, D. M., D. J. Cooper and M. T. Hobbs. 2008. Water tables constrain height recovery of willow on Yellowstone's northern range. Ecological Applications 18: 80-92.

Boyce, M. S. 1991. Natural regulation or the control of nature? In R.B. Keiter and M.S.

Boyce (Eds.), *The Greater Yellowstone Ecosystem*. Yale University Press.

Buckland, S.T., D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers, & L. Thomas. 2001. Introduction to Distance Sampling: Estimating Abundance of Biological Populations. Oxford: Oxford University Press.

Burnham, K.P. and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science+Business Media, Inc., New York, NY. pp: 487.

Canfield, R.H. 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry 39: 388-394.

Cary, K.L. 2005. Willow resilience on Yellowstone's northern elk winter range: a function of environmental gradients. M.S. thesis, Montana State University, Bozeman, Montana.

Cayan, D.R., S.A. Kammerdiener, M.D. Dettinger, J.M. Caprio and D.H. Peterson. 2001. Changes in the onset of spring in the western United States. Bulletin of the American Meteorological Society 83: 399-415.

Chadde, S.W., P.L. Hansen, and R.D. Pfister. 1988. Wetland Plant Communities of the Northern Range, Yellowstone National Park. School of Forestry, University of Montana.

Chadde, S.W. and C.E. Kay. 1991. Tall-willow communities on Yellowstone's northern range: a test of the "natural-regulation" paradigm. In R.B. Keiter and M.S. Boyce (Eds.), *The Greater Yellowstone Ecosystem*. Yale University Press.

Creel, S. and D. Christianson. 2009. Wolf presence and increased willow consumption by Yellowstone elk: implications for trophic cascades. Ecology 90: 2454-2466.

Christiansen, R.L., 2001, The Quaternary and Pliocene Yellowstone Plateau volcanic field of Wyoming, Idaho, and Montana: U.S. Geological Survey Professional Paper: 729-G, 145 p., 3 plates, scale 1:125,000.

Crawley, M.J. 2007. The R. Book. John Wiley & Sons Ltd.

Despain, D.G. 1987. The two climates of Yellowstone National Park. Proceedings of the Montana Academy of Science 47: 11-20.

Donnelly, R. and J.M. Marzluff. 2006. Relative importance of habitat quantity, structure, and spatial patterns to birds in urbanizing environments. Urban Ecosyst 9: 99-117.

Douglas, D.C., J.T. Ratti, R.A. Black, J.R. Alldredge. 1992. Avian habitat associations in riparian zones of Idaho's Centennial Mountains. Wilson Bulletin 104: 486-500.

Engstrom, D.R., C. Whitlock, S.C. Fritz and H.E. Wright, Jr. 1991. Recent environmental changes inferred from the sediments of small lakes in Yellowstone's northern range. Journal of Paleolimnology 5: 139-174.

Finch, D.M. 1989. Habitat use and habitat overlap of riparian birds in three elevation zones. Ecology 70: 866-880.

Finch, D.M. and L.F. Ruggiero. 1993. Wildlife habitats and biological diversity in the Rocky Mountains and northern Great Plains. Natural Areas Journal 13: 191-203.

Fletcher, R.J. and R.L. Hutto. 2008. Partitioning the multi-scale effects of human activity on the occurrence of riparian forests. Landscape Ecology 23: 727-739.

Graumlich, L.J., M.F.J. Pisaric, L.A. Waggoner, J.S. Littell, and J.C. King. 2003. Upper Yellowstone River flow and teleconnections with Pacific basin climate variability during the past three centuries. Climate Change 59: 245-262.

Groshong, L.C. 2004. Mapping riparian vegetation change in Yellowstone's Northern Range using high spatial resolution imagery. M.A. thesis, University of Oregon, Eugene, OR.

Guzy, M. J. & G. Ritchison. 1999. Common Yellowthroat (*Geothlypis trichas*). *In* The Birds of North America, No. 448 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

Hansen, A.J. and J.J. Rotella. 2002. Biophysical factors, land use, and species viability in and around nature reserves. Conservation Biology: 1112-1122.

Hebblewhite, M., C. A. White, C. G. Nietvelt, J. A. McKenzie, T. E. Hurd, J. M. Fryxell, S. E. Bayley, and P. C. Paquet. 2005. Ecology 86: 2135-2144.

Heltzel, J.M. and S.L. Earnst. 2006. Factors influencing nest success of songbirds in aspen and willow riparian areas in the Great Basin. The Condor 108: 842-855.

Houston, D.B. 1982. The northern Yellowstone elk: ecology and management. MacMillan Publishing Co., Inc., N.Y. 474 pp.

Hutto, R.L. 1981. Seasonal variation in the foraging behavior of some migratory western wood warblers. The Auk 98: 765-777.

Hutto, R.L., S.M. Pletschet, and P. Hendricks. 1986. A fixed-radius point count method for nonbreeding and breeding season use. The Auk 103: 593-602.

IPCC, 2007: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* [Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M.Tignor and H.L. Miller (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Jackson, S.G. 1992. Relationships among birds, willows, and native ungulates in and around northern Yellowstone National Park. M.S. thesis, Utah State University, Logan, UT.

Johnson, D.H. 2008. In defense of indices: the case of bird surveys. The Journal of Wildlife Management 72: 857-868.

Knopf, F.L., J.A. Sedgwick, R.W. Cannon. 1988. Guild structure of a riparian avifauna relative to seasonal cattle grazing. Journal of Wildlife Management 52: 280-290.

Kutner, M.H., C.J. Nachtsheim, J. Neter, W. Li. 2004. Applied Linear Statistical Models. The McGraw-Hill Companies, Columbus, Ohio.

Lins, H.F. and J.R. Slack. 1999. Streamflow trends in the United States. Geophysical Research Letters 26: 227-230.

MacArthur, R.H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39: 599-619.

MacArthur, R.H. and J.W. MacArthur. 1961. On bird diversity. Ecology 42: 594-598.

Myneni, R.B., C.D. Keeling, C.J. Tucker, G. Asrar and R.R. Nemani. 1997. Increased Plant growth in the northern high latitudes from 1981 to 1991. Nature 386: 698-702.

National Research Council. 2002. Ecological dynamics of Yellowstone's northern range. National Academy Press, Washington, D.C.

Nemani, R.R., C.D. Keeling, H. Hashimoto, W.M. Jolly, S.C. Piper, C.J. Tucker, R.B. Myneni, and S.W. Running. 2003. Climate-driven increases in global terrestrial net primary productivity form 1982 to 1999. Science 300: 1560-1563.

Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. Applied linear statistical models. McGraw-Hill, Boston, MA.

Nur, N. S.L. Jones, and G.R. Geupel. 1999. A statistical guide to data analysis of avian

monitoring programs. U.S. Department of the Interior, Fish and Wildlife Service, BTP-R6001-1999, Washington, D.C.

Olechnowski, B.F. and D.M. Debinski. 2008. Response of songbirds to riparian willow habitat structure in the Greater Yellowstone Ecosystem. The Wilson Journal of Ornithology 120: 830-839.

Persico, L. and G. Meyer. 2009. Holocene beaver damming, fluvial geomorphology, and climate in Yellowstone National Park, Wyoming. Quaternary Research 71: 340-353.

R Development Core Team. 2007. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ralph, C.J., S. Droege and J. Sauer. 1995. Managing and monitoring birds using point counts: standards and applications USDA Forest Service General Technical Report, PSW-GTR-149.

Regonda, S.K., B. Rajagopalan, M. Clark, and J. Pitlick. 2005. Seasonal cycle shifts in hydroclimatology over the western United States. Journal of Climate 18: 372-384.

Ripple, W.J. and R.L. Beschta. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. Forest Ecology and Management 184: 299-313.

Ripple, W.J. and R.L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems. Bioscience 54: 755-766.

Ripple, W.J. and R.L. Beschta. 2006. Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. Forest Ecology and Management 230: 96-106.

Robel, R.J., J.N. Briggs, A.D. Dayton, and L.C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23: 295-297.

Ruth, J.M. and T.R. Stanley. 2002. Breeding habitat use by sympatric and allopatric populations of Wilson's warblers and yellow warblers. Journal of Field Ornithology 73: 412-419.

Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. Ecological Applications 9: 135-151.

Savage, S. L. and R. Lawrence. 2009. Vegetation dynamics in Yellowstone's northern range: 1985-1999. Photogrammetric Engineering and Remote Sensing.

Scott, M.L., S.K. Skagen, and M.F. Merigliano. 2003. Relating geomorphic change and grazing to avian communities in riparian forests. Conservation Biology 17: 284-296.

Singer, F.J., N.T. Hobbs, D.J. Cooper, D. Smith, J. Mack. 2004. Willow persistence in Yellowstone National Park: interactive effects of climate, hydrology, and herbivory. Annual Report 2003

Singer, F. J., L. C. Mark, and R. C. Cates. 1994. Ungulate herbivory of willows on Yellowstone's northern winter range. Journal of Range Management 47: 435-443.

Singer, F.J., L.C. Zeigenfuss, R.G. Cates, and D.T. Barnett. 1998. Elk, multiple factors, and persistence of willows in national parks. Wildlife Society Bulletin 26: 419-428.

Skagen, S.K., C.P. Melcher, W.H. Howe, F.L. Knopf. 1998. Comparative use of riparian corridors and oases by migrating birds in southeast Arizona. Conservation Biology 12: 896-909.

Smith, C.M. and D.G. Wachob. 2006. Trends associated with residential development in riparian breeding bird habitat along the Snake River in Jackson Hole, WY, USA: implications for conservation planning. Biological Conservation 128: 431-446.

Smith, D. W. and D. B. Tyers. 2008. The beavers of Yellowstone. Yellowstone Science 16: 4-15.

Stevens, L.E., Brown, B.T., Simpson, J.M., Johnson, R.R. 1977. The importance of riparian habitat to migrating birds. In: Jonshon, R.R., Jones Jr., D.A. (Eds.). Importance, preservartion , and management of riparian habitat: A symposium. US Department of Agriculture, Forest Service General Technical Report. RM-43.

Stewart, I.T., D.R. Cayan, and M.D. Dettinger. 2005. Changes toward earlier streamflow timing across western North America. Journal of Climate 18: 1136-1155.

Wolf, E.C., D.J. Cooper, and N.T. Hobbs. 2007. Hydrologic regime and herbivory stabilize an alternative state in Yellowstone National Park 17: 1572-1587.

Yellowstone National Park. 1997. Yellowstone's northern range: complexity and change in a wildland ecosystem. National Park Service, Mammoth Hot Springs, Wyoming.

Zuur, A.F., E.N. Keno, N.J. Walker, A.A. Suavely, and G.M. Smith. 2009. Mixed effects

models and extensions in ecology with R. Springer Science+Business Media, LLC, New York, NY.

CHAPTER 4

WILLOW SPECIES COMPOSITION IN AND AROUND YELLOWSTONE
NATIONAL PARK'S NORTHERN RANGE

Introduction

Willow (*Salix* spp.) in Yellowstone National Park's northern range has been

height suppressed since the early 1900s. Pollen records in lake sediments indicate a

decline in willow since 1920 (Barnosky, 1988; Engstrom et al., 1991) and repeat

photographs show complete loss of willow communities between 1871 and 1988 for 41

of 44 photosets and considerably reduced stature for the remaining three photosets

(Chadde and Kay, 1991). However, since the mid-1990s willow has increased in height

in some locations across the northern range. Beyer et al. (2007) found a two-fold

increase in willow stem growth ring area since 1995. Photo comparisons revealed an

increase in willow and cottonwood (*Populus* spp.) height for six of eight photosets from

1977 to 2002 (Ripple and Beschta, 2003) and high spatial resolution imagery indicated

that riparian vegetation including willow, alder (*Alnus incana*), and cottonwood increased

in areal extent by 279% within a 4 km stretch of the Lamar River-Soda Butte Creek

confluence between 1995 and 1999 (Groshong, 2004). In Chapter 2 we found a 170%

increase in willow, aspen (*Populus tremuloides*), cottonwood, and alder in riparian and

wetlands areas throughout the northern range using air photo comparisons between 1991

and 2006.

Drivers responsible for increased willow growth have received considerable

interest in recent years. One hypothesis is that recent willow growth is the result of a

trophic cascade whereby the reintroduction of wolves (*Canis lupus*) in 1996 has altered

the density and foraging habits of elk (*Cervus elaphus*) resulting in reduced browsing and

increased growth of deciduous woody plants (Ripple and Beschta, 2004). Alternatively,

climate change may be the primary driver of increased willow growth. Longer growing

seasons resulting from warmer spring and fall temperatures have resulted in an increase

in the productivity of deciduous woody vegetation in the Rocky Mountain region (Cayan

et al., 2001; Myneni et al., 1997; Nemani et al., 2003) and warmer spring temperatures

have led to greater (Lins and Slack, 1999) and earlier (Regonda et al., 2005; Stewart et

al., 2005) peak stream flows that may affect patterns of vegetation growth.

Although a number of willow stands have increased in height and areal extent

across the region, changes in growth have not been uniform (R. Renkin, personal

communication, 2005). Some willows stands remain height suppressed while others have

been released from height constraining factors. While all members of the genus *Salix*

share many similar life history characteristics including high seed production, fast growth

rates, and dependence on saturated soils (Karrenberg et al., 2002); individual species

within the genus vary with respect to limits on height growth (USDA - NRCS, 2009),

timing of seed dispersal (Gage and Cooper, 2005), and capacity for vegetative

reproduction (Krasny et al., 1988). Differences between willow species may influence

rates of growth and response to release from height constraining factors.

In this paper we explore willow species composition relative to patterns of willow

growth in Yellowstone's northern range. We asked whether the difference in willow

growth observed in recent years for the northern range may be partially explainable by

differences in willow species composition. If differences in willow growth are related to

species composition then this will have implications for spatial variation in future rates of willow growth across the region and may help inform the debate regarding drivers of willow height release. Our objectives for this study were to 1) compare willow species richness and community similarity across three willow growth conditions: height suppressed, recently released, and previously tall or tall prior to observed increased growth of released willows and 2) compare horizontal cover for willow species occurring across the three willow growth conditions.

Methods

Study Area

This study was conducted in and around Yellowstone's northern range defined as the region occupied by Yellowstone's northern wintering elk herd covering a 153,000 ha area in the Gardner, Lamar, and Yellowstone River watersheds (Figure 4.1) (Houston, 1982). Elevation varies from 1500 to 3209 m (Savage and Lawrence, in press). The majority of the northern range lies within Yellowstone National Park while the remainder lies within the Gallatin National Forest and various private, agricultural, and ranch lands north of the park boundary (Houston, 1982). The semi-arid region receives approximately 260 mm of precipitation per year, most of which falls during the growing season (Despain, 1987).

Relatively nutrient poor rhyolitic soils were deposited across the region two to three million years ago during a period of intense volcanic activity while relatively rich andesite soils found along valley bottoms were deposited approximately 12,000 to 14,000

years ago following the retreat of the Pinedale glacier (Christianson, 2001). Vegetation

in the study region is dominated by non-forested grasslands and sagebrush steppe in the

lower elevations while conifer forests predominate at higher elevations (Houston, 1982).

Deciduous woody vegetation (willow, aspen, cottonwood, and alder) occurs in the

lower elevation regions in four general landscape settings: "1) along stream and river

channels, in overflow channels and on floodplains; 2) in depressions and around kettle

lakes formed by blocks of glacial ice; 3) adjacent to springs and seeps on lower mountain

slopes; and 4) in abandoned beaver channels and ponds" (Chadde et al., 1988). Willows

in particular can be found along portions of the Lamar River, Soda-Butte Creek, and

along lower order streams throughout the northern range, but also occur in small patches

in springs and seeps on toe slopes and especially in flooded channels influenced by

beaver activity (Chadde et al., 1988). Understory vegetation within riparian areas are

dominated by various native sedges (*Carex* spp.), grasses, and forbs.

<u>Study Sites</u>

We examined willow species composition in three willow growth conditions:

suppressed, released, and previously tall described in detail in Chapter 3 and briefly

summarized here. Within each site we surveyed between four and sixteen 40-m radius

sample plots placed at least 100 m apart. In total we sampled 67 plots stratified across

the three willow growth conditions.

The two previously tall sites were located along Obsidian Creek (n = 16 sample

plots) in Yellowstone National Park just south of the northern range and along Tom
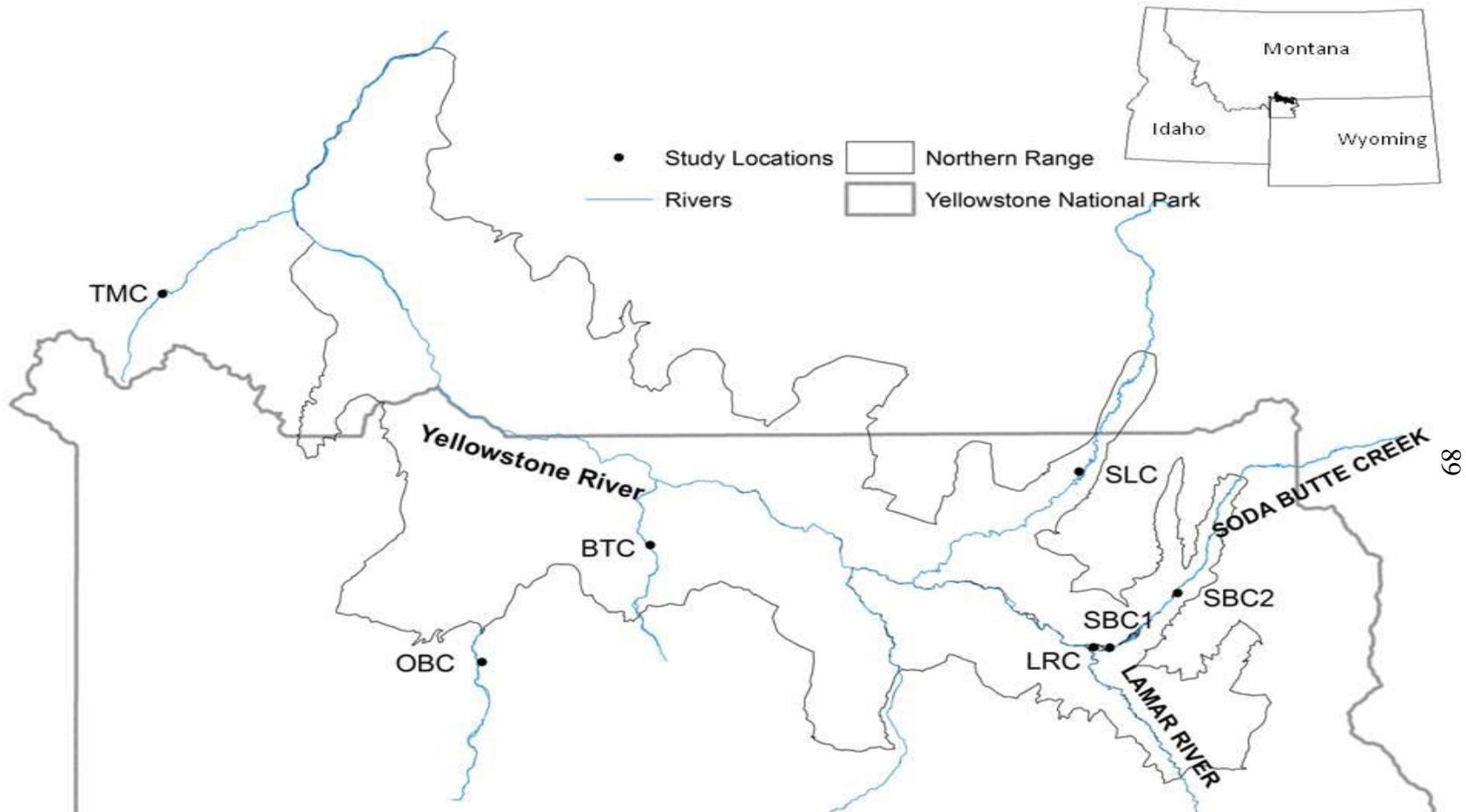
Figure 4. 1. Map of study area and survey locations. Previously tall = TMC (Tom Miner Creek) and OBC (Obsidian Creek); released = BTC (Blacktail Deer Creek), LRC (Lamar River confluence), and SLC (Slough Creek); suppressed = SBC1 (Soda Butte Creek 1) and SBC2 (Soda Butte Creek 2).

Miner Creek (n = 7) in Tom Miner Basin west of the northern range for a total of 23 previously tall sample plots. Previously condition willows are structurally complex tall (180 cm) willows exhibiting high horizontal cover (60%) and have changed little in structure since 1991. Since previously tall willows are absent from the northern range we chose these sites just outside of the northern range for comparison. Released sites were located along upper Slough Creek (n = 9 sample plots), Blacktail Deer Creek (n = 8 sample plots), and along the Lamar River-Soda Butte Creek confluence (n = 4 sample plots) for a total of 21 released sample plots. Released condition willows have increased in structure since 1991 and are currently tall (143 cm) and similar in height and vertical structure to previously tall willows, but lower in horizontal cover (21%). Suppressed sites were situated in two locations along Soda Butte Creek, SBC1 (n = 13 sample plots) and SBC2 (n = 10 sample plots) for a total of 23 suppressed sample plots. Suppressed willows are significantly shorter (62 cm) and limited in distribution (10%) than previously tall or released willows and have been suppressed since at least 1991.

Field Vegetation Sampling

Willow species composition was determined using the line-intercept method (Canfield, 1941) in all 67, 40-m radius sample plots. Line intercept measurements were collected along one transect that originated at the plot center and extended 40 m in a randomly selected cardinal direction. The transect was divided into 1 m intervals along which an observer recorded length and height of each willow species where it intersected with the meter tape.

Generation of Variables: We calculated average species richness and absolute horizontal cover for each sample plot then averaged those values over the number of plots within each growth condition to obtain averages per willow growth condition. Average species richness was calculated as the total number of willow species in each plot divided by the total number of plots for each growth condition. Absolute horizontal cover was determined by the total length of each willow species divided by the total transect length. We calculated the Renkonen index of community similarity per growth condition using the following formula (Nur et al., 1999):

$$ \begin{array}{c} i = s \\ P = \Sigma \text{ minimum } (p^A{}_i, p^B{}_i) \\ i = 1 \end{array} $$

P = Percentage Similarity
pA = percentage of species i in sample A
pB = percentage of species i in sample B
S = the number of species found in either sample

Statistical Analyses

Differences in species richness and absolute horizontal cover for individual willow species were examined using one-way analysis of variance (ANOVA) within a generalized least squares (GLS) framework to account for spatial dependence of errors between sample plots as described in Chapter 3. Briefly, for each variable tested we compared four models of spatial structure (exponential, Gaussian, rational quadratic, and spherical) and a GLS model without spatial structure which yields ordinary least squares (OLS) estimates using Akaike's Information Criterion (AIC_c) corrected for small sample sizes (Burnham and Anderson, 2002). We considered all models with ΔAIC_c of ≤ 2 to

have received substantial support while those models with ΔAIC_c of ≥ 4 to have received

substantially less support (Burnham and Anderson, 2002). For the selected model we

examined semivariograms to ensure that spatial autocorrelation was accounted for in the

model chosen or was not an issue when the OLS models was selected. We log

transformed all variables to meet the assumptions of ANOVA; however, report

untransformed means and standard errors. All analyses were executed using R statistical

software (R, 2007).

Results

Modeling Spatial Autocorrelation

Inclusion of either exponential or rational quadratic spatial autocorrelation

structure significantly improved half of the ANOVA models (Appendix F).

Semivariograms for the selected model indicated that either the inclusion of spatial

autocorrelation structure eliminated spatial dependence or confirmed that spatial

autocorrelation was not an issue for those models where the addition of one of the four

models of spatial structure did not improve the model fit (Appendix G).

Objective 1: Willow Species Richness and Community Similarity

Fourteen species of willow occurred across the three growth conditions. Nine

species were identified in the suppressed condition, 11 in the released condition, and 10

in the previously tall condition. Average willow species richness per sample plot was

significantly greater in the previously tall condition than in either the released or

suppressed condition; however, willow species richness was not significantly different

between the released and the suppressed condition (F = 16.94, P < 0.001; Figure 4.2).

The Renkonen index indicates 74% community similarity between the released and

previously tall condition and 22% similarity between released and suppressed condition.

The suppressed and previously tall conditions were the least similar exhibiting only 16%
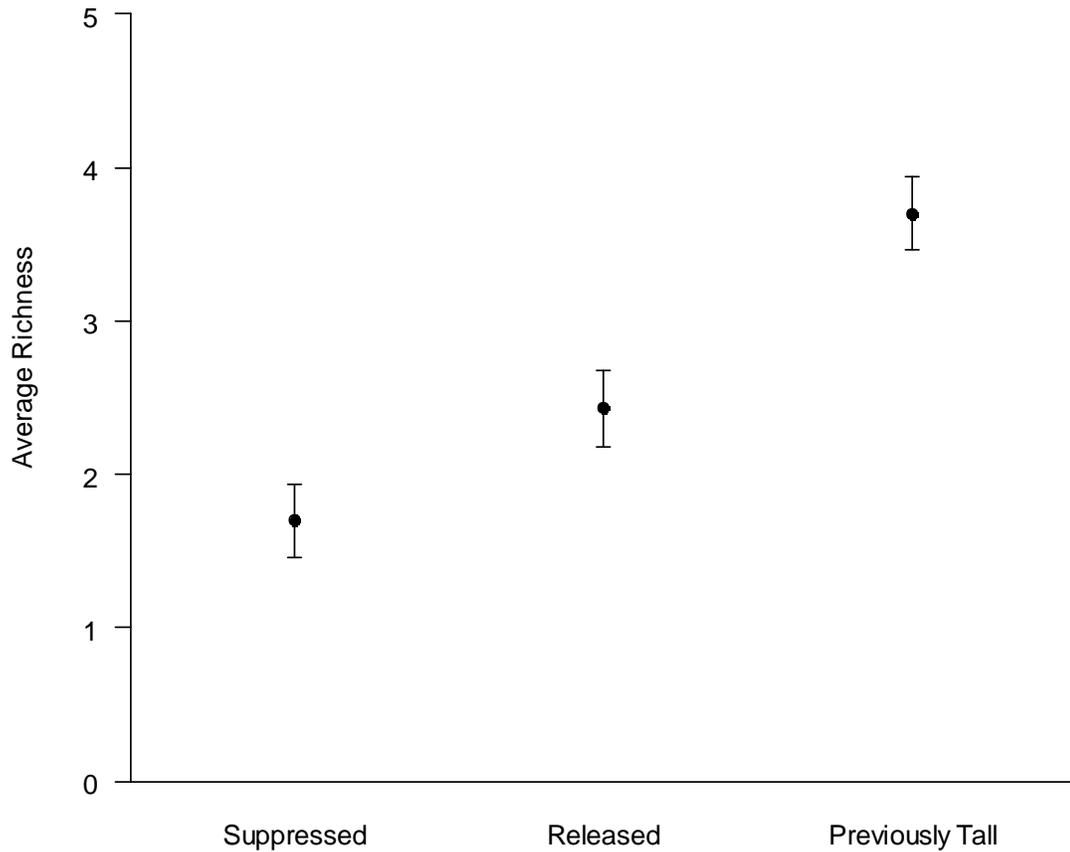
community similarity.

Figure 4.2. Average willow species richness in suppressed, released, and previously tall
willow growth conditions. Mean is shown $\pm$ 1 SE.

Objective 2: Horizontal Willow Cover

Seven species occurred frequently enough to analyze across growth conditions; however, *S. geyeriana* and *S. lemmonii* were absent from the suppressed condition and so those species were only analyzed between the released and previously tall conditions (Table 4.2). Willow species in the previously tall condition were significantly greater in cover than suppressed condition willow species, except for *S. exigua,* the dominant willow cover in the suppressed condition. *S. exigua* was rare in both the released and previously tall conditions. The majority of willow species exhibited similar cover between the released and previously tall willow conditions except for *S. lemmonii* and *S. wolfii* which were both greater in the previously tall condition than in the released condition.

Table 4.1. Summary of mean absolute horizontal cover $\pm$ 1 SE for willow species occurring in suppressed, released, and previously tall growth conditions. Under "Differences" spaces between letters indicate significant differences. Growth conditions are indicated by first letter.

	Suppressed (n = 23) x $\pm$ SE	Released (n = 21) x $\pm$ SE	Previously tall (n = 23) x $\pm$ SE	F	P	Differences	
S. boothii	0.61 $\pm$ 2.45	7.43 $\pm$ 2.57	12.52 $\pm$ 2.45	8.58	< 0.0001	S	P,R
S. drummondiana	0.55 $\pm$ 0.47	1.93 $\pm$ 1.23	5.66 $\pm$ 1.18	6.95	< 0.0019	S,R	P,R
S. eriocephala	0.42 $\pm$ 1.61	1.61 $\pm$ 1.68	4.55 $\pm$ 1.61	3.13	0.0500	S,R,P	
S. exigua	6.11 $\pm$ 0.96	1.01 $\pm$ 0.25	0.96 $\pm$ 0.02	14.58	< 0.0001	S	R,P
S. geyeriana	NA	4.36 $\pm$ 2.95	11.56 $\pm$ 2.82	1.67	0.2031	R,P	
S. lemmonii	NA	1.28 $\pm$ 0.73	17.87 $\pm$ 5.25	4.64	0.0369	R	P
S. wolfi	0.23 $\pm$ 1.07	0.07 $\pm$ 1.12	4.73 $\pm$ 1.07	5.58	0.0058	S,R	P

Discussion

Our results indicate that willow species composition was similar between the released and previously tall conditions and that both differed significantly from willow species composition found in the suppressed condition. However, the suppressed and released conditions were similar in willow species richness. Although nine species were identified in the suppressed condition most plots were dominated by *S. exigua*, a species rarely found in either the released or previously tall condition. Furthermore, species common to both the released and previously tall conditions were rare or absent in the suppressed condition.

While all willow species are able to reproduce asexually, *S. exigua* is unique in that it can produce extensive clones through the production of ramets especially when the flood regime does not allow for reproduction through seed germination (Douhovnikoff et al., 2005). Willow seeds are only viable for a period of a few days and are therefore highly dependent on immediately available favorable conditions for germination (i.e. bare, moist soils) (Karrenberg et al., 2002). If favorable conditions are not present, then asexual propagation often becomes the primary means of reproduction (Douhovnikoff et al., 2005). The dominance of *S. exigua* in the suppressed condition may indicate sites of marginal quality for sexual reproduction. In contrast, the flood disturbance regime in released and previously tall sites may be such that reproduction through seed germination is more common which may have resulted in the greater willow species diversity observed there. However, this is purely speculation since the ratio of plant establishment by seed or clones among growth conditions is unknown.

All willow species identified in this study are able to reach heights of three or more meters except for *S. wolfii* which rarely exceeds 1m in height (USDA - NRCS, 2009); however, this species was rare in the suppressed condition and so does not explain suppressed willows observed there. Elk are the primary browsers of willow in the region and although willow represents <1% of an elk's diet, they can have profound effects on growth and structure (Singer et al., 1994). Although browsing is a factor influencing willow growth in the northern range it is also a mechanism of disturbance that has been shown to influence plant community composition through herbivore selectivity of plant species and species' response to herbivory (Augustine and McNaughton, 1998). While it is well known that browsing has and continues to influence willow structure in the northern range, elk preference for willow species and individual species' responses to selectivity is not well understood and may at least partially explain differences in willow species composition across growth conditions.

Site specific differences in soil quality and nutrient availability are also likely partially responsible for observed differences in willow species composition across growth conditions and may interact with browsing to influence willow communities. For example, differences in the rate of browsing across species may limit the ability of the browsed species to uptake nutrients for growth and chemical defense thereby limiting their distribution and decreasing their abundance (Wagner et al, 1995). Alternatively, sites of poor quality and resulting competition for limited resources may reduce the ability of less competitive species to uptake nutrients for growth and defense against herbivory, thereby promoting browsing and reducing the abundance of heavily browsed species (Singer et al., 1994).

<u>Conclusions</u>

The results of this study raise more questions than it attempts to answer; however, we have identified differences in willow species composition that that may affect future patterns of willow growth as well as inform the debate regarding change in patterns of willow growth for the region. Future research should attempt to 1) determine establishment dates for willow species across growth conditions to construct a historical portrait of changes in willow community composition; 2) establish the role of sexual versus asexual reproduction relative to disturbance regimes (i.e. browse intensity and flood regime); and 3) examine site specific soil characteristics and nutrient availability relative to willow growth and species composition across growth conditions. There is likely a complex interplay and feedback loops among these factors that only carefully controlled, experimental studies will reveal.

Literature Cited

Augustine, D.J. and S.J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance 62: 1165-1183.

Barnosky, C.W. 1988. The relationship of climate to sedimentation rates in lakes and ponds. Page 4 in F. Singer, ed. First annual meeting of research and monitoring on Yellowstone's northern range. USDI, Nat. Park Ser., Yellowstone National Park.

Beyer, H.L., E.H. Merril, N. Varley and M.S. Boyce. 2007. Willow on Yellowstone's northern range: evidence for a trophic cascade? Ecological Applications 17: 1563-1571.

Burnham, K.P. and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science+Business Media, Inc., New York, NY. pp: 487.

Canfield, R.H. 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry 39: 388-394.

Cayan, D.R., S.A. Kammerdiener, M.D. Dettinger, J.M. Caprio and D.H. Peterson. 2001. Changes in the onset of spring in the western United States. Bulletin of the American Meteorological Society 83: 399-415.

Chadde, S.W. and C.E. Kay. 1991. Tall-willow communities on Yellowstone's northern range: a test of the "natural-regulation" paradigm. In R.B. Keiter and M.S. Boyce (Eds.), *The Greater Yellowstone Ecosystem*. Yale University Press.

Chadde, S.W., P.L. Hansen, and R.D. Pfister. 1988. Wetland Plant Communities of the Northern Range, Yellowstone National Park. School of Forestry, University of Montana.

Christiansen, R.L., 2001, The Quaternary and Pliocene Yellowstone Plateau volcanic field of Wyoming, Idaho, and Montana: U.S. Geological Survey Professional Paper: 729-G, 145 p., 3 plates, scale 1:125,000.

Despain, D.G. 1987. The two climates of Yellowstone National Park. Proceedings of the Montana Academy of Science 47: 11-20.

Douhovnikoff, V., J.R. McBride, and R.S. Dodd. 2005. *Salix exigua* clonal growth and population dynamics in relation to disturbance regime variation. Ecology 86: 446-

452.

Engstrom, D.R., C. Whitlock, S.C. Fritz and H.E. Wright, Jr. 1991. Recent environmental changes inferred from the sediments of small lakes in Yellowstone's northern range. Journal of Paleolimnology 5: 139-174.

Gage, E.A. and D.J. Cooper. 2005. Patterns of willow seed dispersal, seed entrapment, and seedling establishment in a heavily browsed montane riparian ecosystem. Canadian Journal of Botany 83: 678-687.

Groshong, L.C. 2004. Mapping riparian vegetation change in Yellowstone's Northern Range using high spatial resolution imagery. M.A. thesis, University of Oregon, Eugene, OR.

Houston, D.B. 1982. The northern Yellowstone elk: ecology and management. MacMillan Publishing Co., Inc., N.Y. 474 pp.

Karrenberg, S., P.J. Edwards, and J. Kollmann. 2002. The life history of Salicaceae living in the active zone of floodplains 47: 733-748.

Krasny, M.E., K.A. Vogt, and J.C. Zasada. 1988. Establishment of four Salicaceae species on river bars in interior Alaska. Holarctic Ecology 11: 210-219.

Lins, H.F. and J.R. Slack. 1999. Streamflow trends in the United States. Geophysical Research Letters 26: 227-230.

Myneni, R.B., C.D. Keeling, C.J. Tucker, G. Asrar and R.R. Nemani. 1997. Increased Plant growth in the northern high latitudes from 1981 to 1991 Nature 386: 698-702.

Nemani, R.R., C.D. Keeling, H. Hashimoto, W.M. Jolly, S.C. Piper, C.J. Tucker, R.B. Myneni, and S.W. Running. 2003. Climate-driven increases in global terrestrial net primary productivity form 1982 to 1999. Science 300: 1560-1563.

Nur, N. S.L. Jones, and G.R. Geupel. 1999. A statistical guide to data analysis of avian monitoring programs. U.S. Department of the Interior, Fish and Wildlife Service, BTP-R6001-1999, Washington, D.C.

R Development Core Team. 2007. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Regonda, S.K., B. Rajagopalan, M. Clark, and J. Pitlick. 2005. Seasonal cycle shifts in hydroclimatology over the western United States. Journal of Climate 18: 372-384.

Ripple, W.J. and R.L. Beschta. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. Forest Ecology and Management 184: 299-313.

Ripple, W.J. and R.L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems. Bioscience 54: 755-766.

Savage, S. L. and R. Lawrence. 2009. Vegetation dynamics in Yellowstone's northern range: 1985-1999. Photogrammetric Engineering and Remote Sensing.

Singer, F. J., L. C. Mark, and R. C. Cates. 1994. Ungulate herbivory of willows on Yellowstone's northern winter range. Journal of Range Management 47: 435-443.

Stewart, I.T., D.R. Cayan, and M.D. Dettinger. 2005. Changes toward earlier streamflow timing across western North America. Journal of Climate 18: 1136-1155.

USDA, NRCS. 2009. The PLANTS Database (http://plants.usda.gov, 12 Nov 2009). National Plant Data Center, Baton Rouge, LA 70874-4490.

Wagner, F.H., R.B. Keigley, and C.L. Wambolt. 1995. Comment: ungulate herbivory of willows on Yellowstone's northern winter range: response to Singer et al., (1994).

CHAPTER 5

CONCLUSIONS

Observations of an increase in deciduous woody vegetation (DWV) across

Yellowstone's northern range since approximately 1998 has stimulated several important

questions regarding change in DWV, three of which guided the research presented in this

thesis. In Chapter 2 I evaluate change in DWV within wetland and riparian areas using

aerial photographs from 1991 and 2006. In Chapter 3 I investigate how an increase in

willow, the dominant component of DWV in the region, has likely influenced bird

diversity and finally, in Chapter 4, I examine willow species composition across the

northern range.

The air photo interpretation revealed a 170% increase in the areal extent of DWV

over the 15-year period. Most (68%) of the sample plots did not change in DWV while

7% decreased and 25% increased. Of the sample plots that remained neutral, most (97%)

did not contain DWV in either date indicating that it is a rare habitat type in the northern

range even within areas of potential growth. Of the plots that increased the majority

(70%) did so by 10 to 20 percentage points revealing that while overall DWV increased,

changes were small, at least with the scale of imagery used. Significantly more plots

appeared to increase by recruitment rather than by densification; however, the accuracy

assessment indicated that DWV below 100 cm was difficult to detect, and therefore

DWV was probably underestimated in some plots suggesting that recruitment may have

been overestimated and densification may have been underestimated. These results

provide the first estimate of change in DWV at the scale of the landscape since

observations of increased growth began.

In Chapter 3 I narrowed my focus to examine how an increase in willow, the

dominant component of DWV, has influenced bird species diversity in the region by

examining willow structural characteristics and bird community variables across three

willow growth conditions. Overall, I found that willows have increased in some

locations in the northern range and that this increase in willow growth has resulted in a

greater amount of structurally complex willow habitat that has in turn allowed for greater

bird richness, abundance, diversity, and abundance of six of the seven focal species

studied. More specifically, vertical willow structural complexity may be more important

than horizontal structural complexity in determining bird community variables at least

within the range of willow growth considered in this study. This was supported by bird

species abundance and diversity which were similar between released and previously tall

willows despite the significantly lower horizontal cover in the released condition than in

the previously tall condition. Additionally, of nineteen *a priori* habitat models describing

bird richness, abundance, and diversity the univariate model of foliage height diversity, a

measure of vertical structural complexity, was selected as the best model with little

support for the other models in the suite. Vertical structural complexity provides a

greater variety of foraging and nesting opportunities that in turn provides a broader

resource base that can be partitioned among multiple species and individuals thereby

reducing competition and potential competitive exclusion.

In the fourth chapter I describe willow species composition among willow growth

conditions. I found that the previously tall and released willow communities were similar in species composition, but that the suppressed condition was dominated by *S. exigua*, a species rarely encountered in the other two growth conditions. The dominance of this species in the suppressed condition may be indicative of site characteristics unfavorable to willow growth and reproduction. *S. exigua* is an extensively clonal species that may be more abundant there as a result of unfavorable conditions for seedling establishment; however this is speculation since it is unknown whether *S. exigua* there established by seed or clonal reproduction. The observation that willow species composition in the suppressed condition is significantly different from that observed in the released or previously tall conditions stimulates several questions regarding drivers of these differences which may be related to disturbance regimes such as browsing and flood events.

APPENDICES

APPENDIX A

MODEL SELECTION RESULTS FOR FIVE MODELS (FOUR INCLUDING
SPATIAL STRUCTURE AND A MODEL WITHOUT SPATIAL STRUCTURE) FOR
ANOVA COMPARISONS OF VEGETATION AND BIRD VARIABLES AMONG
WILLOW GROWTH CONDITIONS

Appendix A: Comparison of four models with spatial structure and a model without spatial structure for ANOVA models for willow variables, bird community variables, and the abundance of each of the seven focal species. Models used for interpretation are in italics. The number of parameters in each model is indicated by 'k'. The weight of evidence for each model given the other models in the suite is indicated by w_i.

Response	Model Structure	AIC_c	ΔAIC_c	w_i	k
HT	Willow condition	92.50	8.97	0.01	1
	Willow condition + exponential structure	*83.53*	*0.00*	*0.49*	2
	Willow condition + Gaussian structure	87.85	4.32	0.06	2
	Willow condition + rational quadratic structure	84.63	1.10	0.28	2
	Willow condition + spherical structure	85.81	2.28	0.16	2
HZ	*Willow condition*	*236.76*	*0.00*	*0.33*	1
	Willow condition + exponential structure	237.69	0.93	0.21	2
	Willow condition + Gaussian structure	238.66	1.90	0.13	2
	Willow condition + rational quadratic structure	237.48	0.72	0.23	2
	Willow condition + spherical structure	239.03	2.27	0.11	2
FREQ	*Willow condition*	*272.54*	*1.13*	*0.21*	1
	Willow condition + exponential structure	271.41	0.00	0.37	2
	Willow condition + Gaussian structure	274.03	2.63	0.10	2
	Willow condition + rational quadratic structure	272.11	0.71	0.26	2
	Willow condition + spherical structure	274.81	3.40	0.07	2
FHD	Willow condition	82.76	8.92	0.01	1
	Willow condition + exponential structure	*73.84*	*0.00*	*0.54*	2
	Willow condition + Gaussian structure	79.22	5.38	0.04	2
	Willow condition + rational quadratic structure	74.62	0.78	0.36	2
	Willow condition + spherical structure	78.38	4.55	0.06	2
PATCH	*Willow condition*	*223.90*	*0.36*	*0.19*	1
	Willow condition + exponential structure	224.24	0.69	0.16	2
	Willow condition + Gaussian structure	223.89	0.34	0.20	2
	Willow condition + rational quadratic structure	223.74	0.19	0.21	2
	Willow condition + spherical structure	223.55	0.00	0.23	2
Vert1	*Willow condition*	*56.84*	*0.19*	*0.25*	1
	Willow condition + exponential structure	57.47	0.81	0.18	2
	Willow condition + Gaussian structure	57.87	1.21	0.15	2
	Willow condition + rational quadratic structure	56.65	0.00	0.27	2
	Willow condition + spherical structure	57.94	1.29	0.14	2
Vert2	*Willow condition*	*571.98*	*0.00*	*0.37*	1
	Willow condition + exponential structure	573.81	1.82	0.15	2
	Willow condition + Gaussian structure	573.73	1.74	0.15	2
	Willow condition + rational quadratic structure	573.57	1.59	0.17	2
	Willow condition + spherical structure	573.65	1.67	0.16	2

Appendix A Continued

Vert3	*Willow condition*	*393.15*	*0.92*	*0.15*	*1*
	Willow condition + exponential structure	392.89	0.66	0.17	2
	Willow condition + Gaussian structure	392.23	0.00	0.24	2
	Willow condition + rational quadratic structure	392.52	0.29	0.21	2
	Willow condition + spherical structure	392.43	0.20	0.22	2
Vert4	*Willow condition*	*209.69*	*0.30*	*0.22*	*1*
	Willow condition + exponential structure	209.71	0.32	0.22	2
	Willow condition + Gaussian structure	210.42	1.04	0.15	2
	Willow condition + rational quadratic structure	209.39	0.00	0.26	2
	Willow condition + spherical structure	210.38	0.99	0.16	2
Richness	Willow condition	-94.76	14.21	0.00	1
	Willow condition + exponential structure	*-108.96*	*0.00*	*0.66*	*2*
	Willow condition + Gaussian structure	-99.83	9.13	0.01	2
	Willow condition + rational quadratic structure	-105.81	3.15	0.14	2
	Willow condition + spherical structure	-106.57	2.40	0.20	2
Abundance	Willow condition	2.38	10.57	0.00	1
	Willow condition + exponential structure	*-8.19*	*0.00*	*0.79*	*2*
	Willow condition + Gaussian structure	-0.37	7.82	0.02	2
	Willow condition + rational quadratic structure	-5.29	2.90	0.19	2
	Willow condition + spherical structure	4.65	12.84	0.00	2
Diversity	Willow condition	-94.76	14.21	0.00	1
	Willow condition + exponential structure	*-108.96*	*0.00*	*0.66*	*2*
	Willow condition + Gaussian structure	-99.83	9.13	0.01	2
	Willow condition + rational quadratic structure	-105.81	3.15	0.14	2
	Willow condition + spherical structure	-106.57	2.40	0.20	2
Common yellowthroat	Willow condition	75.07	15.07	0.00	1
	Willow condition + exponential structure	*60.00*	*0.00*	*0.44*	*2*
	Willow condition + Gaussian structure	65.38	5.38	0.03	2
	Willow condition + rational quadratic structure	61.07	1.07	0.26	2
	Willow condition + spherical structure	60.98	0.98	0.27	2
Lincoln's sparrow	Willow condition	151.83	57.66	0.00	1
	Willow condition + exponential structure	*94.18*	*0.00*	*0.86*	*2*
	Willow condition + Gaussian structure	111.73	17.55	0.00	2
	Willow condition + rational quadratic structure	98.44	4.26	0.10	2
	Willow condition + spherical structure	100.43	6.25	0.04	2
Yellow warbler	Willow condition	75.57	7.62	0.01	1
	Willow condition + exponential structure	*67.95*	*0.00*	*0.57*	*2*
	Willow condition + Gaussian structure	71.78	3.83	0.08	2

Appendix A Continued.

	Willow condition + rational quadratic structure	69.21	1.26	0.30	2
	Willow condition + spherical structure	73.51	5.56	0.04	2
Song sparrow	Willow condition	63.05	25.78	0.00	1
	Willow condition + exponential structure	37.27	0.00	0.67	2
	Willow condition + Gaussian structure	44.22	6.96	0.02	2
	Willow condition + rational quadratic structure	39.75	2.48	0.19	2
	Willow condition + spherical structure	40.70	3.44	0.12	2
Warbling vireo	Willow condition	39.83	35.87	0.00	1
	Willow condition + exponential structure	8.09	4.12	0.07	2
	Willow condition + Gaussian structure	4.71	0.74	0.37	2
	Willow condition + rational quadratic structure	*3.97*	*0.00*	*0.53*	2
	Willow condition + spherical structure	9.37	5.41	0.04	2
Willow flycatcher	Willow condition	24.76	21.29	0.00	1
	Willow condition + exponential structure	*3.47*	*0.00*	*0.62*	2
	Willow condition + Gaussian structure	10.52	7.05	0.02	2
	Willow condition + rational quadratic structure	7.90	4.43	0.07	2
	Willow condition + spherical structure	4.90	1.44	0.30	2

APPENDIX B

MODEL SELECTION RESULTS FOR FIVE MODELS (FOUR INCLUDING
SPATIAL STRUCTURE AND A MODEL WITHOUT SPATIAL STRUCTURE) FOR
GLS *A PRIORI* HABITAT MODELS DESCRIBING BIRD RICHNESS,
ABUNDANCE, AND DIVERSITIY ACROSS WILLOW GROWTH CONDITIONS

Appendix B: Comparison of four models with spatial structure and a model without spatial structure for the global GLS models. The error structure incorporated into the nested models are in italics. The number of parameters in each model is indicated by 'k'. The weight of evidence for each model given the other models in the suite is indicated by w_i.

| Response	Model Structure	AIC_c	ΔAIC_c	w_i	k
Richness	Global model	96.98	7.47	0.01	7
	Global model + exponential error	*89.51*	*0.00*	*0.58*	*8*
	Global model + Gaussian error	93.94	4.43	0.06	8
	Global model + rational quadratic error	90.62	1.12	0.33	8
	Willow condition + spherical error	99.67	10.16	0.00	8
Abundance	Global model	76.18	6.47	0.01	7
	Global model + exponential error	*69.71*	*0.00*	*0.35*	
	Global model + Gaussian error	73.17	3.46	0.06	8
	Global model + rational quadratic error	70.40	0.69	0.25	8
	Willow condition + spherical error	69.81	0.09	0.33	8
Diversity	Global model	8.29	11.00	0.00	7
	Global model + exponential error	*-2.71*	*0.00*	*0.75*	*8*
	Global model + Gaussian error	4.01	6.72	0.03	8
	Global model + rational quadratic error	-0.27	2.44	0.22	8
	Willow condition + spherical error	10.98	13.69	0.00	8

APPENDIX C

SEMIVARIOGRAMS FOR ANOVA MODELS

Appendix C. Semivariograms for vegetation and bird variables use in the ANOVA analysis.
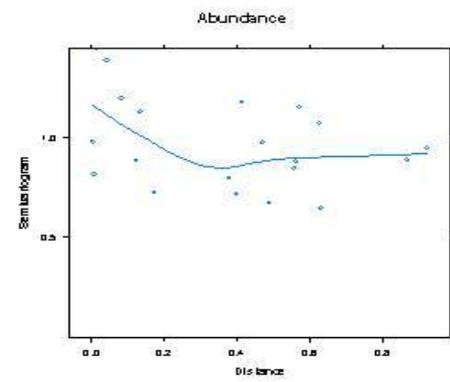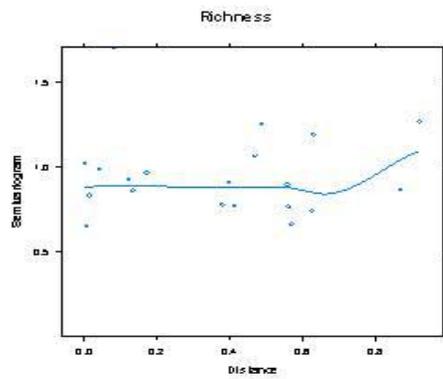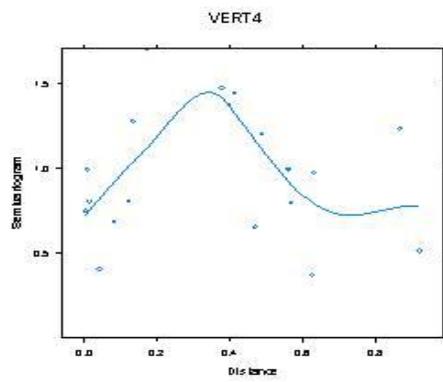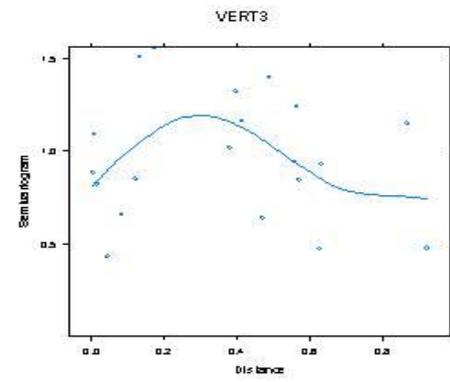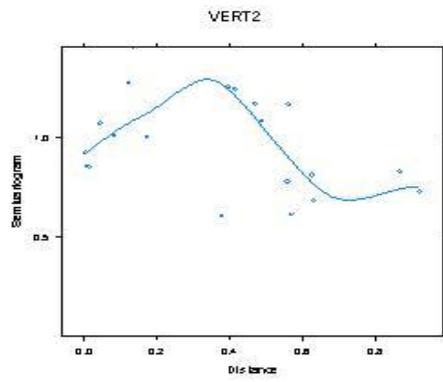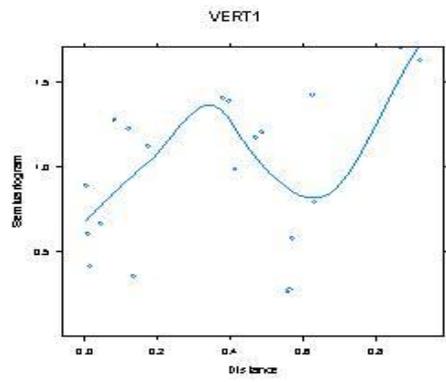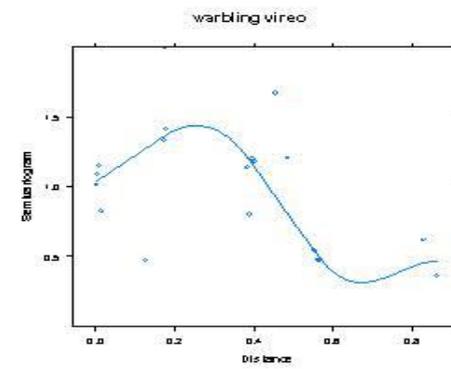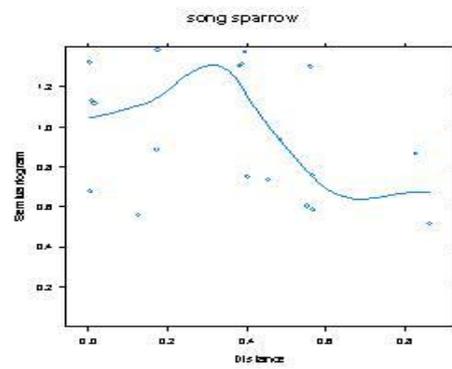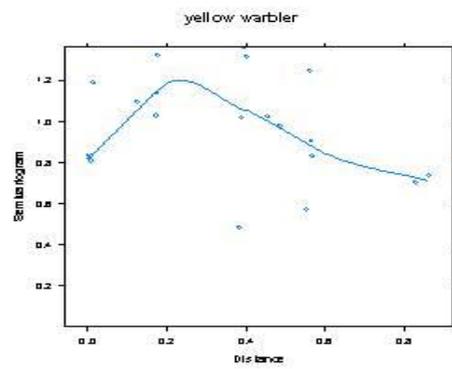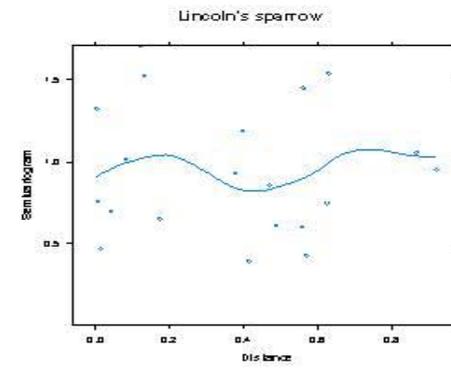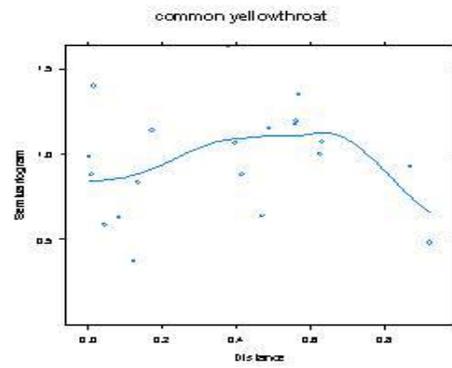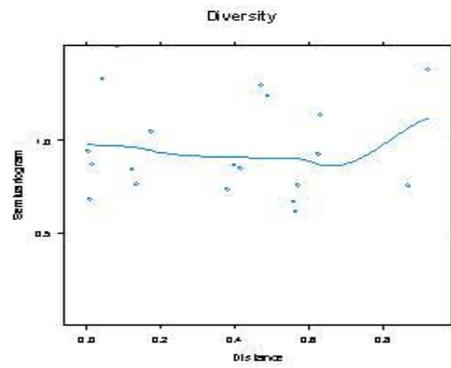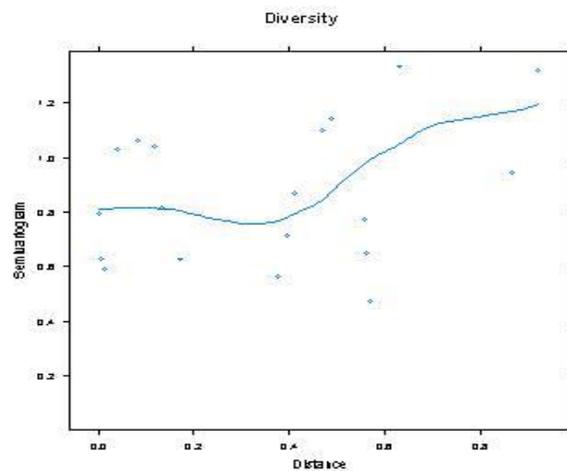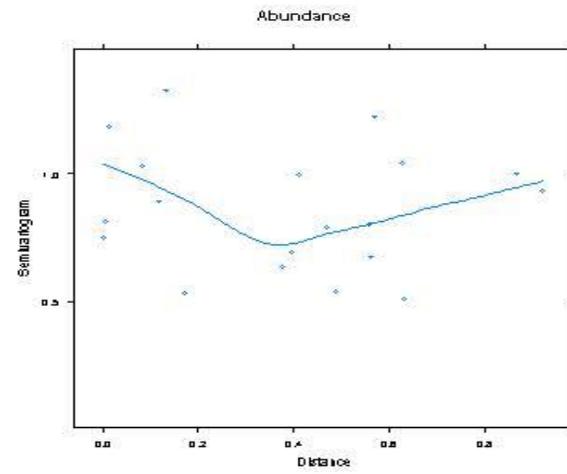
Appendix C Continued.

Appendix C Continued.

willowflycatcher
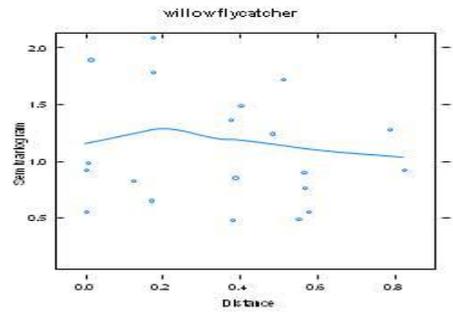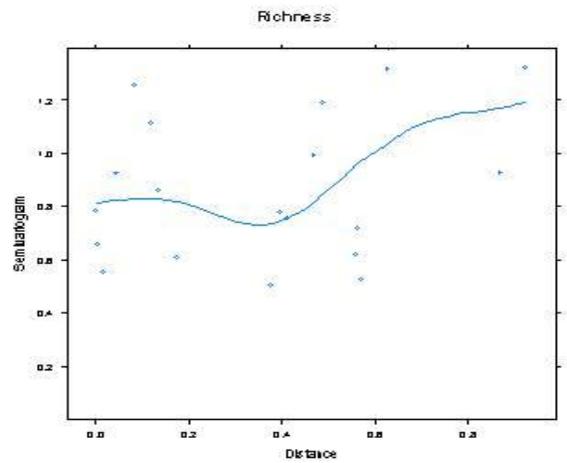
APPENDIX D

SEMIVARIOGRAMS FOR GLOBAL GLS MODELS

Appendix D. Semivariograms for global GLS models

APPENDIX E

BIRDS OBSERVED BY WILLOW GROWTH CONDITION OVER THE THREE
YEARS OF STUDY

Appendix E. Bird species observed in suppressed, released, and previously tall growth conditions in and around Yellowstone's northern range. The list excludes marshbirds, shorebirds, and flyovers since the method of observation is not designed to sample these species. Values indicate number of sample plots occupied with percent of those plots occupied by that species in parentheses.

Common Name	Scientific Name	Suppressed n = 23	Released n = 21	Previously Tall n = 23
American Crow	*Corvus brachyrhynchos*	4 (17)	NA	1 (4)
American Robin	*Turdus migratorius*	5 (22)	14 (67)	13 (57)
Black-billed Magpie	*Pica hudsonia*	NA	NA	5 (22)
Black-capped Chickadee	*Poecile atricapilla*	NA	NA	5 (22)
Brewer's Blackbird	*Euphagus cyanocephalus*	11 (48)	13 (62)	13 (57)
Brown-headed Cowbird	*Molothrus ater*	NA	3 (14)	7 (30)
Chipping Sparrow	*Spizella passerine*	1 (4)	2 (10)	NA
Common Raven	*Corvus corax*	1 (4)	NA	NA
Common Yellowthroat	*Geothlypis trichas*	13 (57)	21 (100)	18 (78)
Dark-eyed Junco	*Junco hyemalis*	1 (4)	NA	2 (9)
Dusky Flycatcher	*Empidonax oberholseri*	NA	2 (10)	5 (22)
Fox Sparrow	*Passerella iliaca*	NA	1 (5)	6 (26)
Gray Catbird	*Dumetella carolinensis*	NA	4 (19)	3 (13)
House Wren	*Troglodytes aedon*	NA	NA	1 (4)
Lincoln's Sparrow	*Melospiza lincolnii*	18 (78)	20 (95)	23 (100)
MacGillivray's Warbler	*Oporornis tolmiei*	NA	NA	6 (26)
Mountain Bluebird	*Sialia currucoides*	1 (4)	1 (5)	NA
Mountain Chickadee	*Poecile gambeli*	NA	NA	1 (4)
Northern Flicker	*Colaptes auratus*	1 (4)	2 (10)	1 (4)
Red-naped Sapsucker	*Sphyrapicus nuchalis*	NA	3 (14)	4 (17)
Red-winged Blackbird	*Agelaius phoeniceus*	9 (39)	9 (43)	3 (13)
Savannah Sparrow	*Passerculus sandwichensis*	22 (96)	9 (43)	13 (57)
Song Sparrow	*Melospiza melodia*	NA	11 (52)	15 (65)
Townsend's Solitaire	*Myadestes townsendi*	1 (4)	NA	NA
Vesper Sparrow	*Pooecetes gramineus*	NA	1 (5)	NA
Warbling Vireo	*Vireo gilvus*	NA	6 (29)	18 (78)
Western Meadowlark	*Sturnella neglecta*	7 (30)	3 (14)	NA
White-crowned Sparrow	*Zonotrichia leucophrys*	1 (4)	6 (30)	15 (65)
Willow Flycatcher	*Empidonax trailii*	NA	10 (48)	10 (43)
Wilson's Warbler	*Wilsonia pusilla*	NA	NA	21 (91)
Yellow Warbler	*Dendroica petechia*	NA	20 (95)	23 (100)
Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*	NA	1 (5)	NA
Yellow-rumped Warbler	*Dendroica coronata*	1 (4)	1 (5)	NA

<u>APPENDIX F</u>

MODEL SELECTION RESULTS FOR FIVE MODELS (FOUR INCLUDING
SPATIAL STRUCTURE AND A MODEL WITHOUT SPATIAL STRUCTURE) FOR
ANOVA MODELS COMPARING WILLOW SPECIES RICHNESS AND
HORIZONTAL COVER FOR SEVEN WILLOW SPECIESACROSS WILLOW
GROWTH CONDITIONS

Appendix F. Comparison of four models with spatial structure and a model without spatial structure for ANOVA models comparing willow species richness and horizontal cover for seven species of willow across willow growth conditions. The error structure incorporated into the nested models are in italics. The number of parameters in each model is indicated by 'k'. The weight of evidence for each model given the other models in the suite is indicated by w_i.
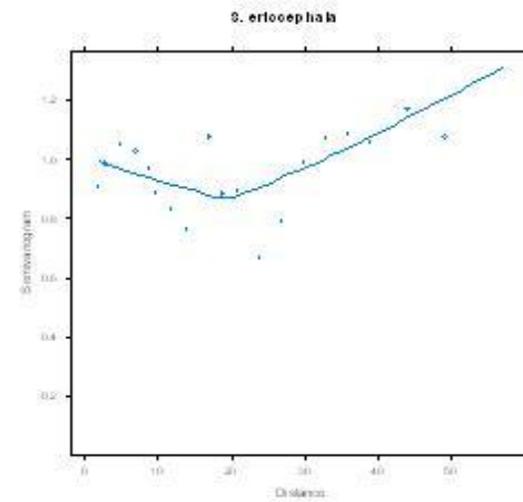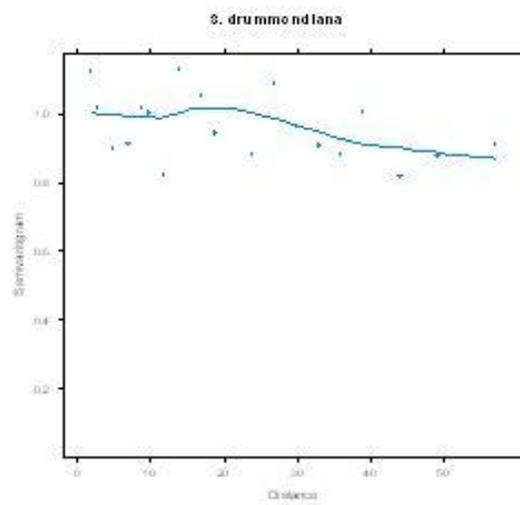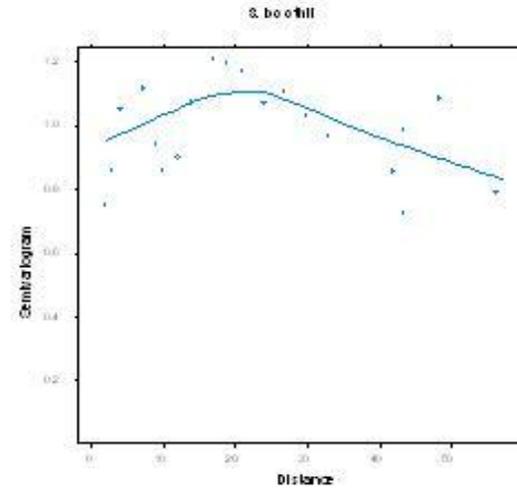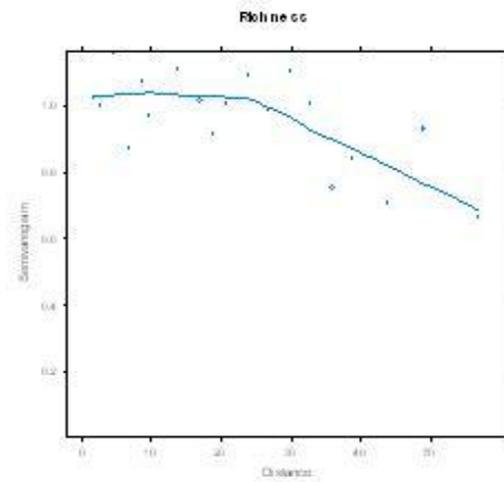
Response	Model Structure	AIC$_c$	ΔAIC$_c$	w_i	k
Richness	*Willow condition*	*61.61*	*0.00*	*0.36*	*1*
	Willow condition + exponential structure	62.93	1.32	0.18	2
	Willow condition + Gaussian structure	63.26	1.65	0.16	2
	Willow condition + rational quadratic structure	62.95	1.34	0.18	2
	Willow condition + spherical structure	63.87	2.27	0.12	2
S. boothii	*Willow condition*	*225.29*	*0.00*	*0.40*	*1*
	Willow condition + exponential structure	227.46	2.17	0.14	2
	Willow condition + Gaussian structure	227.56	2.27	0.13	2
	Willow condition + rational quadratic structure	226.69	1.40	0.2	2
	Willow condition + spherical structure	227.56	2.27	0.13	2
S. drummondiana	*Willow condition*	*189.34*	*0.00*	*0.44*	*1*
	Willow condition + exponential structure	191.60	2.27	0.14	2
	Willow condition + Gaussian structure	191.60	2.27	0.14	2
	Willow condition + rational quadratic structure	191.60	2.27	0.14	2
	Willow condition + spherical structure	191.60	2.27	0.14	2
S. eriocephala	*Willow condition*	*180.44*	*0.00*	*0.23*	*1*
	Willow condition + exponential structure	181.07	0.62	0.20	2
	Willow condition + Gaussian structure	180.74	0.29	0.24	2
	Willow condition + rational quadratic structure	181.02	0.58	0.20	2
	Willow condition + spherical structure	182.71	2.26	0.09	2
S. exigua	Willow condition	161.16	2.57	0.12	1
	Willow condition + exponential structure	*158.59*	*0.00*	*0.42*	*2*
	Willow condition + Gaussian structure	161.79	3.19	0.09	2
	Willow condition + rational quadratic structure	159.05	0.46	0.34	2

Appendix F Continued.

	Willow condition + spherical structure	163.43	4.83	0.04	2
S. geyeriana	Willow condition	157.33	4.10	0.05	1
	Willow condition + exponential structure	153.57	0.34	0.30	2
	Willow condition + Gaussian structure	154.94	1.72	0.15	2
	Willow condition + rational quadratic structure	*153.22*	*0.00*	*0.36*	*2*
	Willow condition + spherical structure	153.20	1.99	0.33	2
S. lemmonii	Willow condition	158.53	23.17	0.00	1
	Willow condition + exponential structure	*135.36*	*0.00*	*0.56*	*2*
	Willow condition + Gaussian structure	140.56	5.20	0.00	2
	Willow condition + rational quadratic structure	137.37	2.01	0.21	2
	Willow condition + spherical structure	137.58	2.21	0.19	2
S. wolfii	Willow condition	161.29	2.36	0.13	1
	Willow condition + exponential structure	159.39	0.46	0.34	2
	Willow condition + Gaussian structure	162.81	3.88	0.07	2
	Willow condition + rational quadratic structure	*158.93*	*0.00*	*0.42*	*2*
	Willow condition + spherical structure	163.18	4.25	0.05	2

APPENDIX G

SEMIVARIOGRAMS FOR ANOVA MODELS OF WILLOW SPECIES RICHNESS
AND HORIZONTAL COVER FOR SEVEN WILLOW SPECIES

Appendix G. Semivariograms for ANOVA models of willow species richness and horizontal cover for seven willow species.

Appendix G Continued.