

Multi-scale Relationships Between Aspen and Birds in the Northern Yellowstone
Ecosystem.

by
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Abstract approved:

William J. Ripple

I conducted a multi-scale evaluation of aspen – bird relationships in the northern ungulate winter range of the northern Yellowstone ecosystem during June 2001-03. Questions addressed were: (1) Does bird diversity increase with conifer presence in aspen stands? (2) Given known habitat selection cues, are migrating birds passively intercepted by aspen patches oriented perpendicular to migratory direction of travel? (3) Are resident (short-distance migrant) birds passively intercepted by aspen patches? and (4) Given the dynamics of wolves, ungulates, and forage plants in the northern Yellowstone ecosystem, what is the present condition of aspen and cavity-nesting birds within Yellowstone National Park (YNP) and how will they change over the next 100+ years?

Regression analyses of migratory bird diversity (species richness or Shannon-Weiner index) on measures of habitat heterogeneity (ratio of conifer to aspen canopy cover, or basal area) suggested no positive relationship with intermediate levels of conifer presence. Migratory birds were most diverse in pure aspen, and least diverse in pure conifer. I found a weak, but significant, positive relationship between most measures of habitat heterogeneity and resident bird diversity. Many residents were habitat generalists or conifer-associated species. To maximize bird diversity and aspen, managers may want to manage for pure aspen stands in a matrix that includes conifer habitat.

Using model selection techniques, long-distance migratory birds did not show evidence of passive interception by aspen patches oriented against northerly or elevational direction of travel. Aspen patch area was most important for migratory birds, given the data and set of models analyzed. Resident (and short-distance migrant) birds showed a marked positive response to patch orientation relative to the elevational gradient of the northern range. Migratory birds appear not to be passively intercepted at high elevation sites such as YNP's northern range. Short distance migrants appear to be passively intercepted.

Northern range aspen stands within YNP have 10cm greater mean live and dead stem diameter, 80% more snags, and greater abundance of many cavity-nesting bird species than northern range stands outside YNP. These conditions fit a conceptual framework of interactions driven by a top-down ecosystem structure that predicts aspen and cavity-nester dynamics over several decades.

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Doctor of Philosophy dissertation of Jeff P. Hollenbeck presented on September 22, 2006.

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

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CONTRIBUTION OF AUTHORS

Dr. William J. Ripple assisted in the interpretation and review of data, and technical reviews of Chapters 1 through 3.

DEDICATION

To my wife and family, whose patience and support have allowed me to pursue my educational and personal goals.

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INTRODUCTION

Aspen (*Populus tremuloides*) is the most widely distributed tree species in North America and one of the most widely distributed deciduous tree species in the world (Jones 1985). Occurring in a variety of ecological settings where climate conditions are suitable, aspen typically prefer moist soils and cool winters. In the western United States and Canada, aspen habitat is disproportionately biologically diverse (Chong et al. 2001). Consequently, aspen habitat is considered ecologically very important among western landscapes, including those in the northern Yellowstone ecosystem. Aspen are dioecious and may reproduce sexually by seed, or asexually (clonally) by root suckers from extensive underground root systems. Seedling establishment is common in the eastern U.S. and Canada, but rare in the west, likely due to seasonal moisture conditions (Jones 1985). Aspen persist in western landscapes primarily as clones that regenerate via root suckers. Some western clones are estimated to be several thousand years old (Jelinski and Cheliak 1992). Aspen clones in the northern Yellowstone ecosystem typically regenerate asexually, although numerous seedlings were observed after extensive fires in 1988 (Romme et al. 1997).

Aspen habitat in the western United States is widely believed to be declining. Evaluation of historical and current distribution indicates losses of >90% of aspen cover in some western states (Bartos 2001b). This decline was first noted in the early-mid 20 century and has slowly become more apparent as aspen contract or even disappear from many western landscapes (e.g., Bartos and Campbell 1998; Di Orio et al. 2005). Most western U.S. and Canadian land management agencies have adopted strategies to address the issue of aspen decline. Public education programs have been instituted, restoration

efforts begun, and research to understand the cause or causes of decline is underway (e.g., Bartos 2001a; Shirley and Erickson 2001; National Research Council 2002). There has been considerable recent research investigating the decline of aspen habitat in the northern Yellowstone ecosystem (Kay 1990; Romme et al. 1995; Yellowstone National Park 1997; Ripple and Larsen 2000; National Research Council 2002; Larsen and Ripple 2005). A decline in aspen has been noted in portions of the northern ungulate winter range (hereafter referred to as northern range) of the northern Yellowstone ecosystem, an area that straddles the northern border of Yellowstone National Park. This area is of interest to aspen researchers since much of it is managed as a natural preserve.

Several mechanisms have been proposed to explain the decline of aspen habitat in the western U.S. Among them are climate change, invasive species, human-altered disturbance regimes, and intensive browsing by domestic and native ungulates. The latter two are favored hypotheses among aspen ecologists (e.g., Kaye et al. 2005).

Several decades of fire suppression has altered the natural disturbance regime in many western landscapes. Aspen appear to be well adapted to periodic fire disturbance that kills overstory competitors, primarily conifers (and overstory aspen stems as well). Following fire, the well-protected underground root system is stimulated to prolific regeneration of new suckers that grow to replace the previously existing stand in the absence of competitors. When conditions are favorable, young aspen can grow quickly to both replace canopy level stems lost during the disturbance, and shade slower growing competitors. In the absence of periodic fire disturbance, shade-tolerant conifers establish within aspen stands, grow, compete, and eventually shade out the remaining aspen canopy (Campbell and Bartos 2001). This process of conifer invasion may lead to the

total displacement of an aspen stand overstory over time. Long periods without disturbance allows invading conifers to dominate and shade young aspen suckers. Lack of new stem recruitment to replace older stems as they die may lead to the eventual death of the entire clone as the underground root system is no longer supported by above ground photosynthesis. Campbell and Bartos (2001) provided guidelines for evaluating the risk posed by invading conifers, and subsequent management priorities.

Ungulate browsing pressure has been shown to affect aspen regeneration, in many cases preventing regeneration completely (e.g., St. John 1995; Kay and Bartos 2000). Intense browsing by ungulates has been proposed as the most likely cause of aspen decline in the northern Yellowstone ecosystem. Within the northern range, a portion of the northern Yellowstone ecosystem that straddles the northern Yellowstone National Park border, there has been considerable research involving interactions between elk, the most abundant ungulate in the region, and forage plants including aspen (National Research Council 2002). Outside Yellowstone National Park, domestic cattle are also implicated in these interactions, both within the northern range (St. John 1995), and elsewhere in the western U.S. (Bartos 2001b). Native ungulate populations in much of North America appear to have increased in size and density during the last century. Deer and elk thrive in many western U.S. landscapes as their predators have been controlled or extirpated, and as human land use changes provide favorable conditions that support larger ungulate populations. In the northern Yellowstone ecosystem, the extirpation of wolves during the 1930's and the adoption of the hands-off "natural regulation" elk herd management policy by the National Park Service have allowed elk numbers to increase considerably (Lemke et al. 1998; Ripple and Larsen 2000).

Aspen habitat is considered very important for both migratory and resident species of birds during the breeding season. Aspen stands offer structure and food resources that are scarce or absent in the conifer, shrub steppe, or grassland habitats that typically comprise western landscapes (Winternitz 1980). Flack (1976) identified several bird species as “aspen obligates” which reflect the dependence these species have on aspen habitat. Water and abundant insects appear to be important, especially for long-distance (neotropical) migrant species during the breeding season (Winternitz 1980). While many species of canopy, shrub, and ground cup-nesting species are well represented in aspen habitat, cavity-nesting species are particularly dependent (e.g., Pinkowski 1981). Large diameter (>20cm) aspen stems are softer than other western tree species and are particularly vulnerable to fungal infection, particularly by aspen heartrot (*Fomes igniarius*) (Basham 1958). These stems, especially those weakened by heartrot, provide critical nesting habitat for primary, and ultimately, secondary cavity-nesting birds (Winternitz and Cahn 1983; Dobkin et al. 1995). The ecological relationships between western aspen and cavity-nesting birds may be quite strong, complex, and far-reaching (Daily et al. 1993).

Understanding relationships between birds and aspen habitat in the western U.S. is immensely helpful for the conservation of both of these important taxa. This is particularly true in the context of aspen decline. Birds likely interact with western aspen habitat at different spatial and temporal scales. Therefore, I evaluated the relationship between aspen habitat and birds in the northern Yellowstone ecosystem at different spatial and temporal scales as well as placing these interactions within the context of declining aspen habitat.

Chapter 1 addresses the fine-scale management question: Do conifers in aspen stands enhance bird diversity? In recognizing the process of conifer invasion, land managers are faced with decisions regarding which aspen stands should receive the focus of their restoration/management efforts. It has been suggested that aspen stands including some conifers present provide a more structurally and floristically diverse habitat which may lead to greater avian diversity within these stands (DeByle 1985). Conversely, allowing conifer invasion to proceed unchecked may accelerate the deterioration of the stand and may even jeopardize the persistence of the stand (Bartos and Campbell 1998). Therefore, it is useful to know if the hypothesized relationship between conifer presence and avian diversity is empirically supported.

Chapter 2 is a coarse-scale examination of aspen patch characteristics and their potential effect on the distribution of birds. The patchy distribution of aspen habitat in the northern range of the greater Yellowstone ecosystem provides an opportunity to better understand relationships between highly mobile organisms and patches of preferred, or required, habitat. Landscape-ecological theory posits a process of passive interception of migrating or dispersing organisms by patches; the level of which is thought to vary with patch characteristics (Forman and Godron 1986). The focus of this investigation is how two patch-level characteristics of aspen stands – patch area and orientation – influence the abundance and/or diversity of migratory bird species within those stands. Covariation of patch orientation and bird abundance/diversity suggest passive interception effects. The only study to date which addresses the effect of passive patch interception of migratory birds (Gutzwiller and Anderson 1992) found greater cavity-nester abundance and diversity in habitat patches with a long axis oriented perpendicular to North-South.

They suggested migratory birds were apparently intercepted at a greater rate by patches oriented perpendicular to the direction of their spring migration. Gutzwiller and Anderson (1992) worked in riparian cottonwood-willow (*Populus-Salix* sp.) habitat in southeastern Wyoming. Cottonwood and aspen are congeneric and have very similar growth habits and structure. In some areas of the western U.S., where they co-occur, they may be largely ecological equivalents. However, Gutzwiller and Anderson (1992) conducted their study in a relatively low-elevation floodplain in southeastern Wyoming. The northern Yellowstone ecosystem is higher in elevation with greater topographic variation. This difference prompted a refinement in patch orientation measurement. Chapter 2 includes a second measure of patch orientation, relative to elevational gradient, in addition to patch orientation relative to true North. As with the previous chapter, knowing which landscape-level patch characteristics are associated with greater abundance or diversity of birds may help prioritize restoration or management efforts.

Chapter 3 is a coarse-scale, synthetic approach to understanding northern Yellowstone's aspen and cavity-nesting bird dynamics in the context of diverse ecosystem processes. Understanding the cascading relationships over several ecological levels over time may help to forecast changes in abundance of aspen-obligate birds, especially cavity-nesting species.

Wolves were re-introduced to the Yellowstone ecosystem in 1995. During the period between ~1930, when wolves were extirpated from the region, and 1995 changes were noted in the condition of vegetation on the northern range in the northern Yellowstone ecosystem (Kay 1990). Among those changes was a decline in aspen, willow, and cottonwood. During this period (1930-1968) elk numbers increased slightly.

Although wolf predation was eliminated, elk abundance was regulated by human hunting and culling by the National Park Service (Barmore Jr. 2003). Elk numbers increased considerably from 1968-1995 with the adoption of the “natural regulation” elk management policy by the National Park Service. During this time, elk were allowed to reach population sizes that were determined by habitat carrying capacity (Huff and Varley 1999). With the re-introduction of wolves in 1995, elk numbers in the northern range have decreased from ~17000 to ~8000 in 2004 (Vucetich et al. 2005).

With wolf re-introduction, it is reasonable to expect changes in the ecological interactions between predators, ungulate prey populations, forage plant populations, and ultimately bird populations. This perturbation (wolf re-introduction) will have lasting impacts on the eventual recovery of the entire ecosystem (Smith et al. 2003). The evidence for top-down structuring of the northern range ecosystem is considerable. Furthermore, the position of the northern range with portions inside and outside YNP allows comparison of aspen and cavity-nesting bird conditions in areas with different elk predation histories. It is in this context that chapter 3 seeks to establish the current position of aspen and cavity-nesting bird dynamics, and develop general predictions for these dynamics over time.

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**Aspen and Conifer Heterogeneity Effects on Bird Diversity in the Northern
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ABSTRACT

We addressed the 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 Shannon-Weiner diversity index, respond 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 inverse linearly related to the extent of conifer invasion. These linear responses were moderate ($R^2 \geq 0.34$, $p < 0.01$, species richness; $R^2 \geq 0.34$, $p < 0.01$, Shannon-Weiner diversity index). 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 marginal for Shannon-Weiner diversity index ($R^2 \leq 0.27$, $p \leq 0.01$). We conclude 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.

KEYWORDS: aspen, bird species diversity, conifer invasion, Yellowstone ecosystem

Aspen (*Populus tremuloides*) is considered important habitat for avifauna, supporting species diversity frequently not found in their respective matrix habitats (Salt 1957, Flack 1976, Winternitz 1980, DeByle 1985). For the western United States, Winternitz (1980) suggested that the deciduous nature and short lifespan of aspen,

combined with the relatively distinct understory and moisture associated with aspen-suitable sites, accounted for a greater bird diversity than that found in surrounding conifer habitat. Flack (1976) made a similar suggestion for aspen occurring in both the mountainous western U. S. 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 sage steppe (Dobkin et al. 1995).

Aspen in the western United States is presently thought to be 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 competing hypotheses). In the western U.S., the disruption of natural disturbance often leads to “conifer invasion”, a process where 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 re-sprouting of aspen suckers once the fire has passed. Thus, aspen stands remain dominant and persist. 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 studies have found relationships between bird species richness and habitat heterogeneity, both in terms of vegetative species composition and structure (MacArthur and MacArthur 1961, Anderson and Shugart 1974, Freemark and Merriam 1986). For example, 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 the 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. They 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-dominant stands than in the combined groups of conifer-dominant, 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 while 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+ yr.) aspen stands compared with young (20-30 yr.) and mature (50-65 yr.) stands. The authors attribute greater bird species richness to spatial structure, including that provided by conifers, 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 ruby-crowned kinglet (*Regulus calendula*) and magnolia warbler (*Dendroica magnolia*) (Hobson and Bayne 2000b). While noting 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, Canada.

Knowing how avian diversity varies with conifer presence among montane aspen in the western United States 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: (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; (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 National Forest (Lemke et al. 1998).

Elevation in the study area ranges from 1560 to 2350 m. Region-wide average annual precipitation is 40 cm/yr with higher elevations receiving more precipitation (up to 66 cm/yr) than lower elevations (as little as 25 cm/yr) (Western Regional Climate Center 2004). Landform and vegetation are typical for the central Rocky Mountains with valleys formed during the Wisconsin glacial period. Benches and playas formed by ancient lahar flows occur southwest of the Yellowstone River near Gardner, Montana. Lodgepole Pine (*Pinus contorta*) is the dominant vegetation at higher elevations, particularly where soils are poor, and Douglas-fir (*Pseudotsuga menziesii*) and Engleman Spruce (*Picea engelmanni*) occur where conditions are suitable. A transition zone occurs at approximately 2200 m elevation where conifer-dominated forest gives way to steppe dominated by sagebrush (*Artemisia* sp.) and grasses, including Idaho fescue (*Festuca idahoensis*), and timothy (*Phleum pratense*). Aspen occurs in a patchy spatial distribution throughout the transition zone and steppe, at sites where moisture conditions are 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 are relatively consistent throughout the study area but management differs 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 aerial photographs (acquired during 1994) where there were gaps in map coverage. Thirty patches were identified in 2001 and 2 more added in 2002. Patch locations were constrained to those ≥ 100 m from primary roads and ≤ 1 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 ≥ 100 m apart. Many stands had changed in composition since they were mapped and may have contained less aspen canopy cover at the time of this study. We later confirmed during sampling that conifer invasion had indeed occurred in some of the selected patches providing a full range of conifer invasion conditions. Patches were randomly selected from the population of patches meeting the previously mentioned criteria. However, 5 of these patches were either mis-identified or no longer extant and replacements were chosen as 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 within YNP and 3 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 pure conifer criteria. We defined pure conifer as 50% or greater canopy cover with no hardwood tree species present in a 100 m radius and evaluated pure conifer status using aerial photographs.

Within each aspen patch, we measured basal area of aspen and conifer stems ≥ 5 cm diameter at breast height (dbh), and canopy cover for aspen and conifer separately. We used a five-point sampling pattern, initiated at the patch centroid with 4 points positioned 25 m 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 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 two variables to represent the relative contribution of aspen and conifers to habitat heterogeneity: the ratio of aspen to conifer basal area (BAR), and aspen to conifer canopy cover (CCR). See Table 1.1 for a summary of patch characteristics.

Bird sampling

We conducted point counts each of 3 years, May 30 – July 1 (breeding season 2001-2003). Counts were 6 min in duration using 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 during analysis. Fly-overs were not counted unless they were considered to be using habitat (aspen patch or conifer site) for foraging. For example, a tree swallow (*Tachycineta bicolor*) or common nighthawk (*Chordeiles minor*) foraging > 10 m above the canopy would not be counted. Counts were not conducted during heavy precipitation or windy conditions (> 16 km/hr), 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; one additional count for each 5 ha. These additional counts were positioned 100 m from centroid point along the major geographic axis of the patch. Only two 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 to 5 aspen patches and/or conifer sites daily during morning hours (sunrise to 10:30 am); an initial patch was randomly chosen, and each nearest patch 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 one observer.

Data analysis

Since migratory birds are often the focus of management directives (Rich et al. 2004), we separated bird observations into migratory and resident categories, and calculated the mean species richness per year per site (aspen patch or conifer point). 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 heterogeneity measure 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.

Response variables were evaluated 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 Shannon-Weiner diversity index was not indicated. We followed the guidelines used by Schieck and Nietfeld (1995) and considered regression coefficients (R^2) of 0.30 to 0.50 moderate, and > 0.50 strong correlation. All regression models and model comparisons were considered significant at $\alpha \leq 0.05$. We used S-Plus statistical software for all analyses (Insightful 2001).

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

$$Diversity = \beta_0 + \beta_1x - \beta_2x^2$$

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:

$$Diversity = \beta_0 - \beta_1x$$

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 would conclude 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 (*Parus gambeli*)) (see Appendix 1.A for a list of species detected). Mean annual species richness (untransformed) ranged from 1.5 to 7.89 for migrants and 0.11 to 1.67 for residents. Shannon-Wiener index values ranged from 1.09 to 2.7 for migrants and 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 1.2). For migratory birds, direct linear models performed better than quadratic models for each combination of species diversity measure and habitat heterogeneity (Table 1.2). 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 Shannon-Weiner diversity index had positive coefficients for β_1 , but were not significantly better than the reduced linear models (see Table 1.2).

Most of the quadratic models of resident bird species richness or Shannon-Weiner diversity were better than direct linear models (Table 1.3). 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-Wiener 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 resident Shannon-Wiener index values 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/year/site), 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 since 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 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 resident Shannon-Wiener index model 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) were critical of diversity indices that are insensitive to species composition due to the risk of including exotic or regionally common species. The starlings discussed above underscore this criticism and managers are advised 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 constitute alpha diversity (local scale) 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, since aspen 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) urged 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 landscapes 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).

Bird diversity in aspen does not appear to increase with conifer invasion in the intermountain western U. S. (Finch and Reynolds 1987, Rumble et al. 2001). However, there is some evidence for greater bird diversity in "mixedwoods" 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, Canada, 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 do 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 affect positive responses in bird diversity by following the guidelines presented by Campbell and Bartos (2001) and 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-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", where browsing mortality is less, and eventually recruit into the overstory (Ripple and Larsen 2001). As these sites increase in aspen dominance, it is likely that increased bird diversity would follow.

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Table 1.1. 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	Mean	SE	Range
Aspen patches (<i>n</i> = 34)			
<i>Patch Size (ha)</i>	1.4	0.53	0.2-16.7
<i>Aspen Canopy Cover (%)</i>	73.1	2.78	31-100
<i>Conifer Canopy Cover (%)</i>	9.3	2.24	0-60
<i>Aspen Basal Area (m²/ha)</i>	33.9	2.97	11-83
<i>Conifer Basal Area (m²/ha)</i>	3.7	0.69	0-10
Conifer sites (<i>n</i> = 6)			
<i>Canopy Cover (%)</i>	95.1	1.95	88-99
<i>Basal Area (m²/ha)</i>	54.1	2.92	41-60
Derived variables (<i>n</i> = 40)			
<i>CCR (Canopy Cover Ratio)</i>	0.27	0.36	0-1
<i>BAR (Basal Area Ratio)</i>	0.28	0.35	0-1

Table 1.2. 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
$\ln(\text{Sp Rich}) = 1.50 - .28(\text{CCR}) - .42(\text{CCR})^2$	0.35	<0.001		
$\ln(\text{Sp Rich}) = 1.53 - .69(\text{CCR})$	0.34	<0.001	0.36	0.55
$\ln(\text{Sp Rich}) = 1.53 - .54(\text{BAR}) - .21(\text{BAR})^2$	0.38	<0.001		
$\ln(\text{Sp Rich}) = 1.54 - .75(\text{BAR})$	0.38	<0.001	0.11	0.75
$\text{SW Index} = 2.22 + .36(\text{CCR}) - 1.01(\text{CCR})^2$	0.39	<0.001		
$\text{SW Index} = 2.29 - .65(\text{CCR})$	0.34	<0.001	2.60	0.12
$\text{SW Index} = 2.25 + .07(\text{BAR}) - .81(\text{BAR})^2$	0.46	<0.001		
$\text{SW Index} = 2.31 - .73(\text{BAR})$	0.43	<0.001	2.01	0.16

Table 1.3. 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
$\ln(\text{Sp Rich}) = -.57 + 2.68(\text{CCR}) - 2.75(\text{CCR})^2$	0.13	0.09		
$\ln(\text{Sp Rich}) = -.38 - .04(\text{CCR})$	0.001	0.89	5.15	0.03
$\ln(\text{Sp Rich}) = -.50 + 1.90(\text{BAR}) - 2.12(\text{BAR})^2$	0.10	0.17		
$\ln(\text{Sp Rich}) = -.33 - .21(\text{BAR})$	0.01	0.48	3.20	0.08
$\text{SW Index} = .89 + 1.69(\text{CCR}) - 2.08(\text{CCR})^2$	0.27	0.004		
$\text{SW Index} = 1.03 - .36(\text{CCR})$	0.10	0.05	8.32	0.007
$\text{SW Index} = .90 + 1.41(\text{BAR}) - 1.81(\text{BAR})^2$	0.25	0.006		
$\text{SW Index} = 1.04 - .39(\text{BAR})$	0.11	0.04	6.71	0.01

APPENDIX

Appendix 1.A. Species detected on the northern ungulate range of the greater Yellowstone ecosystem during June 2001, 2002, and 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>Parus atricapillus</i>	2.4	N	X	X
Brewers Blackbird	<i>Euphagus cyanocephalus</i>	1.5	Y	X	X
Brown-headed Cowbird	<i>Molothrus ater</i>	1.1	Y	X	X
Cassins Finch	<i>Carpodacus cassinii</i>	0.04	Y	--	X
Chipping Sparrow	<i>Spizella passerina</i>	1.3	Y	X	X
Clarks 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>Juncus 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
Green-tailed Towhee	<i>Pipilo chlorurus</i>	0.3	Y	--	X
Hairy Woodpecker	<i>Picoides villosus</i>	0.5	N	X	X
Hammonds Flycatcher	<i>Empidonax hammondii</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
Lincolns Sparrow	<i>Melospiza lincolnii</i>	3.7	Y	X	X
McGillivrays Warbler	<i>Oporornis tolmiei</i>	1.9	Y	X	X
Mountain Bluebird	<i>Sialia currucoides</i>	2.9	Y	X	X
Mountain Chickadee	<i>Parus 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 borealis</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
Starling	<i>Sturnus vulgaris</i>	2.9	N	X	X
Stellars Jay	<i>Cyanocitta stelleri</i>	0.2	N	--	X
Tree Swallow	<i>Tachycineta bicolor</i>	1.5	Y	X	X
Vespers 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
Williamsons Sapsucker	<i>Sphyrapicus thyroideus</i>	0.9	Y	X	X
Willow Flycatcher	<i>Empidonax trailii</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

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Submitted 16 August 2006

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ABSTRACT

We evaluated the effects of aspen patch area and orientation (relative to North and an elevational gradient) on the early breeding season abundance and species richness of migratory and resident birds in the northern ungulate winter range of the Yellowstone ecosystem, USA. Using an information-theoretic model selection approach, we found patch area to be the most important covariate for long distance migrants, and patch orientation relative to elevational gradient the most important covariate for residents/short-distance migrants. Basal area of live aspen and aspen snags was marginally important for all bird species, likely because aspen snags are an important habitat for most cavity-nesting species. Landscape ecological theory provides for the process of passive patch interception of dispersing or migrating organisms. Our results suggest that residents/short-distance migrants appear to be intercepted by patches that are oriented perpendicular to the elevational gradient of the northern range resulting in greater abundances and species richness in those patches. However, long-distance migrants use aspen patches without regard to orientation, but rather to patch area.

KEYWORDS

Aspen, bird migration, interception, patch orientation, Yellowstone National Park

INTRODUCTION

Aspen (*Populus tremuloides*) provide a relatively rare (Bartos 2001) and highly productive habitat which support greater numbers of migratory and resident species of birds than other forest habitat types in the western U.S. (Flack 1976; Winternitz 1980;

Griffis-Kyle and Beier 2005). Studies of aspen habitat in the western U.S. have found them to be important for birds at local, landscape, and regional scales (Johns 1993; Hansen and Rotella 2002; Lawler and Edwards 2002a; Griffis-Kyle and Beier 2003).

Aspen appear to be declining in the western U.S. Several mechanisms have been suggested to explain this decline (Kay 1997; Bartos and Campbell 1998; Ripple and Larsen 2000), but interrupted fire disturbance regimes and increased browsing intensity by ungulates and/or livestock are favored hypotheses. Since aspen habitat typically represents less than 5% of most western landscapes, excluding Colorado and northern Utah (Despain 1990; Barnett and Stohlgren 2001; Barmore Jr. 2003), its reduction or disappearance may have considerable implications for birds. Negative effects may be greatest for migratory birds that use aspen habitat heavily during the breeding season (Flack 1976; Griffis-Kyle and Beier 2005). A better understanding of how birds, particularly migrants, select and interact with aspen habitat may improve the effectiveness of management actions aimed at conserving bird populations and diversity.

Landscape-scale relations between aspen and birds in the western U. S. remain largely unstudied. Lawler and Edwards (2002a; 2002b) demonstrated important landscape context effects of aspen stands for cavity-nesting birds in northern Utah. Turchi et al. (1995) found aspen patch isolation to be a poor predictor of bird species richness in Rocky Mountain National Park, Colorado. However, associated shrub cover was significant. Johns (1993) found long-distance, short-distance, and resident bird diversity increased with aspen patch area in the parklands of Saskatchewan, Canada. Saab (1999) found matrix habitat, and proximity of similar patches, to be important

predictors of bird species richness in riparian cottonwood (*Populus trichocarpa*) habitat in southeastern Idaho.

Landscape ecology theory suggests that interactions between highly mobile organisms and habitat patches, especially those with high contrast edge, may occur as predictable patterns (Forman 1995). Forman and Godron (1986) suggested that the orientation of a non-circular patch, defined as the “angle of interaction” between the patch major axis and the line of travel followed by dispersing or migrating organisms, should influence within-patch abundance and diversity of organisms by means of passive interception. Therefore, with all else being equal, patches that present larger interceptive surfaces (i.e., oriented perpendicular to direction of travel) should contain more individuals and species than patches with smaller interceptive surfaces (see Figure 2.1). The patchy distribution of aspen in most western landscapes, combined with the high value of aspen habitat for birds, may provide a suitable model for investigations of the patch orientation effect.

We know of only one study explicitly evaluating the effect of patch orientation and passive interception of migratory birds. Gutzwiller and Anderson (1992) found significant effects of cottonwood patch area and orientation relative to the northerly direction of travel by migrating birds in spring. These patches were located along the North Platte River in southeastern Wyoming, a low elevation region with little topographic relief. They suggest patches of suitable nesting habitat (riparian cottonwood) intercepted migrating birds. Cottonwood, a congener of aspen, is of value to birds for many of the same reasons as aspen. We speculate that aspen patches intercept migratory birds in a similar manner. However, it is unknown whether passive interception would

exert as strong an influence at higher elevations where aspen typically occur, and where topography is more varied, than Gutzwiller and Anderson's (1992) study area.

Gutzwiller and Anderson (1992) evaluated patch orientation relative to the general northward direction of travel long-distance migrants are assumed to follow during spring. Migrating birds are thought to follow north-south trending river systems with little topographic relief along the general northerly (or southerly) direction of travel (Yong and Finch 1997; Skagen et al. 2005). When migrating birds encounter higher-elevation topographic features, they may change direction of their migratory route to avoid such features. Williams et al. (2001) described the movement of migrants through mountain passes in the northern Appalachian Mountains, New Hampshire, and found that birds avoided direct flights over high elevation features and sought out low elevation passes as part of their migratory route. Other researchers describe elevational migrations for short distance migrant and resident bird species in North America (Presnall 1935; Rabenold and Rabenold 1985; Levey and Stiles 1992; Inouye et al. 2000; Morrissey 2004). These species are thought to avoid harsh winter climates at high elevation, and exploit spring-summer resources when high elevation climate is mild.

It is possible that a final elevational "leg" of spring migration occurs for some long-distance migrants. Hahn et al. (2004) described an altitudinal migration undertaken by white-crowned sparrows (*Zonotrichia leucophrys*), a long-distance migrant, in the Sierra Nevada mountains of California. Here, birds arrived from wintering sites in the south and loitered at lower elevations as conditions at their higher elevation breeding sites improved with the progressing season. This form of multi-stage migration by long-distance migrants is likely to occur for many species which breed in high elevation

habitats. We speculate that some amount of this kind of movement occurs for long-distance migrants breeding in aspen habitat in the northern Yellowstone ecosystem.

Our goal in this study was to determine the landscape-level relationship between birds and aspen habitat in the northern ungulate range of the northern Yellowstone ecosystem, emphasizing the relative importance of patch area and orientation. We hypothesized that, after accounting for within-patch characteristics, patch area and orientation exert an influence on the abundance and species richness of birds via passive interception. Furthermore, we expected the effect of patch orientation to vary with migratory strategy: Since short-distance migrants and residents are known to move along elevational gradients, but long-distance migrants may still arrive directly from the south, we expected the effect of patch orientation relative to the elevational gradient of the landscape to be greater for short-distance migrant (or resident) species than for long distance migrants. Specific objectives were: (1) Develop hypothetical models describing both migratory and resident bird abundance, and species richness, as functions of patch attributes (floristics, structure, and patch characteristics); (2) rank and evaluate fitted hypothetical models; (3) evaluate the relative importance of component variables; and (4) determine the model-averaged effect size and unconditional confidence intervals for patch area and orientation.

STUDY AREA

We conducted our study in the 153,700-ha northern ungulate winter range of the Yellowstone ecosystem, USA (Figure 2.2). Approximately two-thirds of the range is in

Yellowstone National Park (YNP). The remaining one-third is in the Gallatin National Forest (GNF) with a few small private holdings within (Lemke et al. 1998).

Elevation ranges from 1560 to 2350 m. Mean annual precipitation is 40 cm/yr., (from 25 to 66 cm/yr with increasing elevation) (Western Regional Climate Center 2004). Dominant vegetation is Lodgepole Pine (*Pinus contorta*) at higher elevations and where soils are poor, and Douglas-fir (*Pseudotsuga menziesii*) and Engleman Spruce (*Picea englemanni*) where conditions are suitable. Most aspen are distributed as patches at approximately 2200 m elevation where conifer forest transitions to steppe, which is dominated by sagebrush (*Artemisia* sp.) and several grasses, including Idaho fescue (*Festuca idahoensis*) and timothy (*Phleum pratense*).

YNP is managed as a natural preserve. The GNF portion of the northern ungulate range is managed primarily for elk (*Cervus elaphus*) winter range and human recreation (including hunting) with limited resource extraction and livestock grazing (Lemke et al. 1998). Topography and landscape patterns of vegetation are relatively consistent throughout the study area but management differs regarding elk hunting between YNP and GNF portions of the range.

METHODS

Vegetation Data

We randomly selected 32 aspen patches from an existing map (St. John 1995) and aerial photographs (acquired during 1994) where gaps occurred in map coverage. Thirty patches were identified in 2001 and 2 more added in 2002. Patches were constrained to \geq 100 m from primary roads and \leq 1 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 photo acquisition, and were ≥ 100 m apart. During field sampling we found that conifer invasion and changes in canopy cover had occurred in some patches but we retained these in our sample. Five patches from the initial sample were either mis-identified or no longer extant. We chose the nearest extant patches that satisfied location criteria as replacements.

For each patch, we measured basal area of aspen and conifer stems ≥ 1 cm diameter at breast height (dbh). We used a five-point sampling pattern, initiated at the patch centroid with 4 points positioned 25 m in each cardinal direction. We did not sample at points that fell outside the patch. We used variable radius sampling technique with a 5, 10, or 20 Basal Area Factor (BAF) prism to measure tree 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. Tree canopy cover was measured for aspen and conifers separately using a mirror densiometer. Patch characteristics are summarized in Table 2.1.

Patch Attributes

Boundaries of patches selected from the existing map (St. John 1995) were provided in digital format. For those patches that were not selected from the map, we digitized their boundaries using digital orthophotographs in a Geographic Information System (GIS) (Environmental Research Systems Institute 2004).

Patch area and major/minor axes were calculated in the GIS. Patch area was log transformed as a variable for analysis. Patch widths perpendicular to north and

perpendicular to the elevational gradient azimuth were considered as measures of patch interceptive surface. However, similar to Gutzwiller and Anderson (1992), we found this measure to be highly correlated with patch area ($r > 0.9$) and was omitted from our analyses in favor of patch orientation measures. Patch orientation was measured as the acute angle described by the intersection of a direction of travel and the major axis of the patch. Thus orientation could range from 0 to 90 degrees where 0 degrees represented a patch with a major axis parallel to direction of travel, and 90 degrees perpendicular to direction of travel (e.g., Gutzwiller and Anderson 1992). We measured two levels of patch orientation: one relative to true north (regional orientation), and another relative to the azimuth of the elevational gradient for the study area (local orientation). The elevational gradient azimuth of 153° was calculated in a GIS as the average azimuth of lines placed tangential to the course of the Lamar and Yellowstone Rivers at 1-km intervals.

Bird Data

We conducted point counts each of 3 years, May 30 – July 1 (early breeding season 2001-2003). Counts were 6 min. in duration using 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 long-distance migrant or short-distance migrant/resident (McEneaney 1996). For our analyses, we combined short-distant migrant and resident species. Detections known to be outside an aspen patch boundary were flagged for omission during analysis. Fly-overs were not counted unless they were considered to be using habitat for foraging (e.g., tree swallow (*Tachycineta*

bicolor) foraging > 10 m above canopy was excluded). Counts were not conducted during heavy precipitation or windy conditions (> 16 km/hr), but were not constrained by cloud cover. We assumed that bird detectability was similar among sites (e.g., Finch and Reynolds 1987; Schieck and Nietfeld 1995).

Each aspen patch was sampled 3 times during 2001 and 2002, and twice during 2003. We performed 1 count at each patch centroid and additional counts in larger patches; one additional count for each 5 ha of patch area. These additional counts were positioned 100 m from centroid point along the major geographic axis of the patch. Only two patches were > 5 ha. Using the protocol described previously, we collected vegetation data at these additional points and used the average values of all points in the patch for analyses. Additionally, for patches with > 1 point we used the average of bird count data in our analyses. We sampled spatially clustered groups of 3 to 5 aspen patches daily during morning hours (sunrise to 10:30 am); an initial patch was randomly chosen, and each nearest patch 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 one observer (JPH). We assumed bird detections within the 50-m radius point count circle were representative of the entire aspen patch.

Statistical Analyses

We used an information theoretic approach (Burnham and Anderson 2002) to evaluate a set of *a priori* models proposed to explain patterns of migratory and resident bird abundance and diversity. We ranked the candidate models in order of their associated small-sample corrected Akaike's Information Criterion values (AICc) such

that smaller AICc values indicate a better model (Anderson et al. 2001; Burnham and Anderson 2002). Following Anderson and Burnham (2002), we defined AICc as:

$$\text{AICc} = -2(L) + 2K + [2K(K + 1)/(n - K - 1)]$$

where L = the maximum likelihood estimate for the model, K = the number of estimated parameters, including variance, and n = sample size. We evaluated the plausibility of the AICc best model, or group of competing best models, using evidence ratios constructed from Akaike weights. Subsequently, we interpreted the relative importance of covariates, namely patch area and orientation. Using model averaging (Burnham and Anderson 2002) we evaluated the effect size of covariates and their “unconditional” confidence intervals. Akaike weights (ω_i), which indicate the relative plausibility of a given model, given the data and the set of candidate models, were calculated as:

$$\omega_i = \exp(-0.5*\Delta_i) / \sum (\exp(-0.5*\Delta_i))$$

where Δ_i is the difference between AICc of a given model and the AICc of the best model (AICc_{\min}).

We determined *a priori* candidate models from theoretical predictions and known relationships reported in the literature and expressed these as statistical linear models (Table 2.2). For our analysis, we constructed models around two general approaches to habitat selection: within-patch-scale characteristics (floristics/structure), and landscape-scale patch characteristics. Using this approach, we attempted to interpret the relative importance of landscape-level variables, such as patch orientation, and within-patch variables in the context of competitive models selected by AICc. For all models, we regressed covariates on within-year mean bird species richness, or mean bird abundance (average of patch visits within year), resulting in 96 observations.

Candidate Models

Landscape Models

We expected the effect of regional patch orientation to be smaller than that reported by Gutzwiller and Anderson (1992) primarily due to the higher elevation and regional topography of our study area. Because of these characteristics, we hypothesized an alternate route taken by migrants to aspen breeding habitat in Yellowstone's northern ungulate winter range. We conceived that migrants flying over low-elevation, flat topography arrive at their breeding sites from a southerly direction (e.g., Gutzwiller and Anderson 1992), but migrants may avoid high elevation features, such as the Yellowstone Plateau, and follow low elevation routes around such features before subsequently moving up an elevational gradient to their breeding areas. Therefore, we also considered an effect of patch orientation that was relative to the elevational gradient of the study area. We refer to these two orientation measures as "regional orientation" and "local orientation." Models containing each of these covariates, and their interaction with patch area, were present in the candidate model set.

Biogeographic theory and studies have described positive relationships between area and species richness for many taxa for both islands (MacArthur and Wilson 2001) and terrestrial habitats (Martin 1980; Whitcomb et al. 1981; McIntyre 1995; Grant and Berkey 1999). Previous work with aspen habitat suggests the importance of patch area for bird diversity (e.g., Johns 1993; Grant and Berkey 1999), but see Griffis-Kyle and Beier (2003) for an exception. We included patch area as a stand-alone model and as a covariate in all but two landscape-level models of the candidate model set. Furthermore,

since Gutzwiller and Anderson (1992) found a strong and significant interaction between patch area and orientation for both migratory bird abundance and species richness, we included models containing these interaction terms (patch area and both local and regional orientation) in the candidate model set.

Floristic/Structural Models

Once birds have arrived at a patch, we expected several within-patch habitat characteristics to influence site use. Numerous studies have demonstrated relationships between floristic and structural composition of habitat and bird abundance, species richness, and community structure (e.g., MacArthur and MacArthur 1961; Anderson and Shugart 1974; Hobson and Bayne 2000 and others). For our analyses, we considered the within-patch floristic/structural covariates of basal area of live aspen, and basal area of dead aspen. Similar to Gutzwiller and Anderson (1992), we expected better performing models to show landscape-scale patch area and/or orientation effects after accounting for within-patch variables. Within the candidate model set we also provide several models of floristics/structure alone. Thus, the absence of any patch area and/or orientation effects should allow within-patch habitat models to rank higher among AIC values.

We used aspen basal area in candidate models for 3 reasons: (1) aspen canopy cover and basal area were correlated (Pearson's $r \sim 0.70$) which could lead to variable/model redundancy; (2) we did not want to confound the condition assumed to intercept migrating birds (aspen canopy) and the abundance of aspen once in a patch (here measured as basal area); and (3) we considered basal area a more appropriate measure than stem density since each stem, regardless of diameter, is given equal weight

in a density calculation. Several bird species, especially cavity nesters, are known to respond to stem size and basal area. Caton (1996) found that several species of cavity nesters responded positively to basal area of trees surrounding nest sites. Similarly, we used basal area of dead stems as a measure of snag presence to avoid inappropriate weighting of small diameter snags in a density calculation. Among cavity-nesting species, larger diameter snags seem to be preferred (e.g., Dobkin et al. 1995; Caton 1996) and Swallow et al. (1986) found site characteristics, primarily basal area, to be a better predictor of cavity nest presence than variables specific to nest-site trees. Candidate models containing floristic/structural and landscape covariates are shown in Table 2.2.

Global model

The global model is typically the most highly parameterized of the candidate model set. It is assumed to be the most precise, but also the most biased, model and should provide an adequate fit to the data under analysis. With the exception of the interaction between patch area and orientation (e.g., Gutzwiller and Anderson 1992), we did not consider interactions or polynomial models in the candidate model set. These were not supported by our understanding of landscape- or local-scale relationships between birds and aspen habitat. The wholesale inclusion of interactions and unsupported models increases both the number of models in the candidate set, and the number of parameters estimated in larger models, to unacceptable levels (Burnham and Anderson 2002). Thus, the most structurally complex model in our candidate set, which also serves as the global model, is:

$$Y = \beta_0 + \beta_1 \text{BA.Aspen} + \beta_2 \text{BA.Dead} + \beta_3 \text{Area} + \beta_4 \text{Orientation} + \beta_5 (\text{Area} \times \text{Orientation})$$

where BA.Aspen = basal area of aspen, BA.Dead = basal area of dead stems, Area = patch area, Orientation = orientation of patch (may be relative to either North or elevational gradient).

Serial correlation and random intercept effects

We modeled residual error as an unstructured error covariance matrix. This allowed us to model serial correlation of patches among years and account for a random intercept effect of the linear predictor among years. Estimating unstructured serial correlation increased the number of parameters estimated for each model by 4; 1 for the correlation matrix, 3 for each year-wise covariance estimate. The conceptual form was:

$$y_i = X_i \beta_i + \varepsilon_i, \quad \varepsilon_i \sim N(0, \sigma^2, I)$$

where y_i is the individual response, X_i a matrix of fixed effects, β_i the associated coefficients, and ε_i the variance associated with the linear predictor $X_i \beta_i$. I is the unstructured within group variance/covariance matrix where the diagonals are yearly variation of the linear predictor intercept (analogous to a mixed model approach) and the off-diagonals are serial correlation between years. Ultimately, a trade off exists between the effect of additional parameter estimates and the information contained in each year's data. We chose to exploit the information contained in multi-year data.

Model Selection and Interpretation

Using *gls* (generalized least squares regression, Pinheiro and Bates 2000) in S-Plus statistical software (Insightful 2001), we fit each candidate model to log-transformed abundance and species richness response for both migrant and resident species. Of the two most highly parameterized models, we selected the one including local orientation to serve as our global model. We know of no goodness-of-fit test for generalized least squares regression. Therefore we assessed goodness-of-fit for our global models using ordinary least squares regression since sample correlation among years was low. Ordinary least squares regression fits of the global model for each combination of migratory strategy and bird abundance/diversity were adequate to proceed with AICc ranking and evaluation using *gls* (migrant abundance, $R^2 = 0.30$, $F_{5,87} = 7.32$, $p \ll 0.001$; migrant species richness, $R^2 = 0.27$, $F_{5,87} = 6.34$, $p \ll 0.001$; resident abundance, $R^2 = 0.18$, $F_{5,87} = 3.85$, $p = 0.003$; resident species richness, $R^2 = 0.15$, $F_{5,87} = 3.05$, $p = 0.014$) (Burnham and Anderson 2002).

The threshold for including a model as a competing best model was guided by previous studies that applied model selection techniques to bird-habitat questions. Franklin (1997) considered competing best models to be within 2 AICc units of the best (minimum AICc) selected model. This guideline is presented by Burnham and Anderson (2002) as well. Westphal et al. (2003) chose models with Akaike weights ≥ 0.10 as the set of competing models describing landscape effects of bird distributions in southern Australia. We considered models with Akaike weights ≥ 0.10 as competing “best” models.

We determined the relative importance (RI) of covariates in the AICc best model (or competing set of best models). We then calculated slope estimates (β_i) and associated standard errors for these covariates by model averaging. We used “unconditional” 90% and 95% confidence intervals to evaluate these slope estimates (Burnham and Anderson 2002); covariates with confidence intervals that include 0 were not considered important regardless of the ranking of their associated models by AICc. Interpretation of covariates focused on the patch orientation or area, and their importance, if present.

We calculated relative importance of variables as:

$$RI = \sum \omega_i$$

where i is an unique candidate model containing the covariate of interest. Higher RI values indicate greater importance of the target covariate relative to all covariates present in the candidate model set.

We determined unbiased estimates of variable coefficients (β_i) by model averaging (Burnham and Anderson 2002) where the covariate of interest is evaluated in terms of the Akaike weights of the models in which the target covariate occurs. Thus, we calculated model-averaged estimates as:

$$\bar{\hat{\beta}}_i = \sum \omega_i \beta_i$$

where i is an unique candidate model containing the variable of interest.

We constructed 90% and 95% confidence intervals for each model-averaged covariate coefficient using “unconditional” model coefficient standard errors (Burnham and Anderson 2002) calculated as:

$$\hat{SE} = \left[\sum \omega_i \sqrt{SE_{\beta_i} + (\beta_i - \hat{\beta}_i)^2} \right]^2 .$$

The resulting “unconditional” confidence intervals conservatively incorporate model uncertainty and provide a less biased evaluation of the covariate effects.

RESULTS

We detected 2648 birds representing 54 species. Forty-two species were long-distance migrants and 12 were short-distance migrants or residents. The most common long-distance migratory species were Warbling Vireo (*Vireo gilveus*), American Robin (*Turdus migratorius*), and Northern Flicker (*Colaptes auratus*), with 339, 288, and 188 detections respectively. The most numerous resident/short-distance migrants were Mountain Chickadee (*Parus gambeli*), Red-breasted Nuthatch (*Sitta canadensis*), and Starling (*Sturnus vulgaris*), with 131, 78, and 77 detections respectively. Appendix 1 shows a complete list of detected species, their migratory status, and relative abundance.

There were 4 competing best models for migrant abundance, 3 competing best models for migrant species richness, 4 competing best models for resident abundance, and 6 competing best models for resident species richness (Table 2.3). The AICc best model for migrant abundance consisted of patch area only; the AICc best model for migrant species richness contained patch area and basal area of live aspen covariates. The AICc best model for both resident abundance and resident species richness consisted of local patch orientation only.

For bird abundance, patch area was the most important covariate for migrants (99%), and local patch orientation was most important for residents (92%) (Table 2.4).

Local patch orientation, basal area of live aspen, and basal area of dead aspen appear somewhat important for migrants (31%, 28%, and 32% respectively). Patch area, basal area of live aspen, and basal area of dead aspen appeared somewhat important for residents (53%, 42%, and 25% respectively). For both migratory strategies, area-orientation interactions appeared unimportant.

For species richness, patch area was most important for migrants (95%), and local patch orientation was most important for residents (93%). Basal area of live aspen and basal area of dead aspen appeared somewhat important for migrants (51% and 30% respectively). Patch area, basal area of live aspen, and basal area of dead aspen appeared somewhat important for residents (53%, 39%, and 37% respectively). For both migratory strategies, area-orientation interactions appeared unimportant.

Confidence intervals for migratory bird abundance and species richness model covariates showed patch area as the only variable exclusive of zero at either the 95 or 90% level (Table 2.5). For both resident abundance and species richness, only local patch orientation was exclusive of zero at either the 95 or 90% level.

DISCUSSION

Area and Orientation effects

Local patch orientation relative to the elevational gradient of our study area was a key predictor of resident/short-distance migrant abundance and species richness. The AICc best model had local orientation alone for both abundance and species diversity. Local patch orientation had a relative importance value >90% for both resident abundance and species richness. As with long-distance migrants, regional orientation

(relative to north) did not occur in any of the competing best models. Furthermore, confidence intervals (90 and 95%) suggested a lack of support for patch area, basal area of aspen, or basal area of aspen snags as important to the abundance or species richness of resident birds (see Table 2.5).

In contrast, long-distance migrant abundance and species richness responded primarily to patch area. Aspen basal area and aspen snag basal area appeared among the competing best models for both migratory strategies; however, relative importance values and confidence intervals did not suggest a large effect. Notably, neither the regional nor local patch orientation covariates appeared in any of the competing best models for migrant species richness, and local patch orientation occurred in only one competing best model for migrant abundance. Relative importance values and confidence intervals (both 90% and 95%) for migrant model covariate coefficients supported the interpretation that patch area alone was important for migrant abundance and species richness, and that the orientation of patches did not influence migratory birds in the manner described by Gutzwiller and Anderson (1992). Patch area had a relative importance of 99 and 95% for migrant abundance and species richness, respectively, and only patch area had confidence intervals that did not contain zero (Table 2.5).

High elevation winters on Yellowstone's northern range can be cold and severe. Most resident and short-distance migrant birds that breed on the northern range are thought to move to lower elevations during winter months and then back up during spring as climate and foraging conditions improve at higher elevations. This annual elevational migration appears to interact with aspen patches as predicted by Forman and Godron (1986) and as detected by Gutzwiller and Anderson (1992) for long-distance migrants.

However, long-distance migrants did not mirror the patch orientation relationship exhibited by residents/short-distance migrants for either orientation measure. Long-distance migrants appear to encounter and select habitats differently at our high-elevation study area than they would at a low elevation site (i.e., Gutzwiller and Anderson 1992). Diffuse post-arrival movements throughout the study area by long-distance migrants may lead to more uniform settling among patches than occurred with residents/short-distance migrants.

The lack of a regional patch interception (orientation) effect for long-distance migrants might also result from the timing of suitable post leaf-out aspen habitat and the arrival of migrants. Short-distance migrant and resident species likely have greater flexibility in the timing of their altitudinal movements with changing climate, thus are poised to exploit aspen habitats when they are ready, but long-distance migrants likely seek out favorable habitat upon arrival on Yellowstone's northern range. Nevertheless, long-distance migrants were the majority of species found within aspen in the northern range and appeared to use aspen heavily during the breeding season.

We found relationships between patch area and bird species richness that are similar to those found by others. For example, Blake and Karr (1987) found patch (woodlot) area to be the best predictor of species richness for long-distance migrants, but not resident/short distance migrants among hardwood forest fragments in Illinois. Additionally, although they did not evaluate patch orientation, they did find within-patch habitat variables to be most important for resident/short-distance migrant richness. Grant and Berkey (1999) found increased avian richness as patch area increased among aspen patches in North Dakota. In separate evaluations of neotropical migrants and

resident/short-distance migrants, they found that neotropical migrant diversity had a very strong positive relationship with patch area, but residents and short-distance migrants only exhibited a weak relationship. Our results concur with these differences in patch area relationships for different migratory strategies.

While not interpreted as important, it is worth noting that aspen basal area and, in particular, aspen snag basal area covariates have a strong biological basis for appearing among the AICc ranked competing best models. This is because many bird species found in aspen are cavity nesters. Along with burned-over conifer stands, aspen and cottonwood habitats are critically important to these species in the northern Yellowstone ecosystem. The information-theoretic approach used in this study seems to have revealed the relative importance of aspen (and aspen snag) basal area when considered along with patch area and orientation. The AICc ranking, covariate relative importance, and confidence intervals suggest that the landscape-scale measurements of habitat better indicate bird abundance and species richness than within-patch-scale measures.

Limitations

We did not assess the effect of matrix habitat in our analysis. Lawler and Edwards (2002a) found greater bird species richness and abundance of cavity nesters in aspen patches surrounded by meadow matrix in northern Utah (Lawler and Edwards 2002a). They also found fewer cavity nesters in aspen patches surrounded by conifer forest habitat. It is possible that such effects occur within our study area. Certainly, landscape context is a topic in need of further investigation.

Researchers using information-theoretic methods as sensitivity analyses are urged to explicitly state hypothesis(es) in terms of the variables/covariates being evaluated (Guthery et al. 2005). Our focus in this study was not to describe new theoretical models predicting bird abundance or diversity in Yellowstone's northern range. Rather, we evaluated the relative contribution of patch area and orientation in the context of covariates that are known to influence habitat use by birds. In short, we used the information-theoretic model selection approach as a more robust alternative to stepwise regression analysis.

Pinheiro and Bates (2000) cautioned analysts about the potential for over-parameterization of models using a general (i.e., unstructured) error matrix. With the unstructured error covariance matrix, our most highly parameterized (global) model contains 11 estimated parameters (34% of our sample size). Ideally, the number of parameters estimated for the global model in a model selection analysis would be $\leq 30\%$. We should note that all AICc selected competing best models contained ≤ 9 parameters.

Uncertainty about coefficient estimates (Table 2.5) is likely due to small sample size combined with typically variable bird count data. However, our sample size was guided by key literature (Gutzwiller and Anderson 1992) which used 34 patches to detect significant effects of patch area and orientation on abundance and species richness of migratory birds. Furthermore, sampling logistics hindered our ability to include more patches in this study.

CONCLUSIONS

Our study suggests that aspen patches in Yellowstone's northern ungulate range passively intercept resident, or short-distance migrant birds, but not long-distance migrants. Further, our results suggest that at the higher elevation of our study area, patch orientation relative to the elevational gradient is a better measure of patch interceptive surface for resident and short-distance migrants than patch orientation relative to North. Together, the lack of a regional (relative to North) interceptive effect and the lack of response to patch orientation by long-distance migrants suggests that other factors, such as elevation, topography, or possibly aspen phenology, exert a greater influence on landscape-scale bird-habitat relationships at higher elevation sites than at low elevation sites (e.g., Gutzwiller and Anderson 1992).

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Figure 2.1. Effect of patch orientation. Patches viewed from above (a and c) have same area but different orientations relative to direction of bird migration (represented by arrow). Views b and d show the “interceptive surface” of each patch; patches oriented perpendicular to migratory direction have greater surface presentation than those parallel to migratory direction.

Figure 2.2. Location of the northern ungulate range (shown in gray) in northwest Wyoming and southwest Montana, USA.

Table 2.1. Characteristics of aspen patches (n = 32) in the northern ungulate winter range of the Yellowstone ecosystem, 2001-2003. BA.Aspen = basal area of aspen, BA.Dead = basal area of dead stems, Area = patch area, Reg.Orient = patch orientation relative to North, Loc.Orient = patch orientation relative to elevational gradient.

Variable		Mean	SE	Range
CC.Aspen	<i>Aspen Canopy Cover (%)</i>	73.1	2.78	31-100
BA.Aspen	<i>Aspen Basal Area (m²/ha)</i>	33.9	2.97	11-83
BA.Dead	<i>Dead Basal Area (m²/ha)</i>	5.8	0.84	0-18
Area	<i>Patch Size (ha)</i>	1.4	0.53	0.2-16.7
Reg.Orient	<i>Regional Patch Orientation (degrees)</i>	51	5.0	2-87
Loc.Orient	<i>Local Patch Orientation (degrees)</i>	47	4.0	9-83

Table 2.2. List of *a priori* candidate models. Y = Migrant Abundance, Resident Abundance, Migrant Species Richness, Resident or Species Richness. All models applied to data collected during June 2001, 02, 03 in the northern ungulate winter range of the Yellowstone ecosystem. Parameter abbreviations defined in Table 2.1.

Model Structure

$$\log(Y) = \beta_0 + \beta_1 \ln.\text{Area}$$

$$\log(Y) = \beta_0 + \beta_1 \text{Reg.Orient}$$

$$\log(Y) = \beta_0 + \beta_1 \ln.\text{Area} + \beta_2 \text{Reg.Orient}$$

$$\log(Y) = \beta_0 + \beta_1 \ln.\text{Area} + \beta_2 \text{Reg.Orient} + \beta_3 \ln.\text{Area} \times \text{Reg.Orient}$$

$$\log(Y) = \beta_0 + \beta_1 \text{Loc.Orient}$$

$$\log(Y) = \beta_0 + \beta_1 \ln.\text{Area} + \beta_2 \text{Loc.Orient}$$

$$\log(Y) = \beta_0 + \beta_1 \ln.\text{Area} + \beta_2 \text{Loc.Orient} + \beta_3 \ln.\text{Area} \times \text{Loc.Orient}$$

$$\log(Y) = \beta_0 + \beta_1 \text{BA.Death}$$

$$\log(Y) = \beta_0 + \beta_1 \text{BA.Death} + \beta_2 \text{Loc.Orient}$$

$$\log(Y) = \beta_0 + \beta_1 \text{BA.Death} + \beta_2 \text{Reg.Orient}$$

$$\log(Y) = \beta_0 + \beta_1 \text{BA.Aspen}$$

$$\log(Y) = \beta_0 + \beta_1 \text{BA.Aspen} + \beta_2 \text{Loc.Orient}$$

$$\log(Y) = \beta_0 + \beta_1 \text{BA.Aspen} + \beta_2 \text{Reg.Orient}$$

$$\log(Y) = \beta_0 + \beta_1 \text{BA.Aspen} + \beta_2 \text{BA.Death}$$

$$\log(Y) = \beta_0 + \beta_1 \text{BA.Aspen} + \beta_2 \text{BA.Death} + \beta_3 \text{Loc.Orient}$$

$$\log(Y) = \beta_0 + \beta_1 \text{BA.Aspen} + \beta_2 \text{BA.Death} + \beta_3 \text{Reg.Orient}$$

$$\log(Y) = \beta_0 + \beta_1 \ln.\text{Area} + \beta_2 \text{BA.Aspen}$$

$$\log(Y) = \beta_0 + \beta_1 \ln.\text{Area} + \beta_2 \text{BA.Death}$$

$$\log(Y) = \beta_0 + \beta_1 \ln.\text{Area} + \beta_2 \text{BA.Aspen} + \beta_3 \text{Loc.Orient}$$

$$\log(Y) = \beta_0 + \beta_1 \ln.\text{Area} + \beta_2 \text{BA.Death} + \beta_3 \text{Loc.Orient}$$

$$\log(Y) = \beta_0 + \beta_1 \ln.\text{Area} + \beta_2 \text{BA.Aspen} + \beta_3 \text{Reg.Orient}$$

$$\log(Y) = \beta_0 + \beta_1 \ln.\text{Area} + \beta_2 \text{BA.Death} + \beta_3 \text{Reg.Orient}$$

$$\log(Y) = \beta_0 + \beta_1 \ln.\text{Area} + \beta_2 \text{BA.Aspen} + \beta_3 \text{Loc.Orient} + \beta_4 \ln.\text{Area} \times \text{Loc.Orient}$$

$$\log(Y) = \beta_0 + \beta_1 \ln.\text{Area} + \beta_2 \text{BA.Death} + \beta_3 \text{Loc.Orient} + \beta_4 \ln.\text{Area} \times \text{Loc.Orient}$$

$$\log(Y) = \beta_0 + \beta_1 \ln.\text{Area} + \beta_2 \text{BA.Aspen} + \beta_3 \text{Reg.Orient} + \beta_4 \ln.\text{Area} \times \text{Reg.Orient}$$

$$\log(Y) = \beta_0 + \beta_1 \ln.\text{Area} + \beta_2 \text{BA.Death} + \beta_3 \text{Reg.Orient} + \beta_4 \ln.\text{Area} \times \text{Reg.Orient}$$

$$\log(Y) = \beta_0 + \beta_1 \ln.\text{Area} + \beta_2 \text{BA.Aspen} + \beta_3 \text{BA.Death}$$

$$\log(Y) = \beta_0 + \beta_1 \ln.\text{Area} + \beta_2 \text{BA.Aspen} + \beta_3 \text{BA.Death} + \beta_4 \text{Loc.Orient}$$

$$\log(Y) = \beta_0 + \beta_1 \ln.\text{Area} + \beta_2 \text{BA.Aspen} + \beta_3 \text{BA.Death} + \beta_4 \text{Reg.Orient}$$

$$\log(Y) = \beta_0 + \beta_1 \ln.\text{Area} + \beta_2 \text{BA.Aspen} + \beta_3 \text{BA.Death} + \beta_4 \text{Loc.Orient} + \beta_5 \ln.\text{Area} \times \text{Loc.Orient}$$

$$\log(Y) = \beta_0 + \beta_1 \ln.\text{Area} + \beta_2 \text{BA.Aspen} + \beta_3 \text{BA.Death} + \beta_4 \text{Reg.Orient} + \beta_5 \ln.\text{Area} \times \text{Reg.Orient}$$

Table 2.3. Competing best candidate models ranked relative to AICc “best” model for migrant abundance, migrant species richness, resident abundance and resident species richness. LogLik = Maximum log-likelihood for given model, K = number of estimated parameters, Δ AICc = difference in AICc units from best model, ω = Akaike weight.

Parameter abbreviations defined in Table 2.1.

Model	LogLik	K	ΔAICc	ω
Migrant Abundance				
In.Area	-48.34	7	0.00	0.23
In.Area + BA.Dead	-47.73	8	1.24	0.12
In.Area + Loc.Orient	-47.81	8	1.41	0.11
In.Area + BA.Aspen	-47.94	9	1.66	0.10
Migrant Species Richness				
In.Area + BA.Aspen	-34.27	8	0.00	0.19
In.Area	-35.64	7	0.30	0.17
In.Area + BA.Dead	-34.97	8	1.40	0.10
Resident Abundance				
Loc.Orient	-97.87	7	0.00	0.22
In.Area + Loc.Orient	-97.06	8	0.83	0.15
In.Area + BA.Aspen + Loc.Orient	-95.82	9	0.88	0.14
BA.Aspen + Loc.Orient	-97.33	8	1.38	0.11
Resident Species Richness				
Loc.Orient	-70.99	7	0.00	0.18
BA.Dead + Loc.Orient	-70.20	8	0.87	0.12
In.Area + BA.Aspen + Loc.Orient	-68.95	9	0.88	0.12
In.Area + Loc.Orient	-70.29	8	1.06	0.11
BA.Aspen + Loc.Orient	-70.31	8	1.09	0.11
In.Area + BA.Dead + Loc.Orient	-69.07	9	1.12	0.10

Table 2.4. Relative Importance (RI) of covariates for bird abundance and species

richness candidate model sets. Parameter abbreviations defined in Table 2.1. f = number

Covariate	f	RI	
		Migrant	Resident
Bird Abundance			
In.Area	20	0.99	0.53
Loc.Orient	12	0.31	0.92
Reg.Orient	12	0.20	0.03
In.Area x Loc.Orient	4	0.07	0.11
In.Area x Reg.Orient	4	0.05	0.01
BA.Aspen	16	0.28	0.42
BA.Dead	16	0.32	0.25
Bird Species Richness			
In.Area	20	0.95	0.53
Loc.Orient	12	0.22	0.93
Reg.Orient	12	0.24	0.03
In.Area x Loc.Orient	4	0.05	0.11
In.Area x Reg.Orient	4	0.07	0.01
BA.Aspen	16	0.51	0.39
BA.Dead	16	0.30	0.37

of models (out of 31) that includes target covariate.

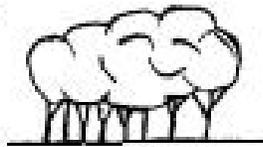
Table 2.5. Model-averaged covariate coefficients and unconditional confidence intervals for migrant abundance, migrant species richness, resident abundance, and resident species richness. Confidence intervals with lower confidence level (LCL) and upper confidence level (UCL) shown in bold do not contain zero. Parameter abbreviations defined in Table 2.1.

	Coefficient	Unconditional 95% CI		Unconditional 90% CI	
		LCL	UCL	LCL	UCL
Migrant Abundance					
In.Area	0.223	0.091	0.354	0.112	0.333
Loc.Orient	0.003	-0.003	0.009	-0.002	0.008
Reg.Orient	0.000	-0.005	0.004	-0.004	0.003
BA.Aspen	0.003	-0.005	0.011	-0.004	0.010
BA.Dead	0.014	-0.013	0.042	-0.009	0.038
In.AreaxLoc.Orient	0.000	-0.005	0.006	-0.004	0.005
In.AreaxReg.Orient	0.001	-0.003	0.005	-0.002	0.004
Migrant Species Richness					
In.Area	0.152	0.042	0.262	0.060	0.244
Loc.Orient	0.001	-0.004	0.006	-0.003	0.005
Reg.Orient	0.001	-0.003	0.005	-0.002	0.004
BA.Aspen	0.005	-0.001	0.012	0.000	0.011
BA.Dead	0.010	-0.014	0.033	-0.010	0.029
In.AreaxLoc.Orient	0.000	-0.005	0.005	-0.004	0.004
In.AreaxReg.Orient	0.001	-0.002	0.004	-0.001	0.004
Resident Abundance					
In.Area	0.127	-0.081	0.335	-0.048	0.302
Loc.Orient	0.013	0.005	0.021	0.006	0.020
Reg.Orient	-0.002	-0.009	0.005	-0.008	0.004
BA.Aspen	-0.008	-0.019	0.003	-0.017	0.002
BA.Dead	0.001	-0.040	0.042	-0.033	0.036
In.AreaxLoc.Orient	0.001	-0.007	0.009	-0.006	0.007
In.AreaxReg.Orient	-0.002	-0.008	0.003	-0.007	0.003
Resident Species Richness					
In.Area	0.093	-0.059	0.246	-0.035	0.222
Loc.Orient	0.009	0.003	0.015	0.004	0.014
Reg.Orient	-0.002	-0.007	0.003	-0.006	0.003
BA.Aspen	-0.005	-0.014	0.003	-0.012	0.002
BA.Dead	-0.024	-0.054	0.006	-0.049	0.001
In.AreaxLoc.Orient	0.000	-0.005	0.006	-0.005	0.005
In.AreaxReg.Orient	-0.002	-0.006	0.003	-0.005	0.002

a.



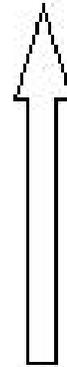
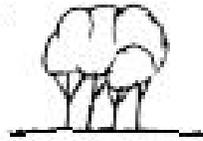
b.

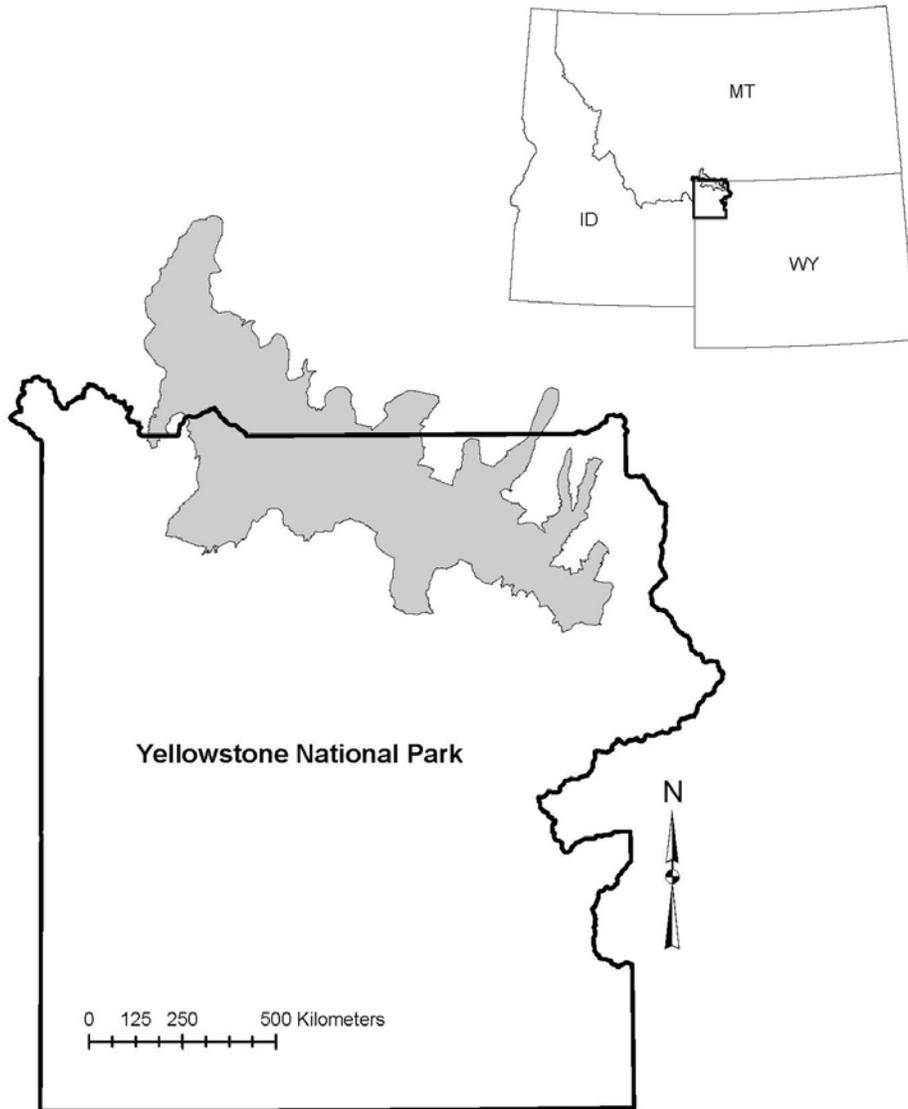


c.



d.





Appendix 1. Birds detected on the northern ungulate range during June of 2001, 02, and 03. Migrant: Y= long-distance migrant, N = resident/short-distance migrant. n = number observed.

Species		Migrant	n
American Kestrel	<i>Falco sparverius</i>	Y	37
American Robin	<i>Turdus migratorius</i>	Y	228
Belted Kingfisher	<i>Ceryle alcyon</i>	N	1
Black-billed Magpie	<i>Pica pica</i>	N	13
Black-capped Chickadee	<i>Parus atricapillus</i>	N	63
Brewers Blackbird	<i>Euphagus cyanocephalus</i>	Y	39
Brown-headed Cowbird	<i>Molothrus ater</i>	Y	30
Cassins Finch	<i>Carpodacus cassinii</i>	Y	1
Chipping Sparrow	<i>Spizella passerina</i>	Y	34
Clarks Nutcracker	<i>Nucifraga columbiana</i>	N	11
Cliff Swallow	<i>Hirundo pyrrhonota</i>	Y	1
Common Raven	<i>Corvus corax</i>	N	10
Common Yellowthroat	<i>Geothlypis trichas</i>	Y	20
Dark-eyed Junco	<i>Juncus hyemalis</i>	Y	41
Downy Woodpecker	<i>Picoides pubescens</i>	N	10
Dusky Flycatcher	<i>Empidonax oberholseri</i>	Y	41
Green-tailed Towhee	<i>Pipilo chlorurus</i>	Y	7
Hairy Woodpecker	<i>Picoides villosus</i>	N	14
Hammonds Flycatcher	<i>Empidonax hammondii</i>	Y	73
House Wren	<i>Troglodytes aedon</i>	Y	163
Indigo Bunting	<i>Passerina cyanea</i>	Y	3
Lazuli Bunting	<i>Passerina amoena</i>	Y	100
Lincolns Sparrow	<i>Melospiza lincolni</i>	Y	98
McGillivrays Warbler	<i>Oporornis tolmiei</i>	Y	49
Mountain Bluebird	<i>Sialia currucoides</i>	Y	77
Mountain Chickadee	<i>Parus gambeli</i>	N	131
Mourning Dove	<i>Zenaida macroura</i>	Y	3
Northern Flicker	<i>Colaptes auratus</i>	Y	188
Olive-sided Flycatcher	<i>Contopus borealis</i>	Y	2
Orange-crowned Warbler	<i>Vermivora celata</i>	Y	8
Pine Siskin	<i>Carduelis pinus</i>	Y	180
Red Crossbill	<i>Loxia curvirostra</i>	N	17
Red-breasted Nuthatch	<i>Sitta canadensis</i>	N	78
Red-naped Sapsucker	<i>Sphyrapicus nuchalis</i>	Y	58
Red-tailed Hawk	<i>Buteo jamaicensis</i>	Y	12
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	Y	1

Ruby-crowned Kinglet	<i>Regulus calendula</i>	Y	24
Ruffed Grouse	<i>Bonasa umbella</i>	N	4
Sandhill Crane	<i>Grus canadensis</i>	Y	1
Sharp-shinned Hawk	<i>Accipiter striatus</i>	Y	1
Song Sparrow	<i>Melospiza melodia</i>	Y	4
Starling	<i>Sturnus vulgaris</i>	N	77
Stellars Jay	<i>Cyanocitta stelleri</i>	N	6
Tree Swallow	<i>Tachycineta bicolor</i>	Y	39
Vespers Sparrow	<i>Pooecetes gramineus</i>	Y	3
Violet-green Swallow	<i>Tachycineta thalassina</i>	Y	70
Warbling Vireo	<i>Vireo gilvus</i>	Y	339
Western Meadowlark	<i>Sturnella neglecta</i>	Y	8
Western Tanager	<i>Piranga ludoviciana</i>	Y	21
Western Wood Pewee	<i>Contopus sordidulus</i>	Y	14
Williamsons Sapsucker	<i>Sphyrapicus thyroideus</i>	Y	23
Willow Flycatcher	<i>Empidonax trailii</i>	Y	1
Yellow Warbler	<i>Dendroica petechia</i>	Y	11
Yellow-rumped Warbler	<i>Dendroica coronata</i>	Y	28

**Aspen snag dynamics and cavity-nesting birds in Yellowstone's northern
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Ecology

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ABSTRACT

We examined current and possible future aspen dynamics and cavity-nesting bird abundances for Yellowstone's northern ungulate winter range. Our measurements suggest aspen stands located within the Yellowstone National Park (YNP) boundary are in a different condition than those located in the Gallatin National Forest (GNF) immediately outside the park. Stands inside YNP were composed of more snags and had fewer small diameter live stems than stands in GNF. Six of the 11 cavity-nesting bird species we analyzed were more abundant inside YNP where aspen snags were more abundant.

We discuss the implications of current and future aspen stand dynamics in the context of wolf re-introduction and trophic cascades ecosystem structuring for cavity nesting birds. Our results suggest aspen stands within YNP will experience a relative abundance of snags in the near future, followed by a snag deficit that will influence the abundance of several cavity-nesting bird species. The relative composition of future aspen stands within YNP will likely differ from historic conditions, and stands outside YNP, for several decades.

KEYWORDS

aspen, aspen decline, cavity-nesting birds, Gallatin National Forest, snags, trophic cascades, Yellowstone National Park

INTRODUCTION

Aspen (*Populus tremuloides*) has been identified as an important breeding habitat for western North American birds (Flack 1976; Winternitz 1980). In addition, aspen is the principal deciduous tree species providing nesting habitat for cavity-nesting birds in the montane western U.S. (Dobkin et al. 1995). The importance of aspen habitat for both primary-excavating and secondary cavity-nesting bird species has been noted by several researchers (Winternitz and Cahn 1983; Li and Martin 1991; Dobkin et al. 1995; Martin and Eadie 1999) as well as its importance as ecological “hot spots” (Hansen and Rotella 2002). Outside Colorado and northern Utah, aspen habitat typically represents less than 5% of most western landscapes (Despain 1990; Barnett and Stohlgren 2001; Barmore Jr. 2003). Thus, its reduction or disappearance may have considerable implications for birds.

Western U.S. aspen typically reproduce asexually. Existing clones produce new ramets (suckers) from an underground root system that grow and recruit into the overstory of an aspen stand consisting of 1 or more clones. In this way, aspen clones are thought to have persisted in western U.S. landscapes for thousands of years (Jelinski and Cheliak 1992; Mitton and Grant 1996). Reproduction by seed is rare in most of the western U.S., occurring only during infrequent “windows of opportunity” (Romme et al. 1997; Stevens et al. 1999) when the timing of disturbance and climate conditions are favorable.

Aspen habitat appears to be in decline in the western U.S. (Kay 1997; Bartos and Campbell 1998). Several mechanisms have been proposed to explain this decline,

including climate change and competition with exotics, but interrupted disturbance regimes and increased browsing intensity by wild and domestic ungulates appear to be the favored hypotheses (Bartos and Campbell 1998; Ripple and Larsen 2000). Some researchers suggest intense browsing by elk (*Cervus elaphus*) has led to the decline of aspen stands within Yellowstone National Park (YNP) (Kay 1990; Ripple and Larsen 2000; National Research Council 2002). The proposed mechanism involves intense ungulate browsing of young suckers, which kills or suppresses them, subsequently preventing recruitment of new stems into the overstory. This hypothesis requires browsing pressure to be greater than historic levels, when aspen recruitment was apparent. The extirpation of wolves (*Canis lupus*), the main predator of elk, in the 1930's, the prohibition of hunting within YNP, and the adoption of the "natural regulation" elk management policy by the National Park Service in 1968 may have led to a larger northern Yellowstone elk herd in recent decades (see Huff and Varley (1999) and Wagner (2006) for discussions of changing elk management on Yellowstone's northern range). Perhaps more importantly, the absence of wolves may have allowed the development of different foraging behavior among herbivores (primarily elk) leading to increased browsing of willows (*Salix* sp.), cottonwood (*Populus* sp.), and aspen suckers (e.g. Ripple et al. 2001; Beschta 2005; Beyer 2006). Furthermore, it has been suggested that this foraging behavior may be changing with the re-introduction of wolves (Ripple et al. 2001; Smith et al. 2003; Ripple and Beschta 2004; Creel et al. 2005; Hebblewhite et al. 2005).

North of the YNP boundary, the Gardner District of the Gallatin National Forest is one of the nation's most popular elk hunting destinations. From 1999 to 2001, an

average of 1375 elk/yr were harvested in the non-park portion of the northern range (Montana Dept. of Fish, Wildlife, and Parks 2004). Human hunting of elk on lands outside the park may influence elk abundance and behavior. During early winter 1989-1999, northern range elk densities outside YNP averaged 7.6 elk/km²; average density inside YNP was 12 elk/km² (Larsen and Ripple 2005). The decline and loss of aspen within the YNP portion of Yellowstone's northern ungulate range is likely due to an altered trophic cascade, or top-down structuring of the ecosystem, involving wolves, native ungulates, and vegetation such as aspen. The loss of a top predator in this system, combined with protection from human predation, apparently allowed changes in the abundance and possibly the behavior of ungulate prey populations. Conversely, the re-introduction of wolves in the northern Yellowstone ecosystem in 1996 seems to have stimulated the recovery of some previously impacted vegetation, such as willows, aspen, and cottonwood. The support for these effects is substantial (e.g. Ripple et al. 2001; National Research Council 2002; Ripple and Beschta 2003; Beschta 2005; Fortin et al. 2005; Hebblewhite et al. 2005; Ripple and Beschta 2005; Beyer 2006; Ripple and Beschta 2006), but role of elk in a trophic cascade continues to be debated (Vucetich et al. 2005).

Assuming the existence of top-down structuring of the northern range ecosystem, and holding disturbance constant or absent, we expect an increase in the relative abundance of aspen snags followed by a decrease as stands continue to deteriorate. Following the decrease, assertion of trophic cascades effects should allow relative snag abundance to recover at or near historical levels, depending on the interim loss of impacted, non-regenerating clones. The pattern of snag abundance is assumed to be

tracked by abundances of cavity nesting birds that use aspen snags heavily in this region. Further, we expect the above-mentioned changes in snag and cavity-nester abundances to be diminished or absent outside YNP, where human hunting appears to keep elk browsing pressure lower than inside YNP. Ultimately, our objective in this study was to evaluate the condition of aspen snags and cavity nesting birds in the context of a potential wolf-elk-aspen trophic cascade on Yellowstone's northern ungulate range. Specific objectives were: (1) to describe relative snag abundance inside and outside YNP; (2) describe relative cavity-nesting bird abundance inside and outside YNP; (3) compare the abundances of snags and cavity nesters inside and outside YNP; and (4) determine the current snag and cavity nester position within a hypothetical framework of aspen dynamics within YNP.

STUDY AREA

The 153,700 ha northern ungulate winter range of the northern Yellowstone ecosystem extends from Dome Mountain in the Gallatin National Forest (GNF) southeast to the Lamar Valley in Yellowstone National Park (YNP), USA (Figure 3.1).

Approximately two-thirds of the range is within YNP and the remaining one-third is in the GNF. A few small private holdings occur within the GNF (Lemke et al. 1998).

Elevation ranges from 1560 to 2350 m. Average annual precipitation is 40 cm/yr and ranges from 25 to 66 cm/yr with increasing elevation (Western Regional Climate Center 2004). Lodgepole Pine (*Pinus contorta*) is the dominant vegetation at higher elevations, particularly in poor soils. Douglas-fir (*Pseudotsuga menziesii*) and Engleman Spruce (*Picea englemanni*) occur where conditions are suitable. Aspen primarily occur

in an elevational band at approximately 2200 m where conifer-dominated forest meets steppe dominated by sagebrush (*Artemisia* sp.) and grasses, including Idaho fescue (*Festuca idahoensis*) and timothy (*Phleum pratense*). Aspen patches are distributed throughout the transition zone and steppe, primarily occurring where moisture conditions are favorable.

YNP is managed as a natural preserve. The GNF portion of the northern 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 are relatively consistent throughout the study area, but management differs regarding elk hunting between YNP and GNF portions of the range.

METHODS

Vegetation Data

From an existing map (St. John 1995) and 1994 aerial photographs (where gaps in map coverage occurred) we randomly selected 32 aspen patches ≥ 100 m from primary roads and ≤ 1 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 photo acquisition, and located ≥ 100 m apart. Thirty aspen patches were selected in 2001 and 2 more added in 2002. During field sampling we found that conifer invasion and changes in canopy cover had occurred in some patches, but retained these in our sample. Five patches from this initial sample were either misidentified or no longer extant. We chose the nearest extant patches that satisfied location criteria as replacements. One patch was located in the Decker Flats area of GNF, bordering YNP.

The very close proximity to YNP and special hunting restrictions for this location were confounding to our hypotheses. Thus we omitted this patch from our analysis. All remaining patches were > 1 km from the YNP boundary with 13 patches inside the park and 18 patches outside.

For each patch, we measured basal area of aspen and conifer stems ≥ 1 cm diameter at breast height (dbh) and canopy cover (%) for aspen and conifer separately. We used a five-point sampling pattern, initiated at the patch centroid with 4 points positioned 25 m in each cardinal direction. We did not sample at points that fell outside the patch. We used variable radius sampling technique with a 5, 10, or 20 Basal Area Factor (BAF) prism to measure tree 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. This provided similar sample precision among patches. At each sampling point, tree canopy cover was measured for aspen and conifer separately, using a mirror densiometer. We measured the dbh of each tree selected by the prism and noted its status as dead (snag) or alive.

Bird Data

We conducted point counts during the early breeding season each of 3 years (May 30 – July 1, 2001-03). Counts were 6 min. in duration, using 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 by migrant status (migratory or resident) (McEneaney 1996), and nesting habit (open cup canopy, open cup shrub, open cup ground, primary cavity, secondary cavity) (Ehrlich et al. 1988).

Detections known to be outside an aspen patch boundary were flagged for omission during analysis. Fly-overs were not counted unless they were considered to be using habitat for foraging (e.g., tree swallow (*Tachycineta bicolor*) or common nighthawk (*Chordeiles minor*) foraging > 10 m above canopy). Counts were not conducted during heavy precipitation or windy conditions (> 16 km/hr), but were not constrained by cloud cover. We assumed that bird detectability was similar among sites (e.g. Finch and Reynolds 1987; Schieck and Nietfeld 1995).

Each aspen patch was sampled 3 times during 2001 and 2002, and twice during 2003. We performed 1 count at each patch centroid and additional counts in larger patches; one additional count for each 5 ha. These additional counts were positioned 100 m from centroid point along the major geographic axis of the patch. Only two patches were > 5 ha. Using the protocol described previously, we collected vegetation data at these additional points and the average values of all points in the patch were used in subsequent analyses. Additionally, for patches with > 1 point we used the average of bird count data in our analyses. We sampled spatially clustered groups of 3 to 5 aspen patches daily during morning hours (sunrise to 10:30 am); an initial patch was randomly chosen, and each nearest patch 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 one observer (JPH).

Analysis

We used Welch's two-sample t-test for samples with unequal variance to assess differences in aspen diameter, canopy cover, snag composition, and the abundance of

cavity-nesting birds, inside and outside YNP. Uniform application of Welch's t-test is a conservative approach that is more likely to accept null hypotheses of no difference when variances are similar. Thus, we avoided the possibility of concluding false differences while increasing our confidence if differences are found. Statistical analyses were done in S-Plus statistical software (Insightful 2001) and differences considered significant at $\alpha = 0.05$. For each species of cavity nesting bird with > 35 detections, we constructed 95% confidence intervals for inside and outside YNP for a visual comparison of abundances. Non-overlapping confidence intervals were interpreted as a significant difference in the abundance of a given species inside and outside YNP.

RESULTS

Aspen condition

Several characteristics differed between aspen stands inside YNP and outside the park (GNF) (Table 3.1, Figure 3.2). Mean live and dead stem diameters were significantly greater inside YNP. Live and dead aspen stem diameters were on average 10 cm greater inside the park when compared to GNF. Aspen canopy cover inside YNP tended to be less than outside the park. The relative abundance of large-diameter snags (≥ 20 cm) was significantly greater in YNP stands with YNP stands containing approximately 80% more large diameter snags (18% versus 10% respectively). YNP stands were typically more open with almost no small diameter live stems, whereas GNF stands contained smaller diameter trees that were recruiting into the overstory (Figure 3.2). Thus, large-diameter live stems (≥ 20 cm) had greater representation as snags in YNP stands when compared to GNF stands.

Birds

We identified 11 bird species that were detected > 35 times during sampling for inclusion in our analyses (Table 3.2): American Kestrel (*Falco sparverius*), Black-capped Chickadee (*Parus atricapillus*), House Wren (*Troglodytes aedon*), Mountain Bluebird (*Sialia currucoides*), Mountain Chickadee (*Parus gambeli*), Northern Flicker (*Colaptes auratus*), Red-breasted Nuthatch (*Sitta canadensis*), Red-naped Sapsucker (*Sphyrapicus nuchalis*), Starling (*Sturnus vulgaris*), Tree Swallow (*Tachycineta bicolor*), and Violet-green Swallow (*Tachycineta thalassina*). Six of 11 species were significantly more abundant inside YNP (Figure 3.3; American Kestrel, $t = 2.41$, $p = 0.02$; House Wren, $t = 2.12$, $p = 0.04$; Mountain Bluebird, $t = 2.72$, $p = 0.01$; Northern Flicker, $t = 3.36$, $p < 0.01$; Red-breasted Nuthatch, $t = 2.21$, $p = 0.03$; Starling, $t = 2.39$, $p = 0.02$). Two species (Tree Swallow and Violet-green Swallow) showed a marginal but non-significant trend toward greater abundance inside YNP (Tree Swallow, $t = 1.41$, $p = 0.17$; Violet-green Swallow, $t = 1.34$, $p = 0.19$). The remaining 3 species (Black-capped Chickadee, Mountain Chickadee, and Red-naped Sapsucker) showed no difference in abundance between YNP and GNF (Black-capped Chickadee, $t = 0.63$, $p = 0.53$; Mountain Chickadee, $t = 0.70$, $p = 0.48$; Red-naped Sapsucker, $t = 0.18$, $p = 0.86$).

DISCUSSION

Aspen condition

We expected and found a sparser canopy among YNP stands as mature trees have converted to snags and have not been replaced by overstory recruitment. In contrast,

GNF stands had more apparent recruitment, resulting in a denser canopy and lower relative snag abundance (see Table 3.1). The smaller mean stem diameter of GNF stands suggests an age class distribution that includes small-diameter trees. Conversely, the larger mean stem diameter found among YNP stands reflects an absence of small-diameter stems. Thus it appeared GNF stands had recently experienced successful recruitment of new stems, and YNP stands had not. The processes leading to these conditions may have profound implications for the future. Assuming the presence of trophic cascades processes, the continued success of wolf re-introduction, and the absence of major disturbance, we expect northern range aspen stands within YNP to follow a path of deterioration and recovery resulting in a relative increase in the abundance of aspen snags followed by a decline in snags before eventual recovery catches up and once again produces snags at or below historic levels. Our results suggest a current abundance of snags within YNP aspen stands that is being tracked by some cavity-nesting bird species.

Over the next 150 years, with the retention of wolves and reduced elk abundance, aspen are expected to recover with subsequent effects on cavity nesting birds (Figure 3.4). It should be noted that aspen clones lost to the present decline cannot be involved in recovery. Thus, northern range aspen habitat within YNP may not recover fully to historic levels (e.g., 1900).

Aspen decline

There is considerable evidence for top-down structuring of the northern Yellowstone ecosystem through a trophic cascade where wolves are the top predator

(Ripple et al. 2001; National Research Council 2002; Ripple and Beschta 2004; Beschta 2005; Fortin et al. 2005; White and Garrott 2005; Beyer 2006; Ripple and Beschta 2006). In the absence of wolves, intense elk browsing of young aspen suckers has severely impacted aspen stands within YNP by reducing or eliminating recruitment of new stems to replace mature aspen as they die. Figure 3.5 shows repeat photographs of a typical aspen stand within YNP during 1986 and 2004. Among the foreground trees, reduced live canopy cover, greater snag abundance, numerous fallen aspen stems, and an apparent lack of regeneration and recruitment is visible in the later photograph. These photographs were taken approximately 10 years prior, and 10 years after wolf re-introduction. The earlier photograph was acquired approximately 55 years after wolf extirpation and 25 years after the adoption of the “natural regulation” elk management policy by the National Park Service. In the approximately 20-year period between these photographs, aspen condition has deteriorated rapidly. And, although wolves had been present for almost 10 years, the later photograph does not yet show signs of aspen recovery due to trophic cascades effects. Wolves, especially where combined with other top predators, such as grizzly bear (*Ursus arctos*), appear to reduce ungulate prey populations in most systems they have been studied (Peterson et al. 2003). Elk densities on Yellowstone’s northern range have declined after wolf re-introduction, likely due to lethal effects of wolf predation, and are expected to continue declining (White and Garrott 2005). Limited aspen and substantial willow recovery have been documented (e.g. Ripple and Beschta 2005; Beyer 2006) as elk densities on Yellowstone’s northern range continue to decline and it seems reasonable to expect a lag in a more widespread aspen recovery.

Live aspen and snag dynamics

Our data (Table 3.1) show a greater percentage of large diameter snags in YNP stands that is not mirrored in GNF stands. Photographs of typical stands sampled during this study show greater abundance of standing and recently fallen snags in YNP stands (Figure 3.2). Outside YNP, where human hunting may affect elk density and/or foraging behavior, aspen stands have continued to recruit new stems into the overstory; stands within YNP have not. St. John (1995) attributes greater aspen recruitment found within 0.5 km of roads outside YNP (within the northern winter range) to human hunting of elk and suggests predation risk by humans has modified the behavior of elk, and subsequent browsing intensity on aspen. In our samples, all stands outside YNP were recruiting new stems into their overstory and most within YNP were not. For YNP stands, the lack of new stem recruitment combined with the dying off of mature stems appears to be producing an abundance of snags. Thus we suggest that at present, stands within YNP have a relative abundance of snags not found outside the park.

We used the following equation, developed by Ripple and Larsen (2000) for aspen occurring on Yellowstone's northern range, to determine the average age of an aspen stem with a 20 cm dbh.

$$AGE \text{ (years)} = -6.8624 + (3.12587 * DBH)$$

Successfully recruiting aspen are expected to reach large diameters (≥ 20 cm dbh) in approximately 56 years. Again, assuming trophic cascades effects will allow aspen recruitment to occur, post wolf re-introduction recruitment of significant numbers of

large diameter live aspen is not expected until 2052 at the soonest (approximately 56 yrs after 1996).

We considered 100-yr. old aspen as mature, thus likely to die and convert to snag status. We arrived at this age as a typical lifespan for aspen in the northern range by determining the mode age of the age class distribution published by Larsen and Ripple (2003). Additionally, an examination of aspen age distributions from several western U.S. sites by Mueggler (1989) reports a modal age of 90-100 years, confirming the Larsen and Ripple (2003) estimate. Thus, any stems recruiting shortly after wolf re-introduction (1996-2000) will not convert to large diameter snags until approximately 2100. Larsen and Ripple (2003; 2005) found > 95% of current living aspen in the YNP portion of the northern ungulate winter range to be >80 yrs old. We can expect many of these trees to die soon since they are at or near the average lifespan. After death, aspen snags do not persist long. Hart and Hart (2001) report an average period of 10.7 yrs. standing after death for aspen snags > 15 cm dbh in the Bridger-Teton National Forest, northwest Wyoming. Consequently, most currently live trees and all currently standing snags will fall and become logs before newly recruited stems can reach larger diameters (≥ 20 cm dbh), mature, and die to create new snags. During the period when most current snags have fallen, and recruiting stems are maturing, there will be a paucity of large diameter snags which are preferred as nest sites by many cavity-nesting birds. We estimate the length of this interval to be about 50 years, beginning approximately 2045 as the remaining large stems mature, die and fall (see Figure 3.4). After this period, we expect the recruitment, maturation, and death of large diameter stems to continue until relative snag abundance approaches historical (1900) levels. Recovery to conditions

resembling those of the historic period (1900-1930) may not occur until approximately 2150 (see Figure 3.4). Note also that the present deterioration of many stands (i.e., the decline and disappearance of clones) within YNP may lead to their permanent disappearance. Subsequently, these stands would not be able contribute to aspen habitat recovery at the landscape scale.

Cavity nesting bird dynamics

Six of the 11 cavity-nesting bird species analyzed in this study are significantly more abundant within YNP. Two species show a non-significant trend toward greater abundance within YNP, and 3 are equally abundant inside and outside YNP. It is reasonable to expect cavity nester abundance to track snag abundance. Winternitz and Cahn (1983) found that nesthole trees in Colorado aspen were mostly dead or decadent (infected with heartrot) with an average age > 100 yrs. Some primary cavity nesters seem to prefer dead aspen to live aspen (e.g. Northern Flicker) and aspen snags, especially those with broken tops, appear highly attractive to a large number of cavity-nesters in general (Li and Martin 1991; Dobkin et al. 1995; Moore 1995; Caton 1996). American Kestrels are dependent on abandoned large primary excavator cavities or suitable natural cavities typically occurring in large snags (Smallwood and Bird 2002). Red-breasted Nuthatches have been shown to strongly prefer snags for nest sites (Harestad and Keisker 1989; Li and Martin 1991; Steeger and Hitchcock 1998; Ghalambor and Martin 1999). Power and Lombardo (1996) state that very little is known about natural nest cavity selection by Mountain Bluebirds. We observed Mountain Bluebirds using cavities in large diameter snags that were not surrounded by dense cover. House Wrens use natural

and abandoned primary-excavator cavities, preferring sites with little or no surrounding foliage (Finch 1989; Johnson 1998). In Yellowstone's northern range, House Wrens appear to be associated with deteriorating aspen stands that have abundant snags and sparse understories. Starlings use any suitable cavity for nesting but are very successful competitors for abandoned, and even occupied, primary excavator nest cavities (Ingold 1989; Dobkin et al. 1995; Moore 1995). Most Starling nests detected in this study appeared to be Northern Flicker cavities located in aspen snags.

Our data suggest that Tree and Violet-green Swallows are more abundant inside YNP. However, due to high variability, the difference was not statistically significant (see Figure 3.3). Swallows are often reported to use existing nest cavities in snags located in open situations (Rendell and Robertson 1989; Robertson et al. 1992; Lawler and Edwards 2002). Aspen stands within YNP are generally more open with sparser canopies.

Of the 3 species with similar relative abundances inside and outside YNP, one is a primary excavator (Red-naped Sapsucker) that prefers large live aspen stems for nest excavation (Crockett and Hadow 1975; Dobkin et al. 1995). The remaining two secondary cavity nesters are taxonomically and behaviorally related (Black-capped and Mountain Chickadees). The similar relative abundance of sapsuckers inside and outside YNP suggests similar occurrence of suitable live-aspen nest sites. Black-capped chickadees and mountain chickadees were found in similar numbers inside and outside YNP. Hill and Lein (1989) found similar habitat use by both species in the Rocky Mountains of southwestern Alberta. Both species used conifer habitat extensively with mountain chickadees using areas with large conifers more frequently than black-capped

chickadees. Yellowstone's northern range habitats are similar to those found in Hill and Lein's (1989) study. Hill and Lein (1989) also found both species of chickadee using cavities excavated by red-naped sapsuckers. If a preference exists for these cavities, it may account for the similar relative abundances of all 3 species in this study.

Limitations

We do not know to what extent cavity nesters that use aspen snags might switch to live aspen or conifers for nest sites as aspen snag abundance declines, but the response is likely to vary by species. Some researchers have found nest-site limitation among western sites (e.g. Zarnowitz and Manuwal 1985). Others have found that nest sites are not limiting, but rather foraging opportunity limits cavity nester abundance (e.g. Brawn and Balda 1988; Welsh and Capen 1992; Caton 1996). A snag deficit within the northern range of the Yellowstone ecosystem likely will affect species differently. For example, Dobkin et al. (1995) and Crockett and Hadow (1975) found that red-naped sapsuckers used live trees more often than dead trees for nesting in eastern Oregon and southern Colorado respectively. Daily et al. (1993) found red-naped sapsuckers in Colorado to be significantly associated with aspen that spatially co-occur with willows. Willows are currently more prevalent outside YNP (Jackson 1992). However, recent studies have documented a release of willows inside YNP attributed to changes in elk herbivory following wolf re-introduction (Beyer 2006; Ripple and Beschta 2006). This may influence the future distribution of red-naped sapsuckers.

Assuming YNP aspen stands follow the course presented above, (Figure 3.4) recruited live aspen will attain large diameters before the end of the snag deficit interval.

Primary excavators, especially those that prefer live aspen, will likely create cavities in these live aspen. In the face of a snag deficit, these live aspen cavities should see use by all cavity-nesting species regardless of their preference for snags.

Fire disturbance may stimulate aspen regeneration by vigorous suckering leading to canopy recruitment, especially if ungulate browsing intensity is at low levels (White et al. 2003). Fire disturbance also may affect cavity-nesting birds, influencing both nest site availability and high-quality foraging habitat (e.g. Caton 1996). The presence and timing of fire-killed aspen and conifer snags complicate the ability to predict cavity-nester abundance. A relatively small portion (< 30%) of YNP's northern range was involved in the extensive wildfires of 1988 and even less area actually burned. We should note however, that the hypothesized dynamics presented in this study (Figure 3.4) assume disturbance, such as fire, is absent. Certainly, the Yellowstone ecosystem experiences disturbances at several scales that would need to be considered when relating the ideas presented here with actual conditions.

CONCLUSIONS

Combining our results describing current aspen and cavity-nesting bird conditions with historical data, recently published data, and an understanding of stand dynamics leads us to conclude that northern range aspen stands within YNP will experience changes over the next several decades that will likely have consequences for cavity-nesting birds. These changes may provide an opportunity for ecologists to better understand the role of trophic cascade processes in ecosystem structuring over long time scales.

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LIST OF FIGURES

Figure 3.1. Location of the northern ungulate winter range (shown in gray) in the greater Yellowstone ecosystem, USA.

Figure 3.2. Typical northern range aspen stands (a) inside and (b) outside YNP during June 2001. Note open stand conditions, abundant snags, and absent small diameter aspen in YNP stand. GNF stand has fewer snags and apparent recruitment of small diameter aspen.

Figure 3.3. Mean abundance and 95% confidence intervals of cavity-nesting birds in aspen stands on Yellowstone's northern range inside (YNP) and outside (GNF) Yellowstone National Park. AMKE = American Kestrel, BCCH = Black-capped Chickadee, HOWR = House Wren, MOBL = Mountain Bluebird, MOCH = Mountain Chickadee, NOFL = Northern Flicker, RBNU = Red-breasted Nuthatch, RNSA = Red-naped Sapsucker, STAR = European Starling, TRSW = Tree Swallow, VGSW = Violet-green Swallow.

Figure 3.4. Hypothesized changes in (a) presence of wolves, (b) elk browsing intensity, (c) large live aspen (> 20cm dbh) abundance, (d) abundance of large aspen snags (> 20cm dbh), (e) relative large snag abundance (% of stand), and (f) cavity-nesting bird abundance within YNP over a 250 yr. interval (1900 to 2150). Gray areas indicate range of condition. Dashed lines indicate projections. Post-reintroduction wolf presence (1996) is assumed to remain constant. Projected elk browsing intensity is assumed to return to historical (pre-wolf extirpation) levels. Projected live aspen and aspen snag dynamics assume an absence of large

disturbance (e.g. fire). Large live aspen and large aspen snags are presented in the same relative scale. Relative abundance of large snags (% of stand) determined by large live aspen and large aspen snag abundances ($\text{Snag abundance} / \text{Snag abundance} + \text{Live abundance}$). Cavity nesting birds are assumed to retain preference for aspen snags during scarcity.

Figure 3.5. Repeat photos of an aspen stand on the northern range in YNP. Top photo (a) was taken during August, 1986 (Photo by Charles Kay), bottom photo (b) was taken during August 2004.

Table 3.1. Northern range aspen stand characteristics for 13 stands inside (YNP) and 18 stands outside (GNF) Yellowstone National Park, June 2001. Variables are: live aspen stem diameter (cm) all stems, dead aspen stem diameter (cm) all stems, overstory canopy cover (%), and large-diameter snags (% of all stems ≥ 20 cm). Comparisons are Welch's t-test for samples with unequal variance.

	YNP		GNF		t	p
	Mean	SD	Mean	SD		
Live Stem Diameter (cm)	37	12	27	9	9.8	<0.01
Dead Stem Diameter (cm)	31	13	21	10	3.6	<0.01
Canopy Cover (%)	66	13	76	18	1.9	0.07
Snags ≥ 20 cm (%)	18	12	10	8	2.3	0.03

Table 3.2. Cavity-nesting birds detected in the northern range of the Yellowstone ecosystem June 2001, 02, 03. Migrant status after McEneaney (1996), YNP = Yellowstone National Park, GNF = Gallatin National Forest.

Species	Migrant	n	YNP	GNF
American Kestrel (<i>Falco sparverius</i>)	Y	37	25	12
Black-capped Chickadee (<i>Parus atricapillus</i>)	N	63	22	41
Downy Woodpecker (<i>Picoides pubescens</i>)	N	10	4	6
Hairy Woodpecker (<i>Picoides villosus</i>)	N	14	7	7
House Wren (<i>Troglodytes aedon</i>)	Y	163	95	68
Mountain Bluebird (<i>Sialia currucoides</i>)	Y	77	44	33
Mountain Chickadee (<i>Parus gambeli</i>)	N	131	48	83
Northern Flicker (<i>Colaptes auratus</i>)	Y	188	112	76
Red-breasted Nuthatch (<i>Sitta Canadensis</i>)	N	78	43	35
Red-naped Sapsucker (<i>Sphyrapicus nuchalis</i>)	Y	58	21	37
Starling (<i>Sturnus vulgaris</i>)	N	77	70	7
Tree Swallow (<i>Tachycineta bicolor</i>)	Y	39	29	10
Violet-green Swallow (<i>Tachycineta thalassina</i>)	Y	70	38	32
Williamsons Sapsucker (<i>Sphyrapicus thyroideus</i>)	Y	23	11	12

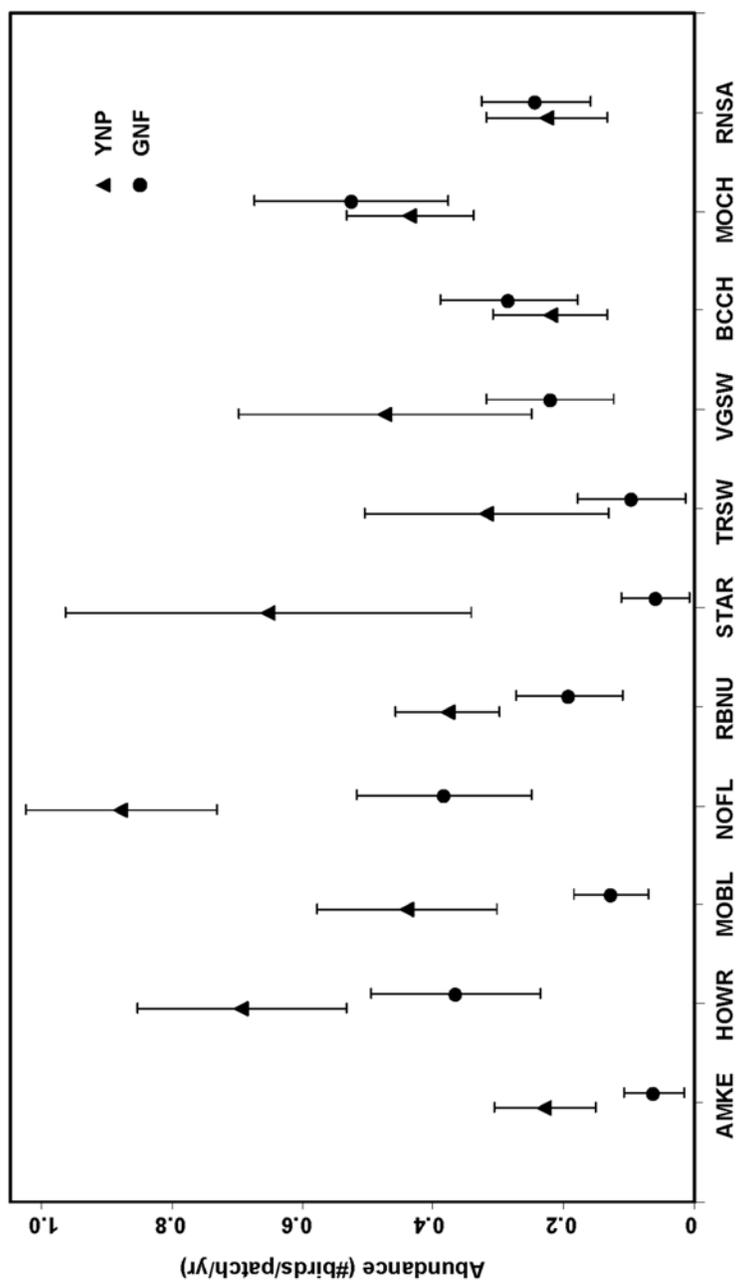


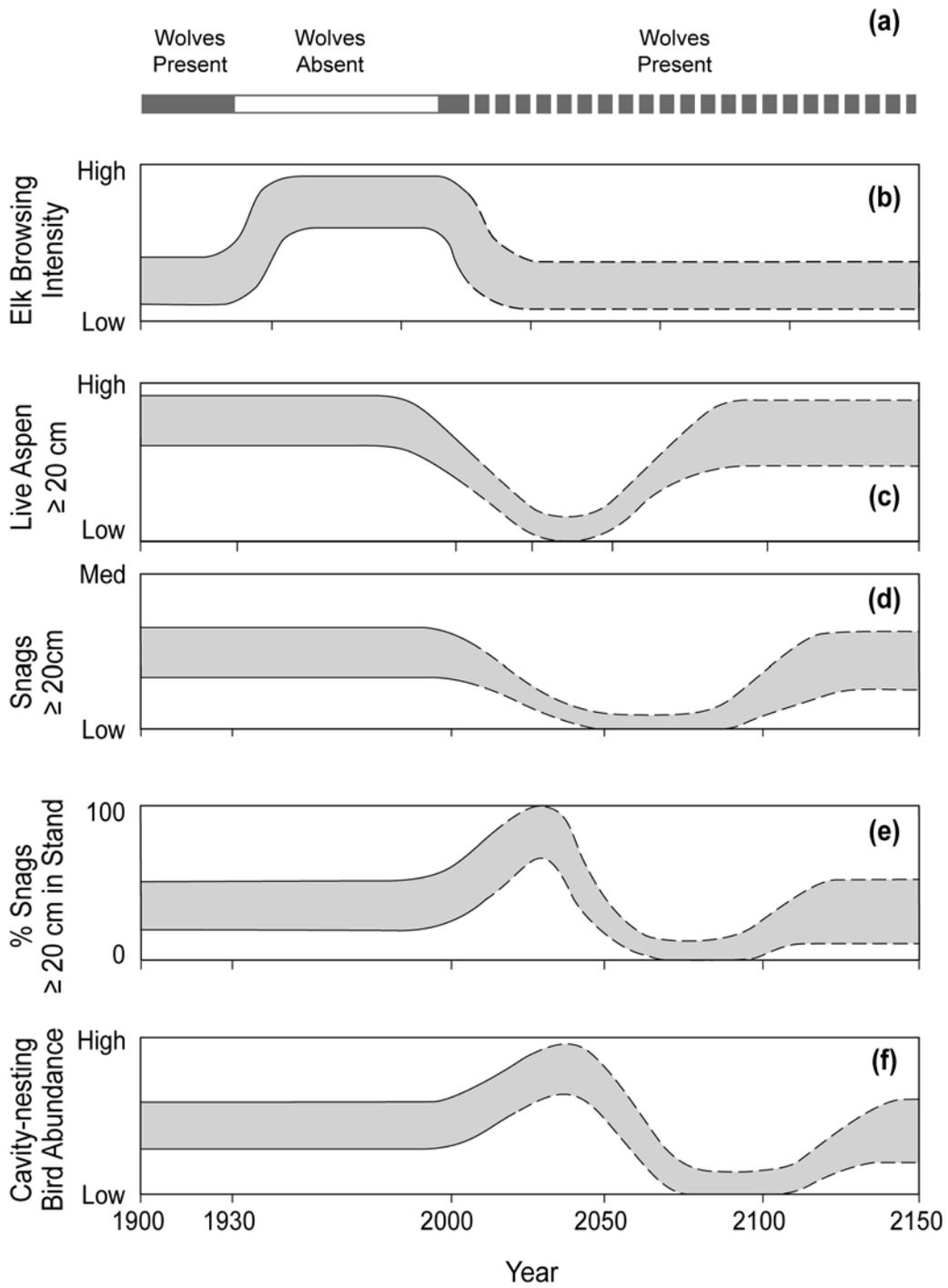
a



b







a.



b.



CONCLUSION

Discernable relationships between birds and aspen habitat in the northern ungulate winter range of the northern Yellowstone ecosystem occurred at every scale considered. The highly mobile nature of birds and the relatively dynamic nature of aspen ecology presented challenges in the form of a variable system. However, with each of the preceding analyses, patterns emerged regarding the abundance or diversity of birds and their occurrence in aspen habitat. Scale, both spatial and temporal, also emerged as an important determinant of pattern.

Fine spatial scale perspective: habitat heterogeneity and avian diversity.

At a relatively fine scale (patch or stand level), it appears that conifer invasion does not enhance avian diversity. Migrant species richness was greater in pure aspen stands than in either mixed conifer/aspen or pure conifer stands with no indication of increased diversity in mixed stands. Bird diversity was measured as both species richness and by the Shannon-Weiner diversity index. Both measures responded similarly in regression analyses. Habitat heterogeneity was measured as the ratio of conifer to aspen canopy cover, or basal area. Both measures of habitat heterogeneity explained bird diversity similarly. Log-ratio tests of quadratic versus first-order linear regression models for migrant bird diversity showed no positive effect of conifer presence in aspen stands. Quadratic models for resident bird diversity were better than first-order models for all combinations of measures of bird diversity and habitat heterogeneity except one. Migrant diversity was moderately well explained by measures of habitat heterogeneity with R^2 values for first-order (linear) regressions of migrant diversity on habitat

heterogeneity ranging from 0.34 to 0.43. Resident diversity was weakly related to habitat heterogeneity. R^2 values ranged from <0.01 to 0.11 for first order (linear) regressions, and 0.10 to 0.27 for quadratic regressions. The weak positive relationship of resident species with habitat heterogeneity likely reflects the generalist, or conifer association, of resident species. Examples of such species are Mountain and Black-capped Chickadees, which are frequently associated with conifer habitat (Hill & Lein, 1989). Conifer habitat is abundant in Yellowstone's northern range and most other western landscapes where aspen occur. Thus, land managers who wish to conserve or restore aspen and maintain high levels of bird diversity, especially migratory species, may want to focus on creating or conserving pure aspen stands. By doing so, the risk of neglected conifer invasion is avoided while ensuring the greatest level of bird diversity achievable at the stand level.

Although the number of studies addressing this question remains small, the strong concordance of results may indicate an adequate state of knowledge for informed management decisions. However, it is worth noting that aspen stands do not occur in isolation; land managers would do well to maintain matrix habitats, including conifer habitat, juxtaposed with aspen to provide for a more appropriate beta, or landscape, approach to bird diversity. This coarser-scale perspective is paramount to management of these systems.

Coarse spatial scale perspective: habitat patch and avian abundance/diversity.

Coarse-scale patterns for migratory and resident bird relationships with aspen habitat patches in Yellowstone's northern range were evident. For migratory birds, there was no support of passive interception by aspen patches. Patches oriented perpendicular

to the northerly travel of long-distance migratory birds had similar migratory bird abundance and diversity as parallel-oriented patches. Furthermore, no pattern emerged for migratory birds and patch orientation relative to elevational gradient. Instead, patch area was the most important predictor of both abundance and species diversity of migratory birds.

Conversely, resident (and short-distance migrant) birds were strongly influenced by the orientation of patches relative to the general elevational gradient. There was no relationship between patch orientation relative to North. Patch area was moderately important for these species. This suggests that resident and short-distance migratory birds are intercepted passively as they move up in elevation during spring.

The effect of passive interception by habitat patches remains largely unstudied. A few studies have addressed the topic for insects (Faeth & Kane, 1978), plants (Buckley & Knedlhans, 1986) or tidal aquatic organisms (Tanner, 2003), but my study is one of only two known addressing patch orientation (passive interception) and birds (see Gutzwiller & Anderson, 1992). As such, my findings should be viewed as an exploratory investigation of the topic. Further research is needed to better understand interactions between migrating birds and aspen habitat at landscape scales. Such research may be directed toward understanding why passive interception appears to affect resident and migrant species differently, and why these effects appear to switch with study area (i.e. Gutzwiller and Anderson 1992). Further, it would be helpful to know if the strength of passive interception effects varies with particular bird species.

Coarse spatial and temporal scale perspective: aspen and cavity-nesting bird dynamics.

Combining historical and current aspen research with an understanding of aspen stand dynamics allows a strictly conceptual evaluation of aspen and cavity nesting bird dynamics in the northern ungulate range over a 150-year interval. Here I found that current aspen and cavity-nesting bird data fit hypothesized conceptual relationships between several ecological entities operating in a top-down (trophic cascade) structured ecosystem. Wolf eradication, and their eventual re-introduction, appears to have triggered changes in several ecosystem processes including, ungulate browsing of aspen, aspen regeneration, aspen snag abundance, and cavity-nesting bird abundance. Tracking these processes over time suggests the effects of wolf eradication and subsequent re-introduction will continue for several decades into the future.

Comparisons of northern ungulate range aspen stand condition, and cavity-nesting bird abundance, inside and outside YNP show that mean diameter at breast height (dbh) of live and dead aspen, relative aspen snag abundance, and cavity-nesting bird abundance is higher among stands within YNP. Mean live aspen stem diameter was 10 cm greater and mean dead aspen stem diameter was 10 cm greater inside YNP, and aspen stands inside YNP had 80% greater snag abundance than outside stands. Six of the 11 species of cavity-nesting birds analyzed were significantly more abundant in stands inside the park. Aspen snags are important as nest sites for many cavity-nesting birds (Winternitz & Cahn, 1983). Among the species that were not more abundant within YNP were species that have little preference for snag nesting sites, or prefer live aspen sites (e.g. Red-naped Sapsucker)(Dobkin *et al.*, 1995).

The larger mean stem diameter of YNP stands reflect the lack of recruitment of regenerating small-diameter stems in recent decades. New stem recruitment has occurred

outside the park. The greater percent snag abundance among stands inside YNP reflects the greater proportion of mature dead and dying stems that occur in stands without recruitment. These snags currently provide nesting sites for several cavity-nesting bird species which is reflected in the greater abundance of most of the bird species analyzed.

Over the last few decades, there has been no wolf or human predation of elk inside YNP. Outside YNP, elk have been consistently hunted by humans. Several researchers have suggested that the lack of predation within YNP has led to either an abundance of elk, or a change in the behavior of elk, which subsequently led to intense browsing of aspen suckers prohibiting successful regeneration of overstory stems (e.g. Kay, 1990). Partial evidence for this comes from the documented regeneration among aspen stands just outside the park (and within the northern range) (St. John, 1995). All aspen stands in the northern range are assumed to experience the same climatic and geophysical conditions. However, an apparent difference between northern range areas inside and outside YNP is elk hunting by humans. The results of my study suggest negative effects of elk browsing on aspen regeneration within YNP.

The re-introduction of wolves in 1995 has potentially changed aspen dynamics, and consequently cavity-nesting bird dynamics, within YNP. The trophic cascades hypothesis of ecosystem structuring in the Greater Yellowstone Ecosystem, including the YNP portion of the northern range has considerable support (Beschta, 2005; Beyer, 2006; National Research Council, 2002; Ripple & Beschta, 2006) although debate still exists regarding the precise effect of wolves on elk abundance (Vucetich *et al.*, 2005). The strength and precise mechanism (elk abundance or behavior) of trophic cascade effects remain active topics of research in the northern range (Creel *et al.*, 2005).

Assuming the northern range ecosystem is structured via top-down effects. The re-introduction of wolves re-establishes a trophic cascade involving wolves, elk, and aspen that subsequently affects cavity-nesting birds within YNP. Using published information about current and historic conditions, aspen stand dynamics, and avian ecology, I constructed a framework of relative abundances of each level over time. Placing current conditions within this framework for YNP's northern range suggests continued adjustments in aspen stand condition and cavity nesting bird abundance for several decades into the future. Currently YNP stands are composed almost entirely of large diameter stems, most of which are dead. Cavity-nesting birds appear to respond to this relative snag abundance. As these stems continue to die and fall, there will be a period of several years before regenerating young aspen may recruit into large diameter canopy trees. During this time, it is likely cavity-nesting bird abundance will decline considerably. Eventually, large diameter stems will be recruited into stands, die and become snags at levels of abundance approaching that of historic conditions (although some aspen stands may be lost in the interim due to intense elk browsing during wolf absence). Cavity-nesting bird abundance is expected to respond positively to greater snag presence.

Further research on this topic may confirm and clarify relationships between aspen and cavity-nesting birds in the context of a top-down structured ecosystem. Future measurements would help with confirmation. Additionally, the aspen and cavity-nesting bird dynamics outlined in this study assume the absence of disturbance, such as large fires. A refinement to the relationships constructed in this study might include effects of

periodic disturbance. It is hoped that this dissertation will provide an initial point from which the complex ecological interactions of the northern range are better understood.

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