Willow–Bird Relationships on Yellowstone's Northern Range

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Some willows (*Salix* spp.) are severely height suppressed, unable to grow taller than a few feet, while others have recently increased in height. Four years ago we asked how the observed increase might affect songbird diversity in the region. Our objective for this article is to share some results of our study of birds and willows in Yellowstone's northern range, but first we offer a brief history of willow growth there.

Background

Willows are wetland plants requiring plenty of water for growth and survival. They can be found along riparian regions throughout Yellowstone, but can grow near springs, seeps, and in any area where water is plentiful. Riparian areas represent transitional zones from rivers, lakes, and streams to adjacent uplands. Because of this intermingling of contrasting environments, riparian zones tend to be some of the most highly productive and ecologically rich environments in the northern Rocky Mountains. An estimated 80% of bird diversity in the northern Rocky Mountains can be found in riparian zones, and several species are found exclusively in these regions (Berger et al. 2001). Moose (*Alces alces*) and beavers (*Castor canadensis*) are dependent on riparian vegetation for forage (Stevens 1970; Wolf et al. 2007). The industrious beaver uses it for dam and lodge building materials as well. In addition to providing important habitat for numerous species, woody riparian vegetation, including willow, alder (*Alnus* spp.), cottonwood (*Populus* spp.), and aspen (*Populus tremuloides*) help stabilize stream banks, maintain nutrient cycles, and regulate water temperatures (Naiman and Décamps 1997).

The majority of willow communities in Yellowstone are found in the Yellowstone River delta, Bechler Meadows, and in areas north of the Madison River. Smaller areas of willow are found in the northern range, a low elevation region in the northern section of the park where the largest Yellowstone elk herd resides during winter. Elk preferentially forage on mature, degenerating grasses and forbs during winter, but also use woody browse including willow, alder, cottonwood, and aspen (Christianson and Creel 2007). Because willow is generally rare in the northern range, even low levels of browsing can have enormous effects on willow growth patterns, which in turn can affect bird diversity. We chose to study willow–bird relationships in the northern range because of the region's unique history of willow growth and recent history of increased willow growth following decades of height suppression.

Photographic comparisons of willow stands in the late 19th and early 20th centuries with current photos of the same area reveal considerable declines in willows (Chadde and Kay 1991). Studies of pollen grains in the northern range lake sediments reveal a decline in willow since 1920 (Barnosky et al. 1988; Engstrom et al. 1991). The loss and low stature of willows has been attributed to factors including extensive elk herbivory, fire history, a warmer and drier climate, and a lower population of beavers, whose activities stimulate willow growth (Yellowstone National Park 1997).

However, biologists have observed that although establishment of new willow plants has been limited, some willow stands in the northern range have increased in height and areal extent since 1997 and 1998. Comparing aerial photos from 1992 to 2006, we found an overall net gain in the areal extent of willow, alder, cottonwood, and aspen across riparian

areas throughout the northern range (Baril 2009). Ripple and Beschta (2003) found increased height in several willow stands between 1977 and 2002, and high spatial resolution imagery indicated that willow, alder, and cottonwood increased in areal extent in the Lamar River-Soda Butte Creek confluence between 1995 and 1999 (Groshong 2004). Biologists regard the recent increases in height growth as an "ecological release" in which some northern range willows, previously unable to reach the height of tall willow stands in other regions of Yellowstone, are now experiencing more favorable conditions that have allowed for the observed increase in growth.

This release of woody vegetation coincides with the reintroduction of wolves (*Canis lupus*) in 1995 and 1996, stimulating the hypothesis that it may be the result of a trophic cascade involving wolves, elk, and willows (Ripple and Beschta 2004; Smith 2005). Elk constitute the majority of wolf diets in the northern range, resulting in a reduction of elk available to browse woody vegetation (Smith 2005). Reduced elk densities could lead to eventual increases in willow growth. Alternatively, elk may behave differently in the presence of wolves by evaluating foraging areas in terms of predation risk. Photo comparisons have revealed that low-risk willow stands in the northern range (i.e., those in uplands with a large viewshed in which to detect predators) remained height suppressed while the majority of willows in high-risk areas (i.e., those in valley bottoms where predators are more difficult to detect) exhibited significant height increases (Ripple and Beschta 2006).

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Released willow along upper Slough Creek.

KATY DUFFY

A distinctively plumaged yellow warbler.

It is also hypothesized that the recent increase in willow is the result of longer growing season temperatures, as willow growth is limited by the number of days during the growing season where temperatures rise above freezing (Despain, pers. comm.). Creel and Christianson (2009) suggest an interaction between biotic (reduced elk densities) and abiotic (decreased snow accumulation) influences on patterns of willow height release in the northern range. Interestingly, increases in willow height growth have not occurred uniformly, indicating that whether recent increases are the ultimate result of climatic factors and/or a trophic cascade, stand-level biophysical characteristics such as nutrient availability, slope, aspect, and other drivers are important proximate factors in determining which stands of willows are significantly increasing in height growth. For example, Tercek et al. (in press) identify a pre-existing suite of abiotic factors contributing to variable willow height release while sampling in two of the three releasing willow sites reported here.

The Effect of Willow Growth on Bird Diversity

Regardless of the causes of willow height increases, the recent expansion of willow may lead to changes in patterns of bird diversity and could have important consequences for bird species in the region associated with willow and other woody riparian vegetation. Since willow-riparian communities are rare in Yellowstone, especially in the northern range, an increase in this habitat type would be beneficial to the guild of species nesting and foraging in willows. A guild refers to a group of species that exploits resources in a similar way (Root 1967). We identified seven species occurring in the region associated with this guild: yellow warbler (*Dendroica petechia*), common yellowthroat (*Geothlypis trichas*), Wilson's warbler (*Wilsonia pusilla*), willow flycatcher (*Empidonax traillii*), warbling vireo (*Vireo gilvus*), song sparrow (*Melospiza melodia*), and Lincoln's sparrow (*Melospiza lincolnii*) (Berger et al. 2001; Jackson 1992). Several of these species also breed in aspen and cottonwood;

however, they are commonly found in willow communities.

To evaluate the potential consequences of increased willow growth on bird diversity, we compared willow structure and bird community composition across three willow growth conditions: short, suppressed; intermediate, released; and previously tall (i.e., tall prior to 1998 when the height release of willow was first observed). Ideally, we would have data on bird assemblages before released willows began to increase in growth; however, as we do not, surveying birds in suppressed willows will shed light on the species most likely inhabiting released sites prior to increased growth. Surveying previously tall willows will provide a frame of reference for the typical bird community associated with a well-established willow stand as well as enable us to make predictions about which species may begin to colonize released sites.

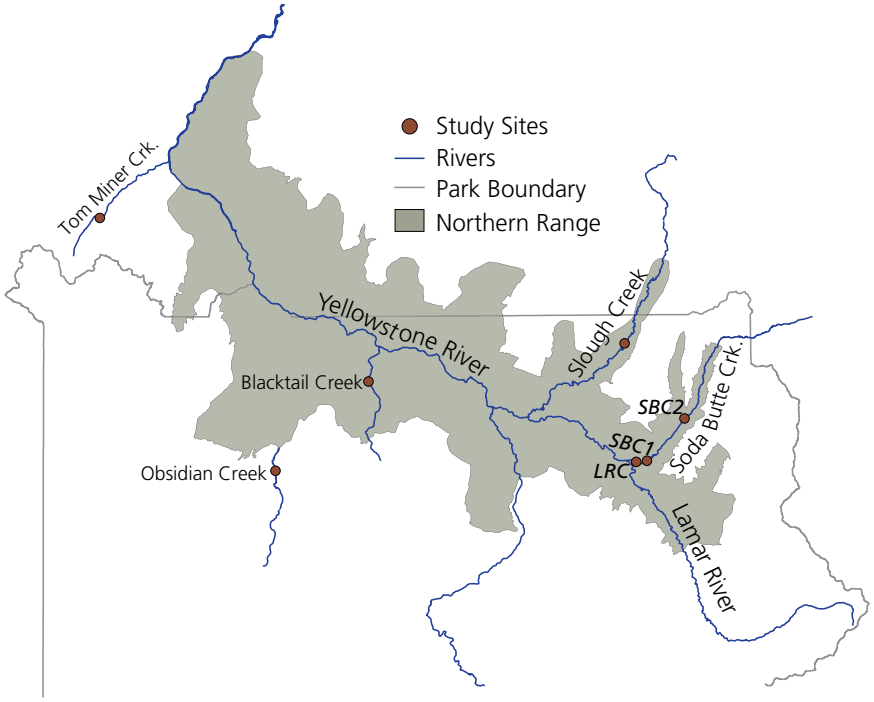

Figure 1. Map of study area and survey locations. Previously tall = Tom Miner Creek and Obsidian Creek; released = Blacktail Deer Creek, Lamar River confluence (LRC), and Slough Creek; suppressed = Soda Butte Creek 1 (SBC1) and Soda Butte Creek 2 (SBC2).

This study was conducted in and around Yellowstone's northern range, defined as the 153,000 hectare area in the Lamar and Yellowstone river watersheds occupied by Yellowstone's northern wintering elk herd (Fig. 1). The majority of the northern range lies within Yellowstone National Park while the remainder lies within the Gallatin National Forest and various private lands north of the park. Vegetation in the region is principally non-forested grasslands and sagebrush steppe in the lower elevations, while conifer forests predominate at higher elevations (Houston 1982). Willows occur along riparian areas and in springs and seeps along valley bottoms.

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Beaver construction along Tom Miner Creek.

Methods

We surveyed two or three sites in each of three willow growth conditions: suppressed, released, and previously tall. Suppressed sites were those with willows that were generally less than 80 centimeters tall and exhibited intense browsing; released sites were formerly height suppressed in part by browsing, but exhibited substantial height gain (>12 inches) and reduced browsing since 1998; previously tall sites were generally 150–200 centimeters tall prior to 1998 and have historically showed little evidence of browsing (Singer et al. 2004 funding report).

Willow sites meeting these criteria were considered for sampling if they were 1) supported by groundwater recharged by a stream; 2) contained enough willow plants for adequate sampling; and 3) were within 15 kilometers of a road for relative ease of access.

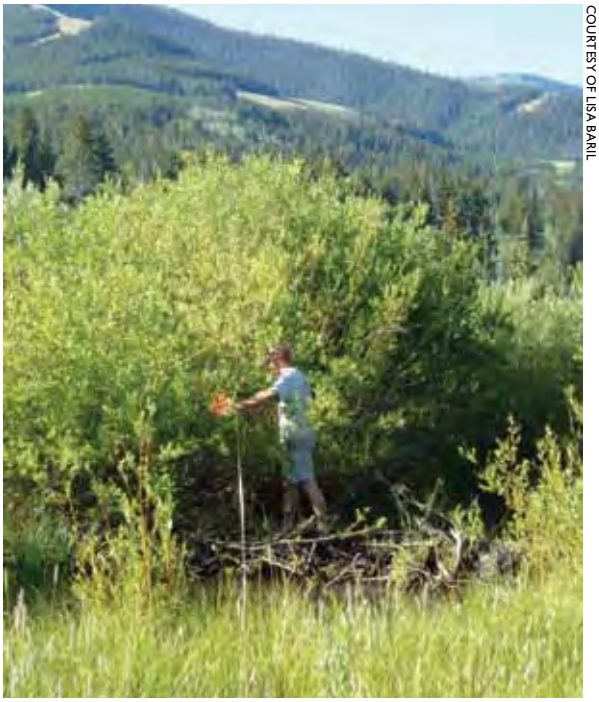
Previously tall sites were located along Obsidian Creek in Yellowstone just south of the northern range and along Tom Miner Creek in Tom Miner Basin west of the northern range because willow sites meeting the previously tall growth condition criteria were absent on the northern range. The slightly higher elevation at these sites, resulting in deeper snows, limits winter use and hence browsing by elk. Additionally, these sites, located outside of Yellowstone, were subject to hunting, potentially changing patterns of elk use there. Released sites were located along upper Slough Creek, Blacktail Deer Creek, and along the Lamar River-Soda Butte Creek confluence. Suppressed sites were situated in two locations along Soda Butte Creek.

At each site, between four and sixteen 40-meter radius circular sample plots were placed at least 100 meters apart. In total, we sampled 67 willow plots stratified across the three willow growth conditions: 23 plots in released sites, 21 plots in suppressed sites, and 23 plots in previously tall sites. In each of these sample plots we surveyed willow structure, species composition, and the bird community. We then averaged values to obtain an overall measure for each of the three growth conditions.

Characterizing Willows

We described the three willow growth conditions in terms of vertical and horizontal vegetation structure. To assess vertical cover or density we used a 5.5 meter Robel pole with 0.5-meter alternating black and white stripes. Measurements were collected at 16 samples point per plot. At each sample point an observer would walk one meter in a random direction from the Robel pole and record the vegetation type (other or willow) and the percentage of the Robel pole obscured by that vegetation in each height class up to the maximum height of the vegetation type present. This technique also allowed us to calculate foliage height diversity, a measure of overall vertical structural complexity. Higher values indicate more complex vegetation while lower values indicate simple vegetation structure.

To assess horizontal vegetation cover, height, and frequency of willow occurrence, we used the line-intercept method, recording the percent willow cover, number intervals containing willow (frequency), and willow height for every 1-meter interval along a 40-meter measuring tape in each sample plot.



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Field technician Mark Paulson taking vegetation measurements.

Lower canopy cover values indicate greater willow patchiness and open spaces between willows, whereas high canopy cover values indicate fewer open spaces and higher canopy closure. All willows encountered were identified to species.

Characterizing Bird Communities

Birds were sampled in the three willow growth conditions using standard point count techniques (Hutto et al. 1986). Three 10-minute rounds of point counts were conducted for each sample plot from June through mid-July of 2005 through 2007. We used four indices for examining differences in birds between growth conditions: richness, abundance, the Shannon-Weiner diversity index, and the Renkonen index of community similarity. Richness is the average number of species observed while abundance is the average number of individuals observed. The Shannon-Weiner diversity index takes into account both richness and evenness in abundance, providing an overall value of bird diversity. The Renkonen index computes the degree of overlap in bird communities between willow growth conditions and is expressed as percent similarity.

We then compared the abundance of each of the seven species identified earlier as belonging to the willow-riparian guild. While other species such as the fox sparrow (*Passerella iliaca*) also belong to this guild, they occur more rarely and are therefore difficult to quantify, so we only included species commonly found in this habitat type that differ in their response to variation in willow structure.

Results

Willows

We found a total of 14 willow species across all three growth conditions (Fig. 2). Eleven species occurred in released sites, ten in previously tall sites, and nine species in suppressed sites. The released and previously tall sites generally contained similar proportions of several species having similar water and soil nutrient requirements (USDA Natural Resources Conservation Service 2007). Suppressed sites, however were dominated by a single species, *S. exigua* (65%), which was rare (<2%) in released and previously tall sites.

S. exigua is an extensively clonal species that reproduces asexually when the flood regime does not create favorable conditions (bare, moist soils) for seed germination (Douhovnikoff et al. 2005). Its presence may indicate that suppressed sites are 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, leading to the greater willow species diversity observed there. However, this is purely speculation, as the ratio of plant establishment by seed versus clones among growth conditions is unknown. Although *S. exigua* and other willow species found in suppressed sites are able to attain heights comparable to those found in previously tall and released sites, they

	Suppressed (n = 23) x ± SE	Released (n = 21) x ± SE	Previously tall (n = 23) x ± SE	F	P	Differences
Height (cm)	61.55 ± 19.03	143.08 ± 18.34	179.17 ± 19.91	15.08	<0.0001	P,R S
Horizontal cover (%)	9.61 ± 3.15	21.42 ± 3.29	60.39 ± 3.15	76.75	<0.0001	P R S
Frequency (%)	26.53 ± 3.95	30.48 ± 4.13	73.48 ± 3.95	31.34	<0.0001	P R,S
Foliage Height Diversity	0.45 ± 0.12	1.39 ± 0.12	1.69 ± 0.13	29.37	<0.0001	P,R S

Table 1. Willow structural characteristics between suppressed (S), released (R) and previously tall (P) willow sites. Under "Differences," spaces between letters indicate significant differences.

have not done so in suppressed sites sampled in the northern range. Differences in height between growth conditions has been largely attributed to ungulate herbivory, but site specific variation in biophysical characteristics such as soil quality, nutrient availability (Tercek et al. in press), and hydrology (Bilyeu et al. 2008) can have significant impacts on willow growth.

Willow frequency was high in previously tall sites. Willows averaged 180 centimeters in height, with high foliage height diversity revealing structurally complex willows (Table 1). Not only were these willows tall, dense, and structurally complex, but they also showed high horizontal cover, representing 60% of the total cover in previously tall sites. In contrast, suppressed sites contained fewer willows and much shorter willows that were structurally simple in nature. Willows in these sites averaged only 62 centimeters in height, a third of previously tall willow height, and represented only 10% of the horizontal cover. Previously tall and suppressed sites represent the two extremes of willow growth in the region and differed significantly from one another in all variables measured.

Released willows were intermediate between suppressed and previously tall sites sharing structural attributes representative of each. Released willows were nearly as tall as previously tall willows (143 centimeters vs. 180 centimeters) with similar vertical structural complexity. Willow frequency, however, was similar between released and suppressed sites. Horizontal cover in released sites was twice that found in suppressed sites and a third of that found in previously tall sites. These findings reveal that while willows in released sites have attained a similar height and vertical structural complexity as in previously tall willows, they have increased only slightly in horizontal cover and have not successfully recruited new willow plants. In other words, existing plants are getting larger, but the population of willows in a given location is not increasing, a finding supported by other studies (Wolf et al. 2007).

Lack of willow recruitment may be partially attributed to prolonged absence of beavers in the northern range since the early to mid 1900s (Jonas 1955). Beaver and willow are mutualists in the region. Willows provide beavers with forage, dam, and lodge building materials, while beaver activity promotes the growth and establishment of willow by raising local water tables and creating favorable conditions for growth and germination (Wolf et al. 2007; Bilyeu et al. 2008).

Following abandonment of riparian areas by beavers, streams banks began to erode and channels became narrower and more incised, causing the groundwater that is important to the establishment and growth of willows to decrease (Wolf et al. 2007). While decreased browsing by elk may be allowing for increased growth of existing willow plants, recruitment of new willow plants may require recolonization of released sites by beavers (Wolf et al. 2007). In recent years, surveys of beavers along northern range streams have shown that they are increasing, which could eventually lead to an increase in the population of willows (Smith and Tyers 2008).

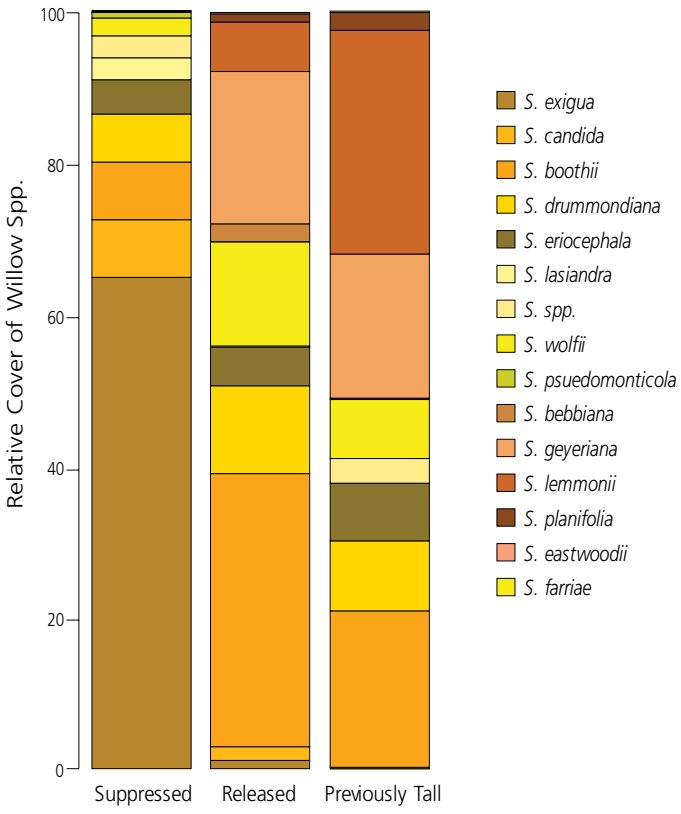

Figure 2. Relative cover of willow species in suppressed, released, and previously tall sites.

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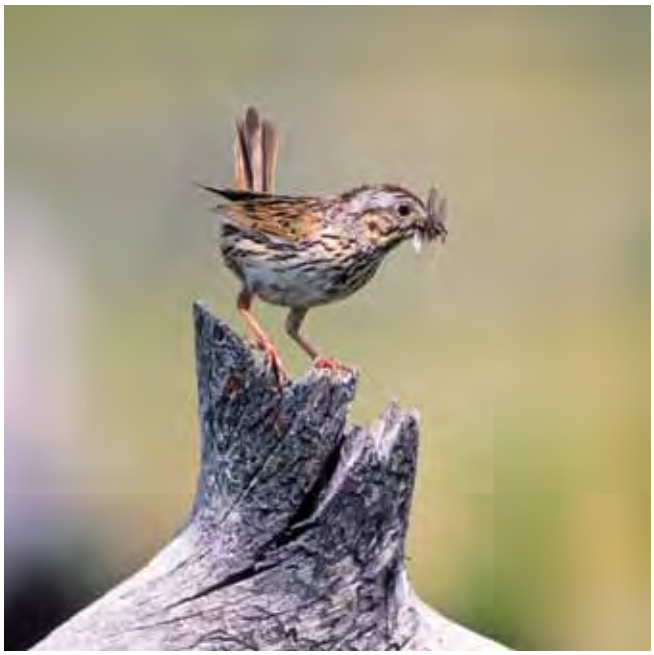
Yellow warbler nest in a released willow stand.

However, the extent to which beaver activity has historically modified northern range stream flow and sedimentation is spatially limited and highly variable over time. (Persico and Meyer 2009). Fluctuating climate and the high velocity of many northern range streams can prevent the construction of dams and subsequent modification of stream flows.



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A Lincoln's sparrow captures a mayfly.

Birds

We recorded 2,724 individuals belonging to 33 species across all three growth conditions over the three years of surveys. Previously tall willows were significantly greater in species richness, abundance, and diversity than suppressed willows (Table 2). Birds reduce competition by foraging and nesting at different vegetation heights. Some species prefer to nest and forage on or near the ground, others the middle vegetation layer, while others prefer the canopy. Even within the same vegetation layer, two or more species can occur simultaneously through differences in foraging and nesting behavior. The relatively complex willow structure found in previously tall sites allows for resources such as food and nesting substrates to be more finely partitioned among a greater number of species than is allowed in the shorter and structurally simple suppressed sites.

The relatively low Shannon-Weiner diversity index indicates that suppressed sites were dominated by a few highly abundant species, primarily savannah sparrows (*Passerculus sandwichensis*) and other species typically associated with wet meadows. This was not the case in previously tall willows. The higher Shannon-Weiner index revealed a more even distribution across several species. Given that suppressed and previously tall sites differed greatly in willow structure, it is not surprising that there was only 34% overlap in species between these two bird communities.

In contrast, released sites were similar (66%) to previously tall sites, but also shared 59% of the species found in suppressed sites. The intermediate structure of released willows provided habitat suitable for species occurring in both growth conditions. Released condition willows were intermediate in richness between the previously tall and suppressed condition, but were similar to the previously tall condition in abundance and diversity. Despite the apparent lack of 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.

Only two bird species in the willow-riparian guild were found in all three willow growth conditions: the common yellowthroat and Lincoln's sparrow (Fig. 3). This suggests that they are somewhat general in their habitat associations, although both occurred more frequently in released and previously tall

	Suppressed *(n = 23)* x ± SE	**Released** *(n = 21)* x ± SE	**Previously tall** *(n = 23)* x ± 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

Table 2. Bird species richness, abundance, and diversity between suppressed (S), released (R) and previously tall (P) willow sites. Under "Differences," spaces between letters indicate significant differences.

sites than in suppressed sites. Both species are ground nesters. Lincoln's sparrows frequently forage on the ground while common yellowthroats forage near the ground, gleaning insects from leaves. As they do not require tall willows for nesting or foraging, they were able to occupy all three growth conditions. The greater horizontal cover in released and previously tall sites afforded more foraging and nesting opportunities than were available in suppressed sites and likely accounts for the higher abundance observed there.

Suppressed willows were unable to support song sparrows, warbling vireos, yellow warblers, willow flycatchers, and Wilson's warblers (Fig. 4). This indicates that each of these species requires willows of at least a certain height and greater horizontal cover than were available in suppressed sites. Song sparrows, warbling vireos, yellow warblers, and willow flycatchers occurred in both released and previously tall willows, however, their abundance was greater in previously tall sites, probably because of the greater horizontal cover there.

Wilson's warblers were found exclusively in previously tall sites. They frequently forage at willow heights of 60 centimeters to 120 centimeters (Hutto 1981). While willows grew this tall in released sites, Wilson's warblers were absent from these areas. This indicates that Wilson's warblers not only require willows of intermediate height, but also a dense horizontal distribution of willow. Because they have specific structural requirements, are restricted to montane willow communities, 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 Wilson's warblers in the region. If released sites increase in horizontal cover, this species may begin to colonize these areas.

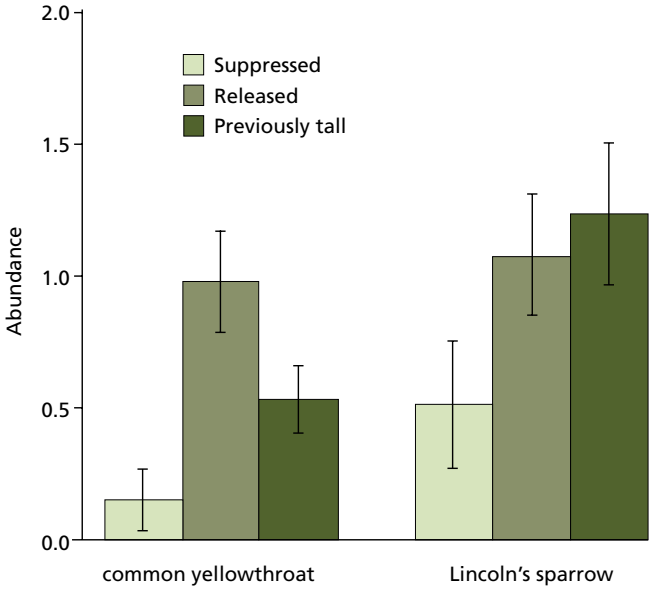

Figure 3. Common yellowthroat and Lincoln's sparrow abundance across the three growth conditions.

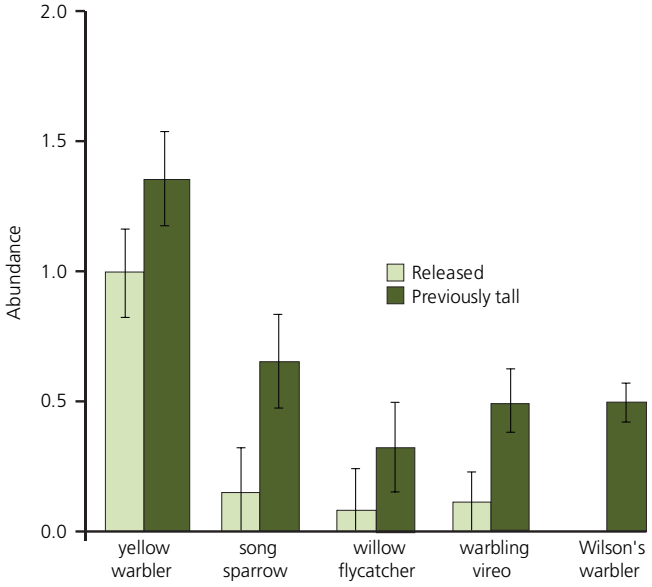

Figure 4. Abundance of bird species in released willows and previously tall willows.

Conclusions

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 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.

The shorter, sparsely distributed suppressed willows prevented the establishment of several species belonging to the willow-riparian guild, except for common yellowthroats and Lincoln's sparrows, which were found to be habitat generalists within the range of willows that we sampled. If suppressed sites attain heights similar to those of released sites, common yellowthroat and Lincoln's sparrow will likely increase in abundance there. An increase in willow frequency and horizontal cover in released sites will likely attract Wilson's warblers to these areas and increase the abundance of willow- and riparian-associated species already occupying these sites.

The majority of focal species in our study appear to have been absent or present in low densities in the northern range during Jackson's (1992) study. Prior to willow height release, song sparrows and yellow warblers both occurred in low densities, while Wilson's warblers, willow flycatchers, and warbling vireos were absent in the sites sampled in the northern range (Jackson 1992). However, it appears that the recent increase in willow growth is not yet sufficient to allow for colonization by Wilson's warblers.

A future goal may be to compare nesting success across sites to determine if those species occurring in all growth conditions, especially released and previously tall, differ in

reproductive success. It may be that released sites, relatively low in willow frequency and cover, have more edge habitat. A greater amount of edge habitat might allow predators to locate nests more easily and decrease reproductive success in these areas. Monitoring nest success would add another dimension to our understanding of willow–bird habitat relationships.

This study represents a snapshot in time of the bird community across a range of willow growth conditions in the region. Yellowstone's bird program is continuing to monitor willow sites surveyed in this study and is now in the fifth year of data collection—the beginning of a long-term dataset on willow–bird relationships in Yellowstone's northern range.

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Dr. Rick Lawrence is a professor of remote sensing in the Land Resources and Environmental Sciences Department at Montana State University. He is also the director of the Spatial Sciences Center there. His work focuses on the use and application of remote sensing technologies in managed and natural ecosystems. His doctorate in remote sensing is from Oregon State University.

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