

Songbird response to increased willow (*Salix* spp.) growth in Yellowstone's northern range

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Abstract. After nearly a century of height suppression, willows (*Salix* spp.) in the northern range of Yellowstone National Park, USA, are increasing in height growth as a possible consequence of wolf (*Canis lupus*) restoration, climate change, or other factors. Regardless of the drivers, the recent release of this rare but important habitat type could have significant implications for associated songbirds that are exhibiting declines in the region. Our objective was to evaluate bird response to releasing willows by comparing willow structure and bird community composition across three willow growth conditions: height suppressed, recently released, and previously tall (i.e., tall prior to the height increase of released willows). Released and previously tall willows exhibited high and similar vertical structure, but released willows were significantly lower in horizontal structure. Suppressed willows were significantly shorter and lower in horizontal cover than released or previously tall willows. Bird richness increased along a gradient from lowest in suppressed to highest in previously tall willows, but abundance and diversity were similar between released and previously tall willows, despite lower horizontal cover in the released condition. Common Yellowthroat (*Geothlypis trichas*) and Lincoln's Sparrow (*Melospiza lincolnii*) were found in all three growth conditions; however, Yellow Warbler (*Dendroica petechia*), Warbling Vireo (*Vireo gilvus*), Willow Flycatcher (*Empidonax traillii*), and Song Sparrow (*Melospiza melodia*) were present in released and previously tall willows only. Wilson's Warbler (*Wilsonia pusilla*) was found in previously tall willows only, appearing to specialize on tall, dense willows. The results of our a priori habitat models indicated that foliage height diversity was the primary driver of bird richness, abundance, and diversity. These results indicate that vertical structure was a more important driver of bird community variables than horizontal structure and that riparian and willow-dependent bird species have responded positively to increased willow growth in the region.

Key words: diversity; foliage height diversity; northern Rocky Mountains, USA; riparian; *Salix* spp.; songbirds; vegetation structure; willow communities; willow-dependent birds; Yellowstone National Park, USA.

INTRODUCTION

Willow (*Salix* spp.) is the dominant woody plant in many riparian zones across the northern Rocky Mountains, USA; however, willow communities are rare, typically comprising <1% of the 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 influences 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 nearly 900 000 ha, Yellowstone National Park is the largest protected area in the western conterminous United States, with many of its riparian areas dominated by willows (National Research Council [NRC] 2002).

Despite this protection, willow communities in Yellowstone National Park's northern range have been

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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 short willow stature and simplified willow structure observed in the region during this time (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 (Yellowstone National Park 1997). Perceptions of overbrowsing led directly to a culling program initiated in 1923 but was replaced with a policy of natural regulation in 1968 after intense public protest (Boyce 1991). Under natural regulation, elk are believed to be limited by density-dependent factors such as competition for forage, therefore reaching eventual equilibrium with vegetation (Boyce 1991); however, it wasn't until 30 years later that woody vegetation began to increase in the northern range.

Beyer et al. (2007) found a twofold 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). High spatial resolution imagery indicated that riparian vegetation, including willow, alder (*Alnus incana*), and cottonwood, increased in areal extent by 279% within a 4-km² area along the Lamar River–Soda Butte Creek confluence between 1995 and 1999 (Groshong 2004). Most recently, aerial photo comparisons revealed a 170% increase in willow, alder, cottonwood, and aspen (*Populus tremuloides*) across riparian and wetland areas throughout the northern range between 1992 and 2006 (Baril 2009).

These observations of increased willow height and areal extent coincided with the reintroduction of wolves

(*Canis lupus*) in 1995 and 1996, stimulating 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, Alberta, Canada, 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 in the northern range also coincided with change in climate. Longer growing seasons, resulting from warmer spring and fall temperatures, have led to increased productivity of deciduous woody vegetation in the Rocky Mountains (Cayan et al. 2001), and warmer spring temperatures have led to greater (Lins and Slack 1999) and earlier peak streamflows (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 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 regulation 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, which may be partially explained by variation in biophysical characteristics among sites (Tercek et al. 2010). Some willow communities 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 goal was to determine the significance of the recent increase in willow growth for bird species diversity in Yellowstone's northern range by addressing the following objectives: (1) quantify willow structure in each of three willow growth conditions occurring in and around the northern range (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) among the three willow growth conditions; (3) examine differences in the abundance of seven focal species known to be associated with willows in the region but that exhibit variation in their response to differences in vegetation structure: Common Yellowthroat (*Geothlypis trichas*), Lincoln's

Sparrow (*Melospiza lincolni*), Yellow Warbler (*Dendroica petechia*), Song Sparrow (*Melospiza melodia*), 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 predicted that willow structure would become increasingly complex along a gradient from suppressed (least complex) to previously tall (most complex) as measured by vertical and horizontal structural characteristics. For the bird community variables, we predicted that richness, abundance, and diversity would increase along a gradient from lowest in suppressed to highest in previously tall willows. For the species-level objective, we predicted that Common Yellowthroat and Lincoln's Sparrow would be present in all three willow growth conditions (i.e., willow generalists) but would increase in abundance along a gradient from lowest in suppressed to highest in previously tall willows. Yellow Warbler, Song Sparrow, and Warbling Vireo would be absent from suppressed willows but would be present in released and previously tall willows, although at a lower abundance in the former (i.e., willow associates). Finally, we predicted that Wilson's Warbler and Willow Flycatcher would be absent from both suppressed and released willows but present in previously tall willows (i.e., willow specialists).

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 (Fig. 1) (Houston 1982). Elevation varies from 1500 to 3209 m (Savage and Lawrence 2010). The majority of the northern range lies within Yellowstone National Park, USA, while the remainder lies within the Gallatin National Forest, Montana, USA, and various private agricultural and ranch lands north of the Yellowstone boundary (Houston 1982). The semiarid region receives ~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 ~12 000–14 000 years ago following the retreat of the Pinedale glacier (Christiansen 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 and Kay 1991:238). Willows, in particular, can be found along portions of the Lamar River and 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 and Kay 1991). 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. 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 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 *Methods: Statistical analyses*).

Study sites

Previously tall condition willow sites were defined as those with >60% of willows currently 150–200 cm tall in addition to being tall prior to 1998. Released condition willow sites were defined as those with formerly height-suppressed willows (<80 cm tall prior to 1998), but where >40% of the willows have exhibited at least 30 cm height gain since 1998. Suppressed condition willow sites were defined as those with currently >60% of the willows <80 cm tall in addition to being height suppressed prior to 1998. Growth conditions were defined by Singer et al. (2004), with slight modification of the released definition, whereby we combined releasing (80–200 cm with 30 cm height gain since 1998) and recently escaped sites (>200 cm and thicket-forming with 30 cm height gain since 1998) into a single released category. A recent ground-based survey of willow distribution across the northern range found that 7% of willows were ≤80 cm, 18% were between 81 and 120 cm, and 75% were >120 cm (Tercek 2010); however, the percentage of willow in each height category based on historic patterns of growth (i.e., stature prior to 1998) is unknown, since information on height growth prior to

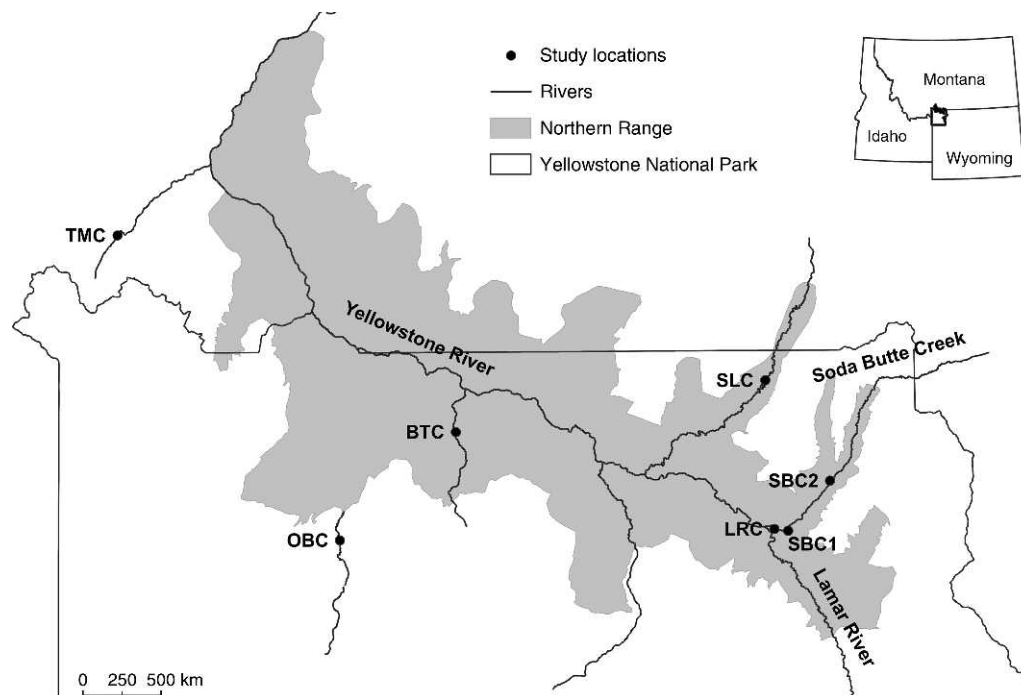


FIG. 1. Map of the willow survey locations in the northern range of Yellowstone National Park, USA. Willows were categorized into three growth conditions: previously tall (>60% of willows currently 150–200 cm tall in addition to being tall prior to 1998), released (>40% of willows <80 cm tall prior to 1998, but with >30 cm height gain since 1998), and suppressed (>60% of the willows currently <80 cm tall in addition to being short prior to 1998). Categorization of sites: 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).

1998 does not exist for all willow patches across the northern range.

We selected two to three willow sites in each growth condition that were at least 400×100 m in area and were within 15 km of a road for relative ease of access. 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 (Garmin International, Olathe, Kansas, USA) global positioning system, we walked in an approximate straight line and placed the center of the plots 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. 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 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 (Fig. 1). All willow sites were previously categorized by Singer et al. (2004) and by the third author's substantial knowledge of willow growth in the region.

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 using the criteria of height stature prior to 1998, we compared land cover for two dates of aerial photography from 1991 and 2006. Areal willow cover as observed in aerial photographs is an indicator of willow height (i.e., low areal cover generally indicates short willow stature; Baril 2009). 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 the USDA's Aerial Photography Field Office

(USDA-APFO). All imagery was obtained through the Yellowstone Center for Resources Spatial Analysis Center in Mammoth, Wyoming, USA.

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 was 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. Since the data were not normally distributed, we used a Wilcoxon signed-rank test to test for significant differences in willow cover between the two dates of imagery for each growth condition.

Since we expected little change between imagery dates in both the previously tall and suppressed willow conditions, we used a two-sided test. Since we expected a significant increase in the released willow condition, we used a one-sided test. We also expected the suppressed willow condition to reveal low percent willow cover for both dates of imagery, while the previously tall willow condition should reveal relatively high percent willow cover for 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 line intercept method (Canfield 1941) in all 67 sample plots of 40 m radius (Fig. 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.

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 four 0.5 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. The Robel pole was placed at each sample point, from which an observer walked 1 m in a random direction from the Robel pole and recorded the cover type (other or willow) and the percentage 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

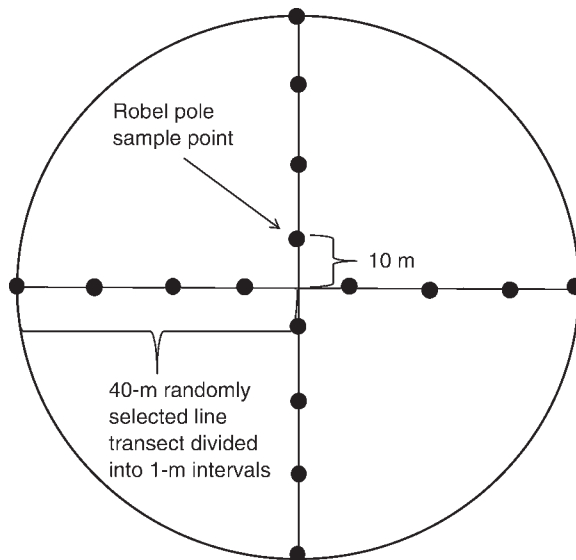


FIG. 2. Plot configuration used to sample vegetation in the 67 circular sample plots of 40 m radius.

randomly selected cardinal direction. An observer recorded the distance over which willow intersected the meter tape and the height of willow where it intersected with the meter tape at 1-m intervals.

Generation of vegetation predictors.—A total of 10 habitat variables were generated from Robel pole and line intercept data. Five of the 10 variables were generated from Robel pole measurements: vertical vegetation density in each of four 0.5-m height classes and foliage height diversity, a measure of overall vertical structural complexity. Vertical vegetation density in each of the four 0.5-m height classes was obtained by averaging the percent cover values across each height class strata per sample plot. Low vertical vegetation cover or density values indicated more open spaces in the vertical structure of willow, while high values indicated 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):

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

where H' is the index of diversity, S is the number of height classes where willow is represented, and p_i is the proportion of total willow cover belonging to the i th height class.

Five of the 10 habitat variables were generated from line intercept measurements: percent horizontal cover, height (cm), percentage 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.

Bird sampling

Birds were sampled in each of the 67 sample plots (40 m radius) 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 2005–2007 except for five plots in 2005 and three plots in 2006, which were sampled only 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 sampled only twice during a season.

Each count lasted 10 minutes, during which 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 09:30. 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. Flyovers, waterfowl, marshbirds, and shorebirds were excluded from analyses because point counts are not designed to adequately survey these species (Ralph et al. 1995). Bird richness and abundance were calculated by summing the number of species or individuals detected per visit per year, then averaging over the visits and then over years. We used the program Distance 5.0 (Thomas et al. 2006) to determine the effective detection radius for the 12 species with >40 detections, and we compared detection radius between each of the three growth conditions (Laake et al. 2006). Although not all species were fully detectable at 40 m, there were no differences in detectability between species occurring in more than one growth condition; therefore, we used uncorrected density estimates to simplify analyses. Although point count stations were 100 m apart, territories for species commonly occurring in willows are generally smaller than the distance between points (Ammon 1995, Guzy and Ritchison 1999, Lowther et al. 1999, Wheelwright and Rising 2008).

The Shannon-Weiner diversity index, which takes into account both richness and evenness, was calculated with the formula given above (see equation in *Methods: Field vegetation sampling: Generation of vegetation predictors*) except that here S is the number of species and p_i is the proportion of species belonging to the i th 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):

$$P = \sum_{i=1}^S \text{minimum}(p_i^A, p_i^B)$$

where P is percentage similarity, p_i^A is the percentage of species i in sample A, p_i^B is the percentage of species i in sample B, and S is the number of species found in either sample.

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 (Zuur et al. 2009). Thus we controlled for spatial autocorrelation using GLS by modeling the spatial dependence present in the data (Zuur et al. 2009). 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). The four models of spatial structure compared were exponential, Gaussian, rational quadratic, and spherical.

We considered all models with $\Delta AIC_c \leq 2$ to have received substantial support, while those models with $\Delta AIC_c \geq 4$ 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 nonspatial model was selected as the best model.

Comparison of vegetation and bird variables among willow growth conditions.—Differences in vegetation variables, bird community variables, and the abundance of the seven focal species 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. 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.

Model development and evaluation.—The relationship between bird response variables (species richness, abundance, and diversity) and willow structural charac-

teristics were examined using GLS regression. We used AIC_c to evaluate a set of a priori models using the model selection criteria described. 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, using the willow structure variables height, foliage height diversity, coefficient of variation in height, horizontal percent cover, percentage frequency, and patch size. We excluded vertical vegetation density in each of the four height classes from model development, since these measures are accounted for by foliage height diversity. This resulted in a set of 19 a priori models for each bird community variable.

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 (Kutner et al. 2004). We assessed multicollinearity 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 (Kutner et al. 2004). We assessed the fit of the global model by examining diagnostic plots for normality of residuals and constant variance.

RESULTS

Confirming the designation of willow sites into the three growth conditions

The change detection results support the classification of the study sites into suppressed, released, and previously tall growth conditions (Fig. 3). Willows across the previously tall condition sample plots did not change significantly between the two dates of imagery ($n = 23$, Wilcoxon signed-rank $W = 239$, $P > 0.57$). Mean willow cover in 1991 was 59% vs. 60% in 2006. Mean willow cover across the suppressed condition sample plots increased from 5% in 1991 to 11% in 2006 ($n = 23$, $W = 199$, $P = 0.11$); however the Wilcoxon signed-rank test indicated no significant difference between the two dates. The released willow condition sample plots 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 ($n = 21$, $W = 16$, $P < 0.001$). The classification accuracy of willow was assessed with field data of willow height at known locations for both 1991 and 2006 in a previous study (see Baril 2009 for complete methods and results). Briefly, accuracy for the classification of willow was generally consistent and reliable, especially when willow was taller than 100 cm (Baril 2009). 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 < 100 cm, slightly above our threshold for inclusion of willows into the suppressed condition.

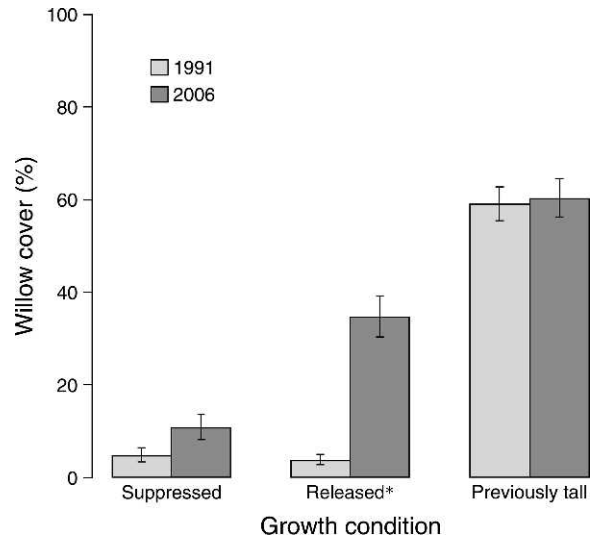


FIG. 3. Willow cover (mean \pm SE) in 1991 and 2006 by willow growth condition as measured from aerial photographs. Ten-dot grids were placed over each bird point count location on 1:24 000 aerial photographs, and the percentage of willow was determined by summing the number of dots encountering willow in 10% increments. Significant differences between pairs were analyzed using the Wilcoxon signed-rank test. An asterisk (*) denotes significant difference ($P < 0.05$) between the two dates of imagery.

It is also 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, low willow cover 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 indicates that at least $\sim 35\%$ of the willows were > 100 cm tall, signifying 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. The exponential spatial structure resulted in the lowest AIC_c score for height and foliage height diversity; however, the differences in AIC_c scores were ≤ 2 for models that included 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 generalized least squares (GLS) models, the exponential spatial structure was selected as the best model and so was incorporated into the suite of a priori models. Semivariograms

TABLE 1. Willow structural characteristics (mean \pm SE) and results of ANOVA among suppressed, released, and previously tall willow growth conditions in the northern range of Yellowstone National Park, USA.

Structural characteristics	Suppressed (<i>n</i> = 23)	Released (<i>n</i> = 21)	Previously tall (<i>n</i> = 23)	<i>F</i> _{2,64}	<i>P</i>	Differences†
Height (cm)	61.55 \pm 19.03	143.08 \pm 18.34	179.71 \pm 19.91	15.08	<0.001	S, R, Pt
CV in height (cm)	0.37 \pm 0.04	0.39 \pm 0.04	0.39 \pm 0.04	0.11	0.895	<u>S, R, Pt</u>
Horizontal cover (%)	9.61 \pm 3.15	21.42 \pm 3.29	60.39 \pm 3.15	76.75	<0.001	S, R, Pt
Frequency (%)	26.53 \pm 3.95	30.48 \pm 4.13	73.48 \pm 3.95	31.34	<0.001	S, R, Pt
Foliage height diversity	0.45 \pm 0.12	1.39 \pm 0.12	1.69 \pm 0.13	29.37	<0.001	S, R, Pt
Patch size	1.05 \pm 2.06	2.95 \pm 2.15	12.49 \pm 2.05	11.31	0.001	S, R, Pt
0–50 cm (%)	59.74 \pm 3.65	69.20 \pm 3.81	68.42 \pm 3.65	14.33	0.246	<u>S, R, Pt</u>
50–100 cm (%)	20.29 \pm 3.83	53.16 \pm 4.01	63.85 \pm 3.83	34.91	<0.001	S, R, Pt
100–150 cm (%)	NA	36.59 \pm 4.90	51.16 \pm 4.69	4.61‡	0.038	R, Pt
150–200 cm (%)	NA	24.88 \pm 5.05	34.98 \pm 4.83	3.92‡	0.054	<u>R, Pt</u>

Notes: CV is the coefficient of variation. The number of point count locations is signified by *n*, derived from measurements taken in the 40 m radius circular sample plots. NA stands for not applicable.

† Underlines indicate nonsignificant differences (*P* > 0.05) between growth conditions (S, suppressed; R, released; Pt, previously tall).

‡ For these two tests, *df* = 1, 42.

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.

Comparison of willow structure across willow growth conditions

In general, willows increased in complexity from least complex in the suppressed condition to most complex in the previously tall condition (Table 1). Previously tall willows averaged 180 cm in height and tended to be relatively dense in all vegetation height classes; however, vertical vegetation density tended to decrease with increasing height. The relatively high foliage height diversity and high patch index indicates structurally complex willows that are organized in few but large willow patches rather than the simplified willows that occur in several small willow patches in the suppressed condition. Previously tall and suppressed willows represent the two extremes of willow growth in the region, differing significantly from one another in most willow structural variables measured. 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 nearly all measures of vertical willow distribution; however, released willows

were significantly lower in all three measures of horizontal willow distribution.

Comparison of bird community variables across willow growth conditions

We recorded 2724 bird detections from 33 species across all three willow conditions over the three years of surveys. Observers recorded 1012 detections belonging to 25 species in previously tall sites, 1042 detections belonging to 23 species in released sites, and 670 detections belonging to 16 species in suppressed sites (see Appendix A).

Previously tall sites were significantly greater in species richness, abundance, and diversity than suppressed sites (Table 2). Not only were there fewer species and individuals of those species, but the relatively low Shannon-Weiner diversity index indicated that suppressed sites were dominated by a few abundant species. The Renkonen community similarity index indicated 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 was similar to the previously tall condition in abundance and diversity. The Renkonen index indicated 66% community similarity between released and previously tall conditions and

TABLE 2. Bird species richness, abundance, and diversity (mean \pm SE) among suppressed, released, and previously tall willow growth conditions.

Bird characteristics	Suppressed (<i>n</i> = 23)	Released (<i>n</i> = 21)	Previously tall (<i>n</i> = 23)	<i>F</i> _{2,64}	<i>P</i>	Differences†
Richness	2.93 \pm 0.34	5.72 \pm 0.33	7.52 \pm 0.34	48.04	<0.001	S, R, Pt
Relative abundance	3.85 \pm 0.39	5.98 \pm 0.37	6.46 \pm 0.41	14.64	<0.001	S, R, Pt
Shannon-Weiner diversity	0.76 \pm 0.06	1.51 \pm 0.06	1.78 \pm 0.07	62.46	<0.001	S, R, Pt

Note: The number of point count locations is signified by *n*, derived from measurements taken in the 40 m radius circular sample plots.

† Underlines indicate nonsignificant differences (*P* > 0.05) between growth conditions (S, suppressed; R, released; Pt, previously tall).

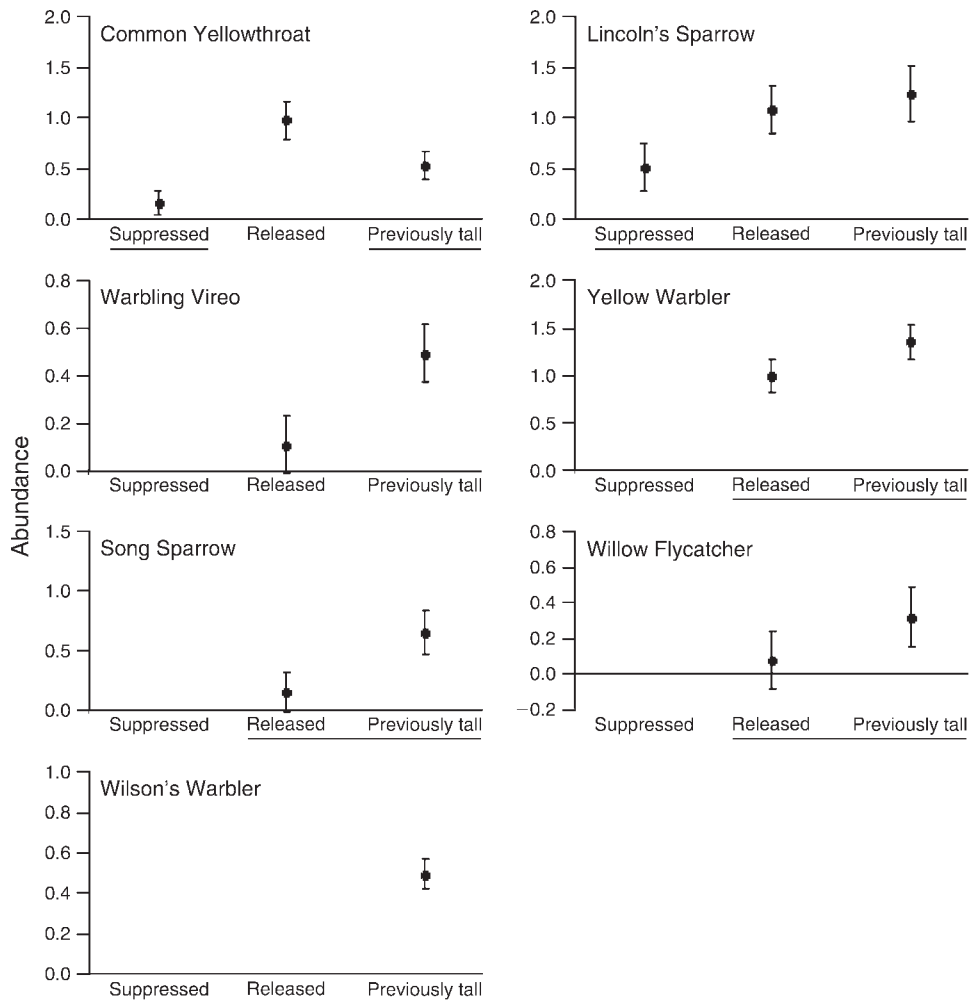


FIG. 4. Comparison of abundance (mean \pm SE) for the seven focal species across suppressed, released, and previously tall willow growth conditions. Significant differences are indicated by the underline method (i.e., nonsignificant differences between pairs are underlined). Note the difference in scale between panels.

59% similarity between released and suppressed conditions. Although abundance and diversity was significantly lower in the suppressed willow condition, neither was significantly different between the released and previously tall condition.

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. Common Yellowthroat (*Geothlypis trichas*) abundance was significantly greater in released than in either previously tall or suppressed willows ($F_{2,64} = 14.01$, $P < 0.001$; Fig. 4). Lincoln's Sparrow (*Melospiza lincolni*) abundance was similar between previously tall and released willows, but both were significantly greater than abundance in suppressed willows ($F_{2,64} = 3.56$, $P = 0.034$). Warbling Vireos (*Vireo gilvus*) were found to be significantly greater in previously tall than in released willows ($F_{1,42} = 4.91$, P

$= 0.032$). Yellow Warbler (*Dendroica petechia*) ($F_{1,42} = 2.11$, $P > 0.05$), Song Sparrow (*Melospiza melodia*) ($F_{1,42} = 3.99$, $P > 0.05$), and Willow Flycatcher (*Empidonax traillii*) abundance ($F_{1,42} = 1.09$, $P > 0.05$) were not significantly different between released and previously tall willows. Wilson's Warblers (*Wilsonia pusilla*) were found exclusively in previously tall willows.

Model evaluation for richness, abundance, and diversity

Three pairs of variables were highly correlated. Foliage height diversity was correlated with height ($R = 0.73$), horizontal percent cover was correlated with percentage frequency ($R = 0.92$), and patch size was correlated with horizontal cover ($R = 0.72$). VIF values for percent horizontal cover and percentage frequency were greater than the threshold (≥ 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

TABLE 3. Model selection results for competing a priori models for species richness, abundance, and diversity.

Model structure	AIC _c	ΔAIC _c	w _i	K
Richness				
Foliage height diversity	25.22	0.00	0.96	1
Coefficient of variation in height	32.56	7.34	0.02	1
Foliage height diversity + patch size	35.93	10.71	0.00	2
Abundance				
Foliage height diversity	-0.4	0.00	0.95	1
Coefficient of variation in height	5.95	6.35	0.04	1
Foliage height diversity + patch size	10.03	10.43	0.01	2
Diversity				
Foliage height diversity	-78.40	0.00	0.97	1
Coefficient of variation in height	-71.51	6.89	0.03	1
Foliage height diversity + patch size	-64.89	13.52	0.00	2

Notes: AIC_c is Akaike's Information Criterion corrected for small sample sizes. ΔAIC_c indicates the difference between the AIC score for a given model and the best model in the suite; w_i indicates the weight of evidence for each model, given the other models in the suite. K is the number of estimated main effects in each model.

residuals and constant variance for all global models, we concluded that each was a good fit to the data.

The best model within our suite of models for richness, abundance, and diversity (Table 3) contained foliage height diversity only. 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 foliage height diversity-only model.

DISCUSSION

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 attained similar height and vertical structural complexity as previously tall willows, horizontal cover was still limited in the released growth condition but was 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 establishment of new willow plants was limited and that differences in horizontal cover were 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 were attributed to prolonged absence of beaver from

some northern range streams, leading to increased stream incision and lowered water tables and resulting in reduced establishment opportunities for willow (Wolf et al. 2007), although the extent to which beaver activity has historically modified northern range streamflow 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 streamflow (Persico and Meyer 2009).

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 were more important than horizontal structure in influencing bird community variables in our study; this was 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 relationships 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 species and individuals, thus accounting for higher diversity associated with complex vegetation (MacArthur and MacArthur 1961); however, individual species respond differently 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, indicating that they are generalists within the range of willow growth sampled; however, the abundance of each varied across growth conditions. 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 threefold increase in horizontal cover from released to previously tall, yet Lincoln's Sparrow abundance increased only slightly. This suggested 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 have been 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, USA, 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.

Yellow Warblers, Song Sparrows, Warbling Vireos, and Willow Flycatchers 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 suggested that these 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 have accounted for higher abundance there. 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 indicated that Willow Flycatchers can tolerate horizontal cover as low as 20% and a wide range of willow density (25 to 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 was relatively rare in the northern range. But evidence suggested that it was 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, 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 suggested that measures of willow distribution such as horizontal cover, frequency, and/or patch size are important for Wilson's Warbler colonization and was 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), 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 indicated that foliage height diversity exhibited better explanatory power than height alone and confirmed 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). 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 among species.

Willow structure in the northern range is in part modified by browsing. 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 of 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 attributed largely to a behaviorally modified trophic cascade whereby wolf presence influences foraging patterns of elk (Ripple and Beschta 2004); however, in a recent study, wolf presence was 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. 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 willows began increasing in height growth. Additionally, warmer spring temperatures have led to earlier (Stewart et al. 2005) and greater peak streamflows (Lins and Slack 1999) that could result in an alternative hydrologic pattern possibly favorable to willow growth, at least in the short term, since climate warming is expected to continue, thereby reducing alpine snowpack responsible for increased flows (Meehl 2007). The colonization of several northern range streams by beavers over the last decade could also influence willow growth (Smith and Tyers 2008). For example, willows gained significantly more height growth under an experimentally elevated water table designed to simulate beaver damming than under the ambient water table condition, even under intense browsing (Bilyeu et al. 2008).

Moreover, underlying abiotic characteristics of an area may interact with these factors. Tercek et al. (2010) identified 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. These associations, combined with the previously recognized climatic influences (longer growing seasons, increased plant productivity [Cayan et al. 2001], earlier peak streamflows [Stewart et al. 2005], consecutive 100-year flood events during the wettest decade in the past three centuries [Graumlich et al. 2003]) represent biotic and abiotic factors that were not present and operating on the landscape at any time over the past century and may have allowed for the height release of willows in the northern range.

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 1998 has, in turn, likely allowed for greater bird richness, abundance, diversity, and abundance of six of the seven focal species studied in the northern range. The increase in willow height has been attributed to a variety of factors, including a wolf-induced trophic cascade, beaver recolonization, climatic changes, or an interaction among these. Regardless of the drivers of willow height release, this study provides the first evidence of the effects of the willow height release on other taxonomic groups. This is especially important, considering the substantial loss of this habitat type at lower elevations, and emphasizes the importance of maintaining ecosystem processes within protected areas.

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APPENDIX

Bird species observed in suppressed, released, and previously tall growth conditions in and around Yellowstone National Park's northern range (*Ecological Archives* A021-103-A1).