

ASPEN AND CONIFER HETEROGENEITY EFFECTS ON BIRD DIVERSITY IN THE NORTHERN YELLOWSTONE ECOSYSTEM

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ABSTRACT.—We addressed the following question: Do conifers within aspen stands (conifer invasion) increase bird species diversity in western landscapes? We tested the hypotheses that bird species diversity, measured as species richness or with the Shannon-Weiner diversity index, responds to aspen-conifer ratios (from 0% to 100% conifer) in a quadratic manner with a maximum occurring at an intermediate ratio of aspen and conifer. Extra sum-of-squares *F* tests comparing quadratic with linear models suggested that migratory bird diversity was inversely linearly related to the extent of conifer invasion. These linear responses were moderate (species richness: $R^2 \geq 0.34$, $P < 0.01$; Shannon-Weiner diversity index: $R^2 \geq 0.34$, $P < 0.01$). Resident species diversity appeared quadratically related to conifer invasion. However, variation was poorly described for species richness ($R^2 \leq 0.13$, $P \geq 0.09$) and was marginal for the Shannon-Weiner diversity index ($R^2 \leq 0.27$, $P \leq 0.01$). We concluded that mixed aspen-conifer stands do not have higher bird species diversity than pure aspen stands and that management activities should focus on heavily conifer-invaded stands to increase bird diversity in western landscapes and help reverse the decline of aspen habitat due to conifer invasion.

Key words: aspen, bird species diversity, conifer invasion, Yellowstone ecosystem.

Aspen (*Populus tremuloides*) is considered important habitat for avifauna, supporting species diversity frequently not found in the respective matrix habitats (Salt 1957, Flack 1976, Winternitz 1980, DeByle 1985). For the western United States, Winternitz (1980) suggests that the deciduous nature and short lifespan of aspen, combined with the relatively distinct understory and moisture associated with aspen-suitable sites, account for a greater bird diversity than that found in surrounding conifer habitat. Flack (1976) makes a similar suggestion for aspen occurring in both the mountainous western United States and the central Canadian parklands. Aspen appears to be significant bird habitat as widely scattered, isolated patches (Griffis-Kyle and Beier 2003) and when it occurs in matrix habitats such as conifer forest (Finch and Reynolds 1987) or sagebrush steppe (Dobkin et al. 1995).

Aspen in the western U.S. is presently in decline (Romme et al. 1995, Kay 1997, Bartos 2001). Hypotheses proposed to explain the decline include climate change, interruption of natural disturbance regimes, and increased browsing by native ungulates and/or domestic livestock (Bartos 2001). Increased browsing intensity and changes in disturbance regime are the most likely mechanisms according to

most aspen ecologists (see Romme et al. 1995 for a discussion of these hypotheses). In the western U.S., the interruption of natural disturbance regimes often leads to “conifer invasion,” a process by which conifers develop within aspen stands and eventually grow to overtop and shade out canopy-height aspen (Bartos and Campbell 1998, Smith and Smith 2005). Natural disturbance, typically fire, kills conifers and stimulates the vigorous resprouting of aspen suckers once the fire has passed. Thus, aspen stands remain dominant and persistent. In the absence of fire, conifers may eventually replace aspen. This has led some land managers to view conifer invasion as detrimental to maintaining biodiversity associated with aspen habitat.

DeByle (1985) suggested that aspen stands with conifers present may sustain higher bird diversity than pure aspen stands due to greater habitat heterogeneity. The basis for this hypothesis is well founded: conifers within aspen stands introduce structural and floristic complexity. Numerous researchers report relationships between bird species richness and habitat heterogeneity, in terms of both vegetative species composition and structure (MacArthur and MacArthur 1961, Anderson and Shugart 1974, Freemark and Merriam 1986). For example,

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Scott et al. (2003) found significant relationships between avian diversity and habitat structure among riparian cottonwood (*P. trichocarpa*, a congener of aspen) patches along the Missouri River north of the Yellowstone ecosystem (Scott et al. 2003). Therefore, it seems reasonable that some level of conifer invasion in aspen stands (habitat heterogeneity) may provide for increased bird diversity.

Few studies have addressed the relationship between bird diversity and aspen-conifer heterogeneity in the western U.S. The most relevant, Rumble et al. (2001), focused on this relationship in ponderosa pine (*Pinus ponderosa*) forests of the Black Hills, South Dakota, where management objectives prompted the evaluation of aspen retention policies in the context of biodiversity goals. These researchers considered 4 groups of habitat: pure aspen, aspen-dominated (>50% aspen), conifer-dominated (<50% aspen), and pure conifer. They found significantly higher bird diversity in the combined groups of pure aspen and aspen-dominated stands than in the combined groups of conifer-dominated and pure conifer stands, but did not find higher bird diversity among aspen-dominated stands as suggested by DeByle (1985).

Finch and Reynolds (1987) found a pattern similar to that found by Rumble et al. (2001) for bird species richness among mixed aspen-conifer and pure aspen stands located near the border of Colorado and Wyoming. However, species richness in pure conifer was not significantly lower than that found in mixed aspen-conifer stands, whereas species richness was significantly lower in pure conifer stands than in pure aspen stands. This suggests a moderate downward trend in species richness as stand composition varies from pure aspen to pure conifer with no increase for intermediate composition.

In a study motivated by conifer invasion in Rocky Mountain National Park, Turchi et al. (1995) found significantly higher bird species richness in aspen than in surrounding conifer habitat. They did not specifically address conifers within aspen patches, but did find a relationship between shrub cover (structural complexity) and bird diversity among the aspen patches studied. Furthermore, they found no significant relationship between bird diversity and aspen patch area or patch isolation.

In the parklands of Alberta, Canada, Schieck and Nietfeld (1995) found higher bird diversity in old (≥ 120 -year-old) aspen stands compared with young (20–30-year-old) and mature (50–65-year-old) stands. The authors attribute greater bird species richness to spatial structure, including structure provided by conifers, which are typically found in old stands. However, several variables contributing to stand structure also varied with stand age. Hobson and Bayne (2000b) found older stands of aspen to have higher bird diversity in Saskatchewan, Canada. In this context, they found that aspen stands with conifers had greater use by bird species that are normally associated with conifers, such as the Ruby-crowned Kinglet (*Regulus calendula*) and the Magnolia Warbler (*Dendroica magnolia*; Hobson and Bayne 2000b). Though they noted the importance of conifers, their analysis also identified canopy structure, understory shrub density, shrub composition, and ground cover as important. Machtans and Latour (2003) reported higher bird species richness in “mixedwoods” than in either pure deciduous or conifer forests in Liard Valley, Northwest Territories.

Knowing how avian diversity varies with conifer presence among montane aspen in the western U.S. is essential for informed management policy. Land managers need to know if, and how much, conifer retention will help them achieve biodiversity goals. Ratios of conifer and aspen canopy cover, or basal area, may provide convenient measures of aspen habitat quality for managers charged with maintaining or increasing bird diversity. The goal of this study was to describe and assess the effect of conifer invasion on avian diversity among aspen stands in the northern ungulate range of the northern Yellowstone ecosystem. Consequently, we considered 2 hypothetical relationships (quadratic and linear) between bird diversity and increasing conifer presence and compared the fit of these hypothesized models to field data. A positive effect of conifer invasion was expected to result in the better fit of a quadratic model that exhibits a maximum at an intermediate level of conifer presence. Conversely, we expected a better fit for the direct linear model in the absence of a positive conifer invasion effect. Specific objectives were to (1) relate aspen-conifer heterogeneity (ratios of conifer and aspen basal area

and canopy cover) to migratory and resident avian species richness, (2) determine the above relationships substituting the Shannon-Weiner diversity index (Margalef 1958) for species richness to mediate the effect of rare species, and (3) evaluate the effect of conifer invasion by comparing the relative fit of quadratic and linear models for each combination of heterogeneity and diversity response described above.

STUDY AREA

The 153,700-ha northern ungulate winter range of the northern Yellowstone ecosystem extends from Dome Mountain in the Gallatin National Forest southeast to the Lamar Valley in Yellowstone National Park (YNP), USA. Approximately two-thirds of the range is within YNP and the remaining one-third is in the Gallatin National Forest. A few small private holdings occur within the Gallatin National Forest (Lemke et al. 1998).

Elevation in the study area ranged from 1560 m to 2350 m. Region-wide average annual precipitation was $40 \text{ cm} \cdot \text{yr}^{-1}$. Higher elevations received more precipitation (up to $66 \text{ cm} \cdot \text{yr}^{-1}$) than lower elevations (as little as $25 \text{ cm} \cdot \text{yr}^{-1}$; Western Regional Climate Center 2004). Landform and vegetation were typical of the central Rocky Mountains, with valleys formed during the Wisconsin glacial period. Benches and playas formed by ancient lahar flows occurred southwest of the Yellowstone River near Gardner, Montana. Lodgepole pine (*Pinus contorta*) was the dominant vegetation at higher elevations, particularly where soils were poor, and Douglas-fir (*Pseudotsuga menziesii*) and Engelman spruce (*Picea englemanni*) occurred where conditions were suitable. A transition zone occurred at approximately 2200 m elevation where conifer-dominated forest gave way to steppe dominated by sagebrush (*Artemisia* spp.) and grasses, including Idaho fescue (*Festuca idahoensis*), and timothy (*Phleum pratense*). Aspen occurred in a patchy spatial distribution throughout the transition zone and steppe at sites where moisture conditions were favorable.

Within YNP, the northern ungulate range is managed as a natural preserve. The national forest portion of the northern ungulate range is managed for elk winter range and human recreation (including hunting), with limited resource extraction and livestock grazing (Lemke

et al. 1998). Thus, general landscape patterns of vegetation were relatively consistent throughout the study area, but management differed regarding elk hunting between YNP and national forest portions of the range.

METHODS

Vegetation

We selected 32 aspen patches from an existing map (St. John 1995) and from aerial photographs (acquired during 1994) that covered gaps in map coverage. Thirty patches were identified in 2001 and 2 more added in 2002. Patch locations were constrained to $\geq 100 \text{ m}$ from primary roads and $\leq 1 \text{ km}$ from a road (primary or secondary) or main trail. We defined aspen patches as contiguous areas of aspen stems with canopy cover $\geq 50\%$ at the time of mapping or delineation, and $\geq 100 \text{ m}$ apart. Many stands have since changed in composition and may have contained less aspen canopy cover at the time of this study. We later confirmed during sampling that conifer invasion had occurred in some of the selected patches such that a full range of conifer invasion conditions existed in the patches. Patches were randomly selected from the population of patches meeting the previously mentioned criteria. However, 5 of these patches were either misidentified or no longer extant; we chose a replacement for each by identifying the nearest extant patch that satisfied location criteria.

We established 6 conifer sites in pure conifer habitat during June 2002. These were spatially distributed throughout the study area so that 3 were inside YNP and 3 were outside. Each site was located, as a point, within 1 km of a previously selected aspen patch. For each of 3 evenly spaced patches inside and outside YNP, we used digital orthophotographs in a geographic information system to select the first random point produced by a random point generator that met the criteria for pure conifer. We defined pure conifer as $\geq 50\%$ canopy cover with no other hardwood tree species present in a 100-m radius, and we evaluated pure conifer status using aerial photographs.

Within each aspen patch, we measured basal area of aspen and conifer stems $\geq 5 \text{ cm}$ in diameter at breast height (dbh). We also determined canopy cover for aspen and conifer separately. We used a 5-point sampling pattern,

TABLE 1. Characteristics of aspen patches and conifer sites sampled in the northern ungulate winter range, Yellowstone ecosystem. CCR—canopy cover ratio (conifer/aspen), BAR—basal area ratio (conifer/aspen).

| Variable | \bar{x} | $s_{\bar{x}}$ | Range |
|--|-----------|---------------|----------|
| ASPEN PATCHES ($n = 34$) | | | |
| Patch size (ha) | 1.4 | 0.53 | 0.2–16.7 |
| Aspen canopy cover (%) | 73.1 | 2.78 | 31–100 |
| Conifer canopy cover (%) | 9.3 | 2.24 | 0–60 |
| Aspen basal area ($\text{m}^2 \cdot \text{ha}^{-1}$) | 33.9 | 2.97 | 11–83 |
| Conifer basal area ($\text{m}^2 \cdot \text{ha}^{-1}$) | 3.7 | 0.69 | 0–10 |
| CONIFER SITES ($n = 6$) | | | |
| Canopy cover (%) | 95.1 | 1.95 | 88–99 |
| Basal area ($\text{m}^2 \cdot \text{ha}^{-1}$) | 54.1 | 2.92 | 41–60 |
| DERIVED VARIABLES ($n = 40$) | | | |
| CCR (canopy cover ratio) | 0.27 | 0.36 | 0–1 |
| BAR (basal area ratio) | 0.28 | 0.35 | 0–1 |

initiated at the patch centroid with 4 points positioned 25 m distant in each cardinal direction. No vegetation sampling was done for points that fell outside the patch. We used the same protocol for conifer sites and limited our sampling to points that occurred within conifer habitat. We used a point sampling technique with a 5, 10, or 20 basal area factor (BAF) prism to measure basal area (Dilworth and Bell 1985). The BAF that included approximately 8–12 trees at the patch centroid was used for all subsequent sampling within a given patch (Wensel et al. 1980). Canopy cover was measured using a mirror densiometer. Because birds may respond to either basal area or canopy cover, we derived 2 variables to represent the relative contribution of aspen and conifers to habitat heterogeneity: the ratio of conifer basal area to aspen basal area (BAR), and conifer canopy cover to aspen canopy cover (CCR). See Table 1 for a summary of patch characteristics.

Bird Sampling

We conducted point counts during the breeding season (30 May–1 July) in 3 years, 2001–2003. Counts were 6 minutes in duration and we used a modified protocol outlined in Ralph et al. (1995). All birds within a 50-m radius were tallied and their species and nesting behavior noted. Species were categorized as migratory or resident (McEneaney 1996). Detections known to be outside an aspen patch boundary were flagged for omission from the analysis. Flyovers were not counted unless the birds were considered to be using the habitat (aspen patch or conifer site) for foraging. Examples include Tree Swallow (*Tachycineta*

bicolor) or Common Nighthawk (*Chordeiles minor*) foraging >10 m above the canopy. Counts were not conducted during heavy precipitation or windy conditions ($>16 \text{ km} \cdot \text{hr}^{-1}$), but were not constrained by cloud cover. Finch and Reynolds (1987) found detection rates for common species to be similar among aspen, mixed, and conifer stands in Wyoming and Colorado; and Shieck and Nietfeld (1995), using a 50-m count radius, found similar detectability among aspen stands of various ages in Alberta. Thus, we assumed bird detectability was similar among sites in this study.

Each aspen patch was sampled 3 times during 2001 and 2002, and twice during 2003. Conifer sites were sampled 3 times during 2002 and twice during 2003. Within aspen patches, 1 count was done at the patch centroid and additional counts were done in larger patches (1 additional count for each 5 ha). These additional counts were positioned 100 m from the centroid point along the major geographic axis of the patch. Only 2 patches were >5 ha. Using the protocol described previously, we collected vegetation data at these additional points and used within-patch average values for analysis. Additionally, we averaged bird count data for patches with >1 point count station.

We sampled spatially clustered groups of 3–5 aspen patches and/or conifer sites daily during morning hours (sunrise–10:30 AM); an initial patch was randomly chosen, and each nearest patch was sampled consecutively as time permitted. This approach varied the order of sampling and was assumed to reduce time-of-day bias. All bird sampling was done by 1 observer.

Data Analysis

Because migratory birds are often the focus of management directives (Rich et al. 2004), we parsed bird observations into migratory and resident categories, and calculated the mean species richness per year per site. Per-site Shannon-Weiner diversity indices were calculated for migrants and residents using observations from all years combined. The Shannon-Wiener diversity index is a measure of heterogeneity that incorporates species richness and evenness. Relative to other diversity indices, such as Simpson's index, it is considered sensitive to the inclusion of rare species (Krebs 1989). Thus, we attempted to reduce the disproportionate effect of a few rare observations (as with species richness) and maintain a level of sensitivity appropriate to our analysis.

We evaluated response variables for normality and constant variance by examining residual plots resulting from both linear and quadratic regressions. A natural-log transformation was applied to species richness. Transformation of the Shannon-Weiner diversity index was not indicated. We followed the guidelines used by Schieck and Niefert (1995) and considered regression coefficients (R^2) of 0.30–0.50 to be moderate correlation, and those >0.50 to be strong correlation. All regression models and model comparisons were considered significant at $P \leq 0.05$. We used S-Plus statistical software for all analyses (Insightful 2001).

For both measures of conifer invasion (CCR and BAR), we modeled the quadratic response hypothesis as

$$\text{Diversity} = \beta_0 + \beta_1x - \beta_2x^2,$$

where β_1 is positive and β_2 is negative. The null hypothesis of a direct linear response with a negative slope was expressed as

$$\text{Diversity} = \beta_0 - \beta_1x.$$

We performed quadratic and linear regression for each of the following combinations: (1) CCR on migrant and resident species richness, (2) BAR on migrant and resident species richness, (3) CCR on migrant and resident diversity index, and (4) BAR on migrant and resident diversity index. For each combination of diversity measure and migrant status, we used likelihood-ratio tests to compare the quadratic (full) and linear (reduced) models. If a

linear model was found to be the better representation of the data (fit and parsimony), we concluded that there was no significant positive response of species diversity at intermediate values of aspen-conifer heterogeneity. We used least squares regression to fit models to our data and the extra sum-of-squares F test (a likelihood-ratio test) for model comparisons (Ramsey and Schafer 1997). Lack-of-fit tests were not attempted due to insufficient repeated observations among the range of aspen-conifer heterogeneity levels.

RESULTS

We detected 2648 birds representing 54 species (42 migratory, 12 resident); 42% of detections occurred in sites with $<10\%$ BAR (pure aspen) and 3% in sites with $>90\%$ BAR (pure conifer). Observations of long-distance (neotropical) and short-distance migratory species outnumbered residents by 3.5 times. This is consistent with previous studies extolling the value of aspen as breeding habitat for migrants. Resident species in the northern ungulate range are generally considered habitat generalists (e.g., Common Raven [*Corvus corax*]) or are typically associated with conifer habitat (e.g., Mountain Chickadee [*Poecile gambeli*]; see Appendix for a list of species detected). Mean annual species richness (untransformed) ranged from 1.5 to 7.89 for migrants and from 0.11 to 1.67 for residents. Shannon-Wiener index values ranged from 1.09 to 2.7 for migrants and from 0 to 1.51 for residents.

Both linear and quadratic models moderately explained variability in migratory species richness or Shannon-Weiner diversity ($R^2 \geq 0.34$) with respect to CCR and BAR (Table 2). For migratory birds, direct linear models performed better than quadratic models for each combination of species diversity measure and habitat heterogeneity (Table 2). These direct linear models described a moderate negative relationship between species diversity and increasing conifer presence. The quadratic models for migratory species richness had negative coefficients for β_1 indicating no increase in species richness over the range of habitat heterogeneity. The quadratic models for the Shannon-Weiner diversity index had positive coefficients for β_1 , but were not significantly better than the reduced linear models (Table 2).

TABLE 2. Models of migratory bird species diversity as a function of aspen-conifer ratio. Sp Rich—species richness, SW index—Shannon-Weiner diversity index, CCR—canopy cover ratio (conifer/aspen), BAR—basal area ratio (conifer/aspen). Model comparisons are extra sum-of-squares F tests ($df = 1$ and 35 for all comparisons).

| Model | R^2 | P -value | Model comparison | |
|--|-------|------------|------------------|------------|
| | | | $F_{1,35}$ | P -value |
| $\ln(\text{Sp Rich}) = 1.50 - 0.28(\text{CCR}) - 0.42(\text{CCR})^2$ | 0.35 | 0.0006 | | |
| $\ln(\text{Sp Rich}) = 1.53 - 0.69(\text{CCR})$ | 0.34 | 0.0001 | 0.36 | 0.55 |
| $\ln(\text{Sp Rich}) = 1.53 - 0.54(\text{BAR}) - 0.21(\text{BAR})^2$ | 0.38 | 0.0002 | | |
| $\ln(\text{Sp Rich}) = 1.54 - 0.75(\text{BAR})$ | 0.38 | 0.00004 | 0.11 | 0.75 |
| $\text{SW index} = 2.22 + 0.36(\text{CCR}) - 1.01(\text{CCR})^2$ | 0.39 | 0.0002 | | |
| $\text{SW index} = 2.29 - 0.65(\text{CCR})$ | 0.34 | 0.0001 | 2.60 | 0.12 |
| $\text{SW index} = 2.25 + 0.07(\text{BAR}) - 0.81(\text{BAR})^2$ | 0.46 | 0.00002 | | |
| $\text{SW index} = 2.31 - 0.73(\text{BAR})$ | 0.43 | 0.00001 | 2.01 | 0.16 |

TABLE 3. Models of resident bird species diversity as a function of aspen-conifer ratio. Sp Rich—species richness, SW index—Shannon-Weiner diversity index, CCR—canopy cover ratio (conifer/aspen), BAR—basal area ratio (conifer/aspen). Model comparisons are extra sum-of-squares F tests ($df = 1$ and 35 for all comparisons).

| Model | R^2 | P -value | Model comparison | |
|---|-------|------------|------------------|------------|
| | | | $F_{1,35}$ | P -value |
| $\ln(\text{Sp Rich}) = -0.57 + 2.68(\text{CCR}) - 2.75(\text{CCR})^2$ | 0.13 | 0.09 | | |
| $\ln(\text{Sp Rich}) = -0.38 - 0.04(\text{CCR})$ | 0.001 | 0.89 | 5.15 | 0.03 |
| $\ln(\text{Sp Rich}) = -0.50 + 1.90(\text{BAR}) - 2.12(\text{BAR})^2$ | 0.10 | 0.17 | | |
| $\ln(\text{Sp Rich}) = -0.33 - 0.21(\text{BAR})$ | 0.01 | 0.48 | 3.20 | 0.08 |
| $\text{SW index} = 0.89 + 1.69(\text{CCR}) - 2.08(\text{CCR})^2$ | 0.27 | 0.004 | | |
| $\text{SW index} = 1.03 - 0.36(\text{CCR})$ | 0.10 | 0.05 | 8.32 | 0.007 |
| $\text{SW index} = 0.90 + 1.41(\text{BAR}) - 1.81(\text{BAR})^2$ | 0.25 | 0.006 | | |
| $\text{SW index} = 1.04 - 0.39(\text{BAR})$ | 0.11 | 0.04 | 6.71 | 0.01 |

Most of the quadratic models of resident bird species richness or Shannon-Weiner diversity were better than direct linear models (Table 3). All resident bird models had poor or marginal coefficients of determination, suggesting no relationship between CCR or BAR and resident bird species richness ($R^2 \leq 0.13$), and a weak quadratic relationship between CCR or BAR and Shannon-Weiner diversity index ($R^2 \leq 0.27$).

DISCUSSION

We found a moderate negative linear relationship between migratory bird species diversity (both species richness and Shannon-Weiner index) and conifer presence, with the greatest diversity occurring in pure aspen. This is consistent with other western U.S. studies (Finch and Reynolds 1987, Rumble et al. 2001). We found no relationship between conifer presence and resident bird species richness, but Shannon-Weiner index values for

residents suggested a weak increase of diversity at intermediate levels of conifer presence. These findings are limited to the breeding season. Different relationships between conifers in aspen and bird diversity may occur during winter when migrants are absent, as well as during spring or fall when itinerant migrants are moving through the region. Another limitation of our analyses is the unequal sampling of aspen and conifer patches/sites across years. Although the response has been standardized (diversity $\cdot \text{year}^{-1} \text{site}^{-1}$), aspen patches and conifer sites were sampled for 3 and 2 years, respectively, and bias from unequal sampling effort may be present.

As expected, BAR and CCR were highly correlated ($r = 0.92$). Models for each were considered because it was unknown whether birds use canopy or boles as cues for habitat assessment. The similar performance of models containing BAR and CCR confirms the usefulness of either as measures of habitat heterogeneity by land managers. However, CCR

is an easier variable to measure in the field. High correlation between species richness and the Shannon-Weiner diversity index ($r = 0.87$, all species) suggests that few rare species were included in our samples. Indeed, we detected species typical for the northern ungulate range (McEneaney 1996), and few rarities were noted in the field.

The Shannon-Wiener index model for residents indicated a quadratic response to conifer invasion. This may be misleading. European Starlings (*Sturnus vulgaris*) were very abundant in 3 aspen patches that contained few to no conifers. The Shannon-Wiener index, which incorporates both species evenness and richness, may have assigned lower index values for these patches than for patches without starlings due to the relative lack of evenness, resulting in the appearance that pure aspen stands were relatively less diverse than invaded stands. Knopf and Samson (1994) are critical of diversity indices that are insensitive to species composition due to the risk of including exotic or regionally common species. The discussion about starlings underscores this criticism, and we advise managers to collect species-specific information when assessing biodiversity.

Rumble et al. (2001) concluded that the co-occurrence of "conifer" and "aspen" bird species in heterogeneous sites constitutes alpha (local-scale) diversity, which may not be an appropriate approach to measuring bird diversity in aspen habitat since it does not reflect an increase in beta diversity (landscape scale). We acknowledge this, but find that in the northern Yellowstone ecosystem, because aspens occur as discrete patches in the landscape, it may be useful to approach these patches as potential management units, each with unique attributes, including species diversity provided by conifers present within them. Furthermore, Samson and Knopf (1993) urge managers and conservationists to consider both alpha and beta diversity across the landscape, with an emphasis on beta diversity. Consequently, it seems appropriate to manage aspen and its matrix habitats such that the unique diversity of each is maximized. Currently, conifer and steppe habitats appear to be abundant and stable in Yellowstone's northern range, but aspen comprises only about 2% of the vegetative land cover (Despain 1990) and is in decline (Larsen and Ripple 2003). Many land-

scapes in the Intermountain U.S. have similar relative habitat compositions and are experiencing aspen decline (Barnett and Stohlgren 2001, Bartos 2001). Thus, it would appear that managers in the western U.S. should focus on restoration and maintenance of pure aspen in the landscape. Such actions would likely benefit the diversity of other taxa as well (e.g., Chong et al. 2001).

Samson and Knopf (1993) also suggest that managers focus on the restoration or conservation of ecological processes as a means of managing for biodiversity. The decline of aspen in western landscapes has been attributed to the disruption of 1 or more ecological processes, namely conifer invasion resulting from fire suppression and heavy browsing pressure from increasing ungulate populations (Romme et al. 1995, Ripple and Larsen 2000, Bartos 2001). Site-specific aspen restoration has met with mixed success (see Shirley and Erickson 2001). However, studies demonstrating stand-level processes, such as coarse woody debris ("jack-straw") refugia (Ripple and Larsen 2001), and ecosystem-level processes, such as the trophic cascade effect of wolf reintroduction (Ripple and Larsen 2000, Hebblewhite et al. 2005), appear promising.

Bird diversity in aspen does not appear to increase with conifer invasion in the Intermountain West. (Finch and Reynolds 1987, Rumble et al. 2001). However, there is some evidence for greater bird diversity in "mixed-woods" of the boreal forests and aspen parklands of central Canada (Schieck and Nietfeld 1995, Hobson and Bayne 2000b, Machtans and Latour 2003). This may be due to regional differences in the relative composition of habitats. Aspen typically comprise <5% of the vegetative cover in western U.S. landscapes (Barnett and Stohlgren 2001), but may represent >20% of vegetative cover in the aspen parklands of central Canada. However, the evidence is equivocal. Hobson and Bayne (2000a) found that mixed-species forests in central Saskatchewan supported higher bird diversity generally, but when aspen habitat was considered alone, pure aspen stands supported higher diversity than combinations of aspen and any of the other tree species considered in their analysis. The authors suggested that shrub cover in pure aspen, used by ground-nesting species less common in other stand types, may account for the observed pattern.

CONCLUSIONS

We conclude that the presence of conifers in aspen stands does not significantly increase bird diversity in the northern Yellowstone ecosystem, and that aspen appears to be a high-value habitat for migratory birds. Consequently, land managers may effect positive responses in bird diversity by following the guidelines presented by Campbell and Bartos (2001) and by selecting heavily invaded stands (>50% conifer canopy) for restoration. Reducing conifer invasion in these stands may simultaneously address the decline in aspen condition and increase stand- and landscape-scale bird diversity. A technique that may accomplish these goals in the presence of heavy ungulate browsing pressure, as occurs in Yellowstone's northern range, involves killing and felling invading conifers so that they lie in "jackstraw" piles within the aspen stand (e.g., Ripple and Larsen 2001). The immediate effect of killing these conifers is a change in the ratio of aspen canopy to conifer canopy. It is unknown when bird diversity would respond to these treatments. Long-term stand condition should improve as regenerating suckers, protected from browsing by jackstraw refugia, grow to "escape height," at which browsing mortality is less, and eventually recruit into the overstory (Ripple and Larsen 2001). As aspen dominance increases at these sites, it is likely that increased bird diversity would follow.

ACKNOWLEDGMENTS

We thank Jennifer Gervais, Betsy Glenn, Vicky Hollenbeck, and 2 anonymous reviewers for thoughtful reviews. We also thank Roy Renkin of the Yellowstone Center for Resources, and Dan Tyers of the Gallatin National Forest, Gardner District, for data and logistical support. Funding was provided by the National Science Foundation, Landscape Studies Fellowship 9452810-GER.

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Received 22 August 2005

Accepted 5 June 2006

APPENDIX. Species detected on the northern ungulate range of the Greater Yellowstone Ecosystem during June 2001, June 2002, and June 2003. N = relative abundance (% of total individuals detected); migrant status follows McEneaney (1996). YNP—Yellowstone National Park, GNF—Gallatin National Forest.

| Species | | N (%) | Migrant | YNP | GNF |
|------------------------|-------------------------------|-------|---------|-----|-----|
| American Kestrel | <i>Falco sparverius</i> | 1.4 | Y | X | X |
| American Robin | <i>Turdus migratorius</i> | 8.6 | Y | X | X |
| Belted Kingfisher | <i>Ceryle alcyon</i> | 0.04 | N | X | |
| Black-billed Magpie | <i>Pica pica</i> | 0.5 | N | X | X |
| Black-capped Chickadee | <i>Poecile atricapilla</i> | 2.4 | N | X | X |
| Brewer's Blackbird | <i>Euphagus cyanocephalus</i> | 1.5 | Y | X | X |
| Brown-headed Cowbird | <i>Molothrus ater</i> | 1.1 | Y | X | X |
| Cassin's Finch | <i>Carpodacus cassinii</i> | 0.04 | Y | | X |
| Chipping Sparrow | <i>Spizella passerina</i> | 1.3 | Y | X | X |
| Clark's Nutcracker | <i>Nucifraga columbiana</i> | 0.4 | N | X | X |
| Cliff Swallow | <i>Hirundo pyrrhonota</i> | 0.04 | Y | | X |
| Common Raven | <i>Corvus corax</i> | 0.4 | N | X | X |
| Common Yellowthroat | <i>Geothlypis trichas</i> | 0.8 | Y | X | X |
| Dark-eyed Junco | <i>Juncos hyemalis</i> | 1.5 | Y | X | X |
| Downy Woodpecker | <i>Picoides pubescens</i> | 0.4 | N | X | X |
| Dusky Flycatcher | <i>Empidonax oberholseri</i> | 1.5 | Y | X | X |
| European Starling | <i>Sturnus vulgaris</i> | 2.9 | N | X | X |
| Green-tailed Towhee | <i>Pipilo chlorurus</i> | 0.3 | Y | | X |
| Hairy Woodpecker | <i>Picoides villosus</i> | 0.5 | N | X | X |
| Hammond's Flycatcher | <i>Empidonax hammondi</i> | 2.8 | Y | X | X |
| House Wren | <i>Troglodytes aedon</i> | 6.2 | Y | X | X |
| Indigo Bunting | <i>Passerina cyanea</i> | 0.1 | Y | | X |
| Lazuli Bunting | <i>Passerina amoena</i> | 3.8 | Y | X | X |
| Lincoln's Sparrow | <i>Melospiza lincolnii</i> | 3.7 | Y | X | X |
| McGillivray's Warbler | <i>Oporornis tolmiei</i> | 1.9 | Y | X | X |
| Mountain Bluebird | <i>Sialia currucoides</i> | 2.9 | Y | X | X |
| Mountain Chickadee | <i>Poecile gambeli</i> | 5.0 | N | X | X |
| Mourning Dove | <i>Zenaida macroura</i> | 0.1 | Y | X | X |
| Northern Flicker | <i>Colaptes auratus</i> | 7.1 | Y | X | X |
| Olive-sided Flycatcher | <i>Contopus cooperi</i> | 0.08 | Y | X | |
| Orange-crowned Warbler | <i>Vermivora celata</i> | 0.3 | Y | X | X |
| Pine Siskin | <i>Carduelis pinus</i> | 6.8 | Y | X | X |
| Red Crossbill | <i>Loxia curvirostra</i> | 0.6 | N | X | |
| Red-breasted Nuthatch | <i>Sitta canadensis</i> | 2.9 | N | X | X |
| Red-naped Sapsucker | <i>Sphyrapicus nuchalis</i> | 2.2 | Y | X | X |
| Red-tailed Hawk | <i>Buteo jamaicensis</i> | 0.5 | Y | X | X |
| Red-winged Blackbird | <i>Agelaius phoeniceus</i> | 0.04 | Y | X | |
| Ruby-crowned Kinglet | <i>Regulus calendula</i> | 0.9 | Y | X | X |
| Ruffed Grouse | <i>Bonasa umbella</i> | 0.2 | N | | X |
| Sandhill Crane | <i>Grus canadensis</i> | 0.04 | Y | X | |
| Sharp-shinned Hawk | <i>Accipiter striatus</i> | 0.04 | Y | | X |
| Song Sparrow | <i>Melospiza melodia</i> | 0.2 | Y | | X |
| Stellar's Jay | <i>Cyanocitta stelleri</i> | 0.2 | N | | X |
| Tree Swallow | <i>Tachycineta bicolor</i> | 1.5 | Y | X | X |
| Vesper Sparrow | <i>Poocetes gramineus</i> | 0.1 | Y | | X |
| Violet-green Swallow | <i>Tachycineta thalassina</i> | 2.6 | Y | X | X |
| Warbling Vireo | <i>Vireo gilvus</i> | 12.8 | Y | X | X |
| Western Meadowlark | <i>Sturnella neglecta</i> | 0.3 | Y | X | X |
| Western Tanager | <i>Piranga ludoviciana</i> | 0.8 | Y | X | X |
| Western Wood-Pewee | <i>Contopus sordidulus</i> | 0.5 | Y | X | X |
| Williamson's Sapsucker | <i>Sphyrapicus thyroideus</i> | 0.9 | Y | X | X |
| Willow Flycatcher | <i>Empidonax traillii</i> | 0.04 | Y | | X |
| Yellow Warbler | <i>Dendroica petechia</i> | 0.4 | Y | X | X |
| Yellow-rumped Warbler | <i>Dendroica coronata</i> | 1.1 | Y | X | X |