RESEARCH ARTICLE

Aspen patch and migratory bird relationships in the northern Yellowstone ecosystem

Jeff P. Hollenbeck · William J. Ripple

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 and basal area of aspen to be the most important covariates 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 both migratory strategies, likely because aspen snags are an important habitat for most cavity-nesting species. Landscape ecological theory postulates passive interception of dispersing or migrating organisms by patches of suitable habitat. Our results suggest that residents/ short-distance migrants are intercepted by patches that are oriented perpendicular to the elevational gradient of our study region resulting in greater abundances and species richness in those patches. However, long-distance migrants appear to use aspen patches without regard to orientation, but rather to patch area.

Keywords Aspen · Bird migration · Interception · Patch orientation · *Populus tremuloides* · 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 2003), its persistence in these landscapes may be risk. The reduction or disappearance

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of this habitat would likely have considerable implications for bird diversity. 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 studies of bird and habitat relations have demonstrated effects for many species and habitat types worldwide (e.g., Graham and Blake 2001; Fischer and Lindenmayer 2002; Davis 2004; Tubelis et al. 2004; Taft and Haig 2006), including the western U.S. There are relatively few studies that focus on relations between birds and aspen in western U.S. landscapes. Some of these studies concentrate on landscape context or enrichment. For example, Lawler and Edwards (2002a,b) demonstrated the importance of landscape context for aspen stands (dominant matrix of conifer forest or open grassland/steppe) for cavity-nesting birds in northern Utah. Other studies focused explicitly on aspen habitat as patches. For example, Turchi et al. (1995) found aspen patch isolation to be a poor predictor of bird species richness in Rocky Mountain National Park, Colorado, and Johns (1993) found that long-distance, short-distance, and resident bird diversity increased with aspen patch area in the parklands of Saskatchewan, Canada. All landscape-scale studies of birds in western aspen appear to acknowledge the importance of aspen habitat relative to respective matrix habitats.

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 Fig. 1). The patchy distribution of aspen in most
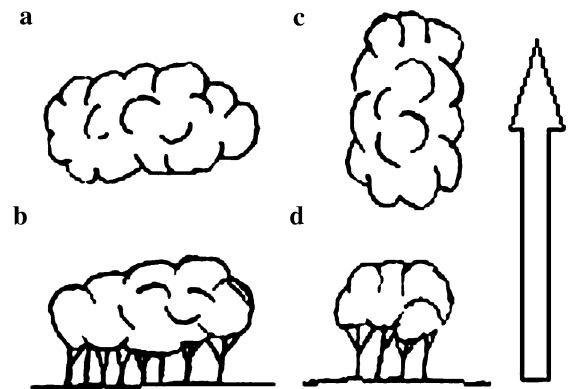

Fig. 1 Effect of patch orientation. Patches viewed from above (a and c) have same area but different orientations relative to direction of bird migration (represented by arrow). Views b and d show the ''interceptive surface'' of each patch; patches oriented perpendicular to migratory direction have greater surface presentation than those parallel to migratory direction

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. Gutzwiller and Anderson (1992) found strong evidence that suggested patches of suitable nesting habitat (riparian cottonwood) intercepted some migrating birds. Since cottonwood, a congener of aspen, is of value to birds for many of the same reasons as aspen (such as canopy structure, associated invertebrate abundance, natural and easily excavated cavities), 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 (Yong and Finch 1997), or routes along a general northerly (or southerly) direction of travel within biogeographic constraints (such as topographic relief or suitable stopover habitat) (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 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 (Fig. 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 2007). 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 deeper, moist soil occurs. Most aspen are distributed as patches at approximately 2200 m elevation where conifer forest transitions to steppe, which is dominated by sagebrush (*Artemesia* 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.

Fig. 2 Location of the
northern ungulate range
(shown in gray) in
northwest Wyoming and
southwest Montana, USA
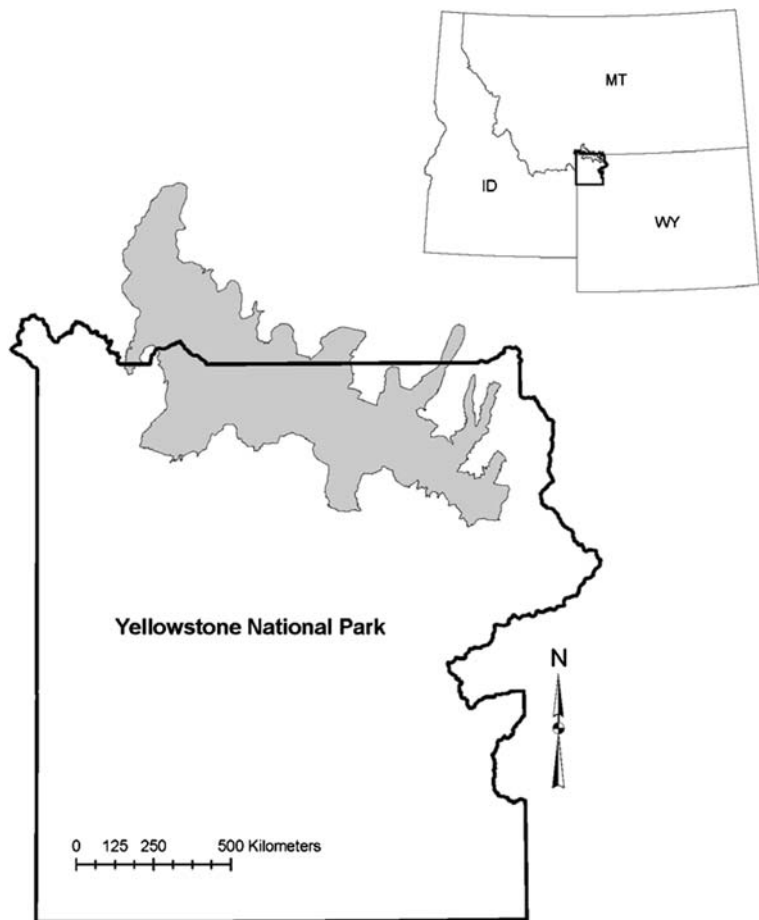
Methods

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
two more added in 2002. Patches were constrained to
≥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 ≥50% at the time of mapping or photo acqui-
sition, 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, initi-
ated 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 1.

Patch attributes

Boundaries of patches selected from the existing map
(St. John 1995) were available in digital format. For
those patches that were not selected from the map, we

Table 1 Characteristics of aspen patches ($n = 32$) in the northern ungulate winter range of the Yellowstone ecosystem, 2001–2003. Reg.Orient = patch orientation relative to North, Loc.Orient = patch orientation relative to elevational gradient

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

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 following the protocol outlined in Ralph et al. (1995). We allowed 30 s after the arrival of the observer for bird activity to resume, then 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) and acknowledge that some bird species which may have been present during sampling were not be detected (e.g., owls).

Each aspen patch was sampled thrice 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 three to five 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 (AIC_c) such that smaller AIC_c values indicate a better model (Anderson et al. 2001; Burnham and Anderson 2002). Following Anderson and Burnham (2002), we defined AIC_c as:

$$AIC_c = -2\ln(L) + 2K + [2K(K+1)/(n-K-1)]$$

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 AIC_c 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:

$$\omega_i = \exp(-0.5 * \Delta_i)/\Sigma\left(\exp(-0.5 * \Delta_i)\right)$$

where Δ_i is the difference between AIC_c of a given model and the AIC_c of the best model (AIC_{c-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). 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 AIC_c. For all models, we

regressed covariates on the 3-year patch average of bird species richness, or bird abundance for each migratory group (resident/short-distance migrant and long-distance migrant).

Using ordinary least squares regression, we also fit full models (all variables) for each combination of response (abundance or species richness) and migratory strategy, assessed interaction terms and re-fit as necessary. The resulting model coefficients and their significance (alpha = 0.05) were used to evaluate model selection results and interpretation. The objective of this comparison was confirmation and support for model selection results.

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

Table 2 List of a priori candidate models applied to migrant bird abundance, resident bird abundance, migrant bird species richness, and resident bird species richness. All models applied to data collected during June 2001, 02, 03 in the northern Yellowstone ecosystem. Parameter abbreviations defined in Table 1. ln.Area = log patch area

Model structure
$\beta_0 + \beta_1$ln.Area
$\beta_0 + \beta_1$Reg.Orient
$\beta_0 + \beta_1$ln.Area + β_2Reg.Orient
$\beta_0 + \beta_1$ln.Area + β_2Reg.Orient + $\beta_3$ln.Area x Reg.Orient
$\beta_0 + \beta_1$Loc.Orient
$\beta_0 + \beta_1$ln.Area + β_2Loc.Orient
$\beta_0 + \beta_1$ln.Area + β_2Loc.Orient + $\beta_3$ln.Area x Loc.Orient
$\beta_0 + \beta_1$BA.Dead
$\beta_0 + \beta_1$BA.Dead + β_2Loc.Orient
$\beta_0 + \beta_1$BA.Dead + β_2Reg.Orient
$\beta_0 + \beta_1$BA.Aspen
$\beta_0 + \beta_1$BA.Aspen + β_2Loc.Orient
$\beta_0 + \beta_1$BA.Aspen + β_2Reg.Orient
$\beta_0 + \beta_1$BA.Aspen + β_2BA.Dead
$\beta_0 + \beta_1$BA.Aspen + β_2BA.Dead + β_3Loc.Orient
$\beta_0 + \beta_1$BA.Aspen + β_2BA.Dead + β_3Reg.Orient
$\beta_0 + \beta_1$ln.Area + β_2BA.Aspen
$\beta_0 + \beta_1$ln.Area + β_2BA.Dead
$\beta_0 + \beta_1$ln.Area + β_2BA.Aspen + β_3Loc.Orient
$\beta_0 + \beta_1$ln.Area + β_2BA.Dead + β_3Loc.Orient
$\beta_0 + \beta_1$ln.Area + β_2BA.Aspen + β_3Reg.Orient
$\beta_0 + \beta_1$ln.Area + β_2BA.Dead + β_3Reg.Orient
$\beta_0 + \beta_1$ln.Area + β_2BA.Aspen + β_3Loc.Orient + $\beta_4$ln.Area x Loc.Orient
$\beta_0 + \beta_1$ln.Area + β_2BA.Dead + β_3Loc.Orient + $\beta_4$ln.Area x Loc.Orient
$\beta_0 + \beta_1$ln.Area + β_2BA.Aspen + β_3Reg.Orient + $\beta_4$ln.Area x Reg.Orient
$\beta_0 + \beta_1$ln.Area + β_2BA.Dead + β_3Reg.Orient + $\beta_4$ln.Area x Reg.Orient
$\beta_0 + \beta_1$ln.Area + β_2BA.Aspen + β_3BA.Dead
$\beta_0 + \beta_1$ln.Area + β_2BA.Aspen + β_3BA.Dead + β_4Loc.Orient
$\beta_0 + \beta_1$ln.Area + β_2BA.Aspen + β_3BA.Dead + β_4Reg.Orient
$\beta_0 + \beta_1$ln.Area + β_2BA.Aspen + β_3BA.Dead + β_4Loc.Orient + $\beta_5$ln.Area x Loc.Orient
$\beta_0 + \beta_1$ln.Area + β_2BA.Aspen + β_3BA.Dead + β_4Reg.Orient + $\beta_5$ln.Area x Reg.Orient

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). 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 three 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 site characteristics, primarily basal area, appear to be a better predictor of cavity nest presence than variables specific to nest-site trees (Swallow et al. 1986). Candidate models containing floristic/structural and landscape covariates are shown in Table 2.

Global model

In the model selection context, the global model is typically the most highly parameterized of the candidate model set (Burnham and Anderson 2002). 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 since these were not supported by our

understanding of landscape- or local-scale relationships between birds and aspen habitat. Additionally, 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, was:

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

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).

Model selection and interpretation

Using ordinary least squares regression in S-Plus statistical software (Insightful 2001), we fit each candidate model to the 3-year mean abundance and species richness response for both migrant and resident species. Of the most highly parameterized candidate models, we selected those including local patch orientation (as opposed to regional orientation) to serve as the global model for each response. We assessed goodness-of-fit for global models using the regression coefficient of determination (R^2). The resulting regression fits of global models for each combination of migratory strategy and bird abundance/diversity were adequate to proceed with AIC$_c$ ranking and evaluation (migrant abundance, $R^2 = 0.43$, $F_{5,26} = 3.97$, $p < 0.01$; migrant species richness, $R^2 = 0.47$, $F_{5,26} = 4.60$, $p < 0.01$; resident abundance, $R^2 = 0.34$, $F_{5,26} = 2.61$, $p = 0.05$; resident species richness, $R^2 = 0.22$, $F_{5,26} = 1.49$, $p = 0.22$) (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 AIC$_c$ units of the best (minimum AIC$_c$) 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 AIC_c best model (or competing set of best models). Subsequently, we calculated model-averaged slope estimates (β_i) and associated standard errors for these covariates as well as their ''unconditional'' 90% and 95% confidence intervals (Burnham and Anderson 2002); covariates with confidence intervals that include 0 were not considered important regardless of the ranking of their associated models by AIC_c. Interpretation of covariates focused on the patch orientation or area, and their importance, if present.

We calculated relative importance of variables as:

$$RI = \Sigma \, \omega_i$$

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:

$$\bar{\bar{\beta}}_i = \Sigma \, \omega_i \beta_i$$

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:

$$\widehat{SE} = \left[\Sigma \, \omega_i \sqrt{ SE_{\beta_i} + \left(\beta_i - \bar{\bar{\beta}}_i \right)^2 } \right]^2 .$$

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 five competing best models for migrant abundance, two competing best models for migrant species richness, two competing best models for resident abundance, and two competing best models for resident species richness (Table 3). The AIC_c best model for migrant abundance consisted of patch area and aspen basal area; the AIC_c best model for migrant species richness contained patch area and aspen basal area covariates. The AIC_c 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 (98%) (Table 4). Local patch orientation, basal area of live aspen, and basal area of dead aspen appear moderately to marginally important for migrants (28%, 46%, and 28%, respectively). Patch area and basal area of live aspen appeared somewhat important for residents (35% and 25%, respectively). For both migratory strategies, area-orientation interactions were unimportant.

For species richness, patch area and basal area of live aspen were most important for migrants (96% and 82%, respectively), and local patch orientation was most important for residents (86%). Local patch orientation and basal area of dead aspen appeared somewhat important for migrants (30% and 26%, respectively). Patch area, basal area of live aspen, and basal area of dead aspen appeared somewhat important for residents (39%, 24%, and 23%, respectively). For both migratory strategies, area-orientation interactions were unimportant.

Confidence intervals for migratory bird abundance covariates showed patch area and live aspen basal area exclusive of zero at both the 95% or 90% level (Table 5). Confidence intervals for

Table 3 Competing best candidate models ranked relative to AIC$_c$ ''best'' model for migrant abundance, migrant species richness, resident abundance and resident species richness. $-2LogLik = -2 *$ maximum log-likelihood for given model, K = number of estimated parameters, ΔAIC_c = difference in AIC$_c$ units from best model, w = Akaike weight, R^2 = coefficient of determination

Model	$-2LogLik$	K	ΔAIC_c	w	R^2
Migrant abundance					
ln.Area + BA.Aspen	141.51	4	0.00	0.19	0.41
ln.Area	144.26	3	0.12	0.18	0.36
ln.Area + BA.Dead	142.66	4	1.15	0.11	0.39
ln.Area + BA.Aspen + Loc.Orient	140.31	5	1.62	0.09	0.43
ln.Area + Loc.Orient	143.21	4	1.70	0.08	0.38
Migrant species richness					
ln.Area + BA.Aspen	98.52	4	0.00	0.33	0.44
ln.Area + BA.Aspen + Loc.Orient	97.17	5	1.48	0.16	0.46
Resident abundance					
Loc.Orient	78.18	3	0.00	0.38	0.29
ln.Area + Loc.Orient	77.32	4	1.77	0.16	0.31
Resident species richness					
Loc.Orient	31.15	3	0.00	0.33	0.18
ln.Area + Loc.Orient	30.08	4	1.55	0.15	0.20

migratory bird species richness showed only patch area exclusive of zero (Table 5). For both resident abundance and species richness, only local patch orientation was exclusive of zero at either the 95% or 90% level.

Table 4 Relative Importance (RI) of covariates for bird abundance and species richness candidate model sets. Parameter abbreviations defined in Table 1. f = number of models (out of 31) that includes target covariate

Covariate	f	RI	
		Migrant	Resident
Bird abundance			
ln.Area	20	0.99	0.35
Loc.Orient	12	0.28	0.98
Reg.Orient	12	0.17	0.01
ln.Area x Loc.Orient	4	0.05	0.07
ln.Area x Reg.Orient	4	0.03	0.00
BA.Aspen	16	0.46	0.25
BA.Dead	16	0.28	0.21
Bird species richness			
ln.Area	20	0.96	0.39
Loc.Orient	12	0.30	0.86
Reg.Orient	12	0.16	0.05
ln.Area x Loc.Orient	4	0.06	0.06
ln.Area x Reg.Orient	4	0.03	0.00
BA.Aspen	16	0.82	0.24
BA.Dead	16	0.26	0.23

Regression fits of full models (all variables) indicated interaction terms for patch area and either measure of patch orientation were not significant for all combinations of migratory strategy and bird response. Subsequent fits excluding interaction terms showed significant effects (alpha = 0.05) for the same covariates that emerged from model selection results (Table 5) for all combinations of bird response and migratory strategy (Table 6).

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 AIC$_c$ best models for both abundance and species diversity consisted of local orientation alone or local orientation and patch area. Local patch orientation had very high relative importance values of 98% and 86% for resident abundance and species richness, respectively. Patch area was moderately to marginally important with values of 35% and 39% for abundance and species richness, respectively (Table 4). As with long-distance migrants, regional orientation (relative to North) was not important and did not occur in any of the competing best models. Additionally, confidence

Table 5 Model-averaged covariate coefficients and unconditional confidence intervals that do not contain zero for migrant abundance, migrant species richness, resident abundance, and resident species richness. LCL = lower confidence level and UCL = upper confidence level. Parameter abbreviations defined in Table 1.

	Coefficient	Unconditional 95% CI		Unconditional 90% CI	
		LCL	UCL	LCL	UCL
Migrant abundance					
ln.Area	1.52	0.60	2.43	0.75	2.29
Migrant species richness					
ln.Area	0.65	0.22	1.19	0.30	1.11
BA.Aspen	0.03	0.01	0.06	0.01	0.06
Resident abundance					
Loc.Orient	0.02	0.01	0.04	0.01	0.04
Resident species richness					
Loc.Orient	0.02	0.01	0.02	0.02	0.02

Table 6 Coefficient of determination (R^2) for ordinary least squares regression fits of full models (all explanatory variables, excluding interactions) and coefficients of significant covariates contained in each model. Covariate abbreviations defined in Table 1

	Model R^2	Covariate	Coefficient	p-value
Migrant abundance	0.46			
		ln.Area	1.44	<0.01
Migrant species richness	0.48			
		ln.Area	0.64	0.01
		BA.Aspen	0.03	0.04
Resident abundance	0.39			
		Loc.Orient	0.04	<0.01
Resident species richness	0.30			
		Loc.Orient	0.02	0.01

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 5).

In contrast, long-distance migrant abundance and species richness responded primarily to patch area. Although aspen basal area, aspen snag basal area, and local patch orientation also appeared among the competing best models for this migratory strategy, the relative importance values and confidence intervals only supported the inclusion of aspen basal area as a considerable effect. Relative importance values and confidence intervals for migrant model covariate coefficients supported the interpretation that patch area and aspen basal area were most important for migrant abundance and patch area alone for species richness. Patch area had a relative importance of 99 and 96% for migrant abundance and species richness, respectively, and aspen basal area had a relative importance of 82% for migrant abundance (Table 4). Confidence intervals (90 and 95%) for patch area and aspen basal area did not contain zero for migrant abundance, and only patch area intervals were exclusive of zero for migrant species richness (see Table 5). Orientation of patches, relative to either North or the regional elevational gradient, did not influence migratory birds in the manner described by Gutzwiller and Anderson (1992).

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 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 less important than patch area, it is worth noting that aspen basal area and aspen snag basal area covariates have a strong biological basis for appearing among the AIC_c ranked competing best models for long-distance migrants. This is because many long-distance migrant 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. Models selected by the information-theoretic approach may have been influenced the relative importance of aspen (and

aspen snag) basal area when considered along with patch area and orientation. However, the AIC_c ranking of candidate models, covariate relative importance, unconditional confidence intervals, and confirmatory regression fits of full models suggest that the landscape-scale measurements of habitat better indicated 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.

Uncertainty about coefficient estimates (Table 5) may be 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

The results of our study suggest 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).

Appendix 1 Birds detected in the northern Yellowstone ecosystem 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	*Falco sparverius*	Y	37
American Robin	*Turdus migratorius*	Y	228
Belted Kingfisher	*Ceryle alcyon*	N	1
Black-billed Magpie	*Pica pica*	N	13
Black-capped Chickadee	*Parus atricapillus*	N	63
Brewers Blackbird	*Euphagus cyanocephalus*	Y	39
Brown-headed Cowbird	*Molothrus ater*	Y	30
Cassins Finch	*Carpodacus cassinii*	Y	1
Chipping Sparrow	*Spizella passerina*	Y	34
Clarks Nutcracker	*Nucifraga columbiana*	N	11
Cliff Swallow	*Hirundo pyrrhonota*	Y	1
Common Raven	*Corvus corax*	N	10
Common Yellowthroat	*Geothlypis trichas*	Y	20
Dark-eyed Junco	*Juncus hyemalis*	Y	41
Downy Woodpecker	*Picoides pubescens*	N	10

Appendix 1 continued

Species		Migrant	n
Dusky Flycatcher	*Empidonax oberholseri*	Y	41
Green-tailed Towhee	*Pipilo chlorurus*	Y	7
Hairy Woodpecker	*Picoides villosus*	N	14
Hammonds Flycatcher	*Empidonax hammondii*	Y	73
House Wren	*Troglodytes aedon*	Y	163
Indigo Bunting	*Passerina cyanea*	Y	3
Lazuli Bunting	*Passerina amoena*	Y	100
Lincolns Sparrow	*Melospiza lincolnii*	Y	98
McGillivrays Warbler	*Oporornis tolmiei*	Y	49
Mountain Bluebird	*Sialia currucoides*	Y	77
Mountain Chickadee	*Parus gambeli*	N	131
Mourning Dove	*Zenaida macroura*	Y	3
Northern Flicker	*Colaptes auratus*	Y	188
Olive-sided Flycatcher	*Contopus borealis*	Y	2
Orange-crowned Warbler	*Vermivora celata*	Y	8
Pine Siskin	*Carduelis pinus*	Y	180
Red Crossbill	*Loxia curvirostra*	N	17
Red-breasted Nuthatch	*Sitta canadensis*	N	78
Red-naped Sapsucker	*Sphyrapicus nuchalis*	Y	58
Red-tailed Hawk	*Buteo jamaicensis*	Y	12
Red-winged Blackbird	*Agelaius phoeniceus*	Y	1
Ruby-crowned Kinglet	*Regulus calendula*	Y	24
Ruffed Grouse	*Bonasa umbella*	N	4
Sandhill Crane	*Grus canadensis*	Y	1
Sharp-shinned Hawk	*Accipiter striatus*	Y	1
Song Sparrow	*Melospiza melodia*	Y	4
Starling	*Sturnus vulgaris*	N	77
Stellars Jay	*Cyanocitta stelleri*	N	6
Tree Swallow	*Tachycineta bicolor*	Y	39
Vespers Sparrow	*Pooecetes gramineus*	Y	3
Violet-green Swallow	*Tachycineta thalassina*	Y	70
Warbling Vireo	*Vireo gilvus*	Y	339
Western Meadowlark	*Sturnella neglecta*	Y	8
Western Tanager	*Piranga ludoviciana*	Y	21
Western Wood Pewee	*Contopus sordidulus*	Y	14
Williamsons Sapsucker	*Sphyrapicus thyroideus*	Y	23
Willow Flycatcher	*Empidonax trailii*	Y	1
Yellow Warbler	*Dendroica petechia*	Y	11
Yellow-rumped Warbler	*Dendroica coronata*	Y	28

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