Landscape Ecology **16:** 71–83, 2001.

Research Article

A comparison of satellite data and landscape variables in predicting bird species occurrences in the Greater Yellowstone Ecosystem, USA

Erika Hasler Saveraid[1], Diane M. Debinski[1]*, Kelly Kindscher[2] and Mark E. Jakubauskas[3]
[1]*Department of Animal Ecology, Iowa State University, Ames, IA 50011, USA;* [2]*Kansas Biological Survey, University of Kansas, Lawrence, KS 66047-2906, USA;* [3]*Kansas Applied Remote Sensing (KARS) Program, University of Kansas, Lawrence, KS 66045-2969, USA; (*Corresponding author: Phone: 515-294-2460; Fax: 515-294-7874; E-mail: debinski@iastate.edu)*

Received 23 August 1999; Revised 31 May 2000; Accepted 27 June 2000

Key words: heterogeneous landscapes, predicting bird species occurrences, remote sensing, satellite imagery, wildlife species habitats

Abstract

We compare the accuracy of predicting the occurrence of 11 bird species in montane meadows of the Greater Yellowstone National Park ecosystem, in the states of Montana and Wyoming, USA. We used remotely sensed, landscape, and habitat data. The meadow type, as determined from the remotely sensed data, was highly correlated with abundances of six of the 11 bird species. Landscape variables significant in predicting occurrence were selected using a stepwise multiple regression for each bird species. These variables were then used in a multiple regression with the variable meadow type. As expected, the abundances of the generalist species (American Robin, Dark-eyed Junco, White-crowned Sparrow, Brewer's Blackbird, and Chipping Sparrow) were not strongly correlated with landscape variables or meadow type. Conversely, abundances of the Common Snipe, Common Yellowthroat, Lincoln's Sparrow, Savannah Sparrow, Vesper Sparrow, and Yellow Warbler were highly correlated with meadow type and landscape variables such as percent cover of willow (*Salix* spp.), graminoid, woody vegetation, sagebrush (*Artemisia* spp.), and graminoid and shrub biomass. The results from our study indicate that remotely sensed data are applicable for estimating potential habitats for bird species in the different types of montane meadows. However, to improve predictions about species in specific sites or areas, we recommend the use of additional landscape metrics and habitat data collected in the field.

Introduction

The field of landscape ecology has increased ecologists' awareness of landscape mosaics and how patch size, patch context, and other habitat characteristics affect local species distribution patterns and the communities within the landscape. Variations in climate, edaphic factors, resource distribution, and physical disturbances are natural factors that determine landscape patterns (Wiens et al. 1985). Because of heterogeneity of the environment, the conservation of patchy communities must be examined from the perspective of landscape spatial structure and landscape relationships among patches of habitat in order to fully understand the relationships and processes of a community (Fahrig and Merriam 1994).

Landscape ecology emphasizes the spatial and temporal arrangements of ecosystems and the resulting ecological effects at broad spatial scales (Turner 1989). A landscape is defined by Dunning et al. (1992) as a mosaic of habitat patches in which a patch of interest is embedded, and this is the definition we used in our study. Patch size, patch type, and patch context are important factors to consider when studying a community. The application of landscape ecology to conservation biology has resulted in a myriad of studies on habitat patchiness caused by both natural and human induced changes (agricultural transformation of landscapes, harvesting of forests, urban development, etc.). The spatial arrangement, size, type, and diversity of patches can interact to influence species abundances within those patches (Turner 1989; Pearson 1993). Species may also be influenced by the presence and quality of dispersal routes within a landscape (van Dorp and Opdam 1987). The landscape matrix around habitat patches is rarely an inhospitable environment, and the boundaries may affect processes within the patch (Wiens 1995). Estimates of species abundance and diversity are crucial when designing conservation programs for threatened communities, so understanding the factors that may be controlling species distribution patterns has important implications for conservation biologists.

There has been considerable study of landscape effects on the populations of forest dwelling birds (Blake and Karr 1987; Haila et al. 1993; Lescourret and Genard 1994; Hagan et al. 1996), but a review of the literature shows there have been few studies of patchiness in grassland or meadow habitats (Herkert 1994; Vickery et al. 1994). In forest fragmentation studies, habitat area has been found to be one of the major factors relating to species number (Freemark and Merriam 1986; van Dorp and Opdam 1987; Lescourret and Genard 1994). Van Dorp and Opdam (1987) studied forest patches in an agricultural matrix and determined that woodlot size was the best predictor of species number and probability of occurrence. Habitat variables such as isolation, amount of woods, and proximity and density of connecting elements also influenced species number, although they had less effect than area (Freemark and Merriam 1986; van Dorp and Opdam 1987). Lescourret and Genard (1994) determined that both bird species composition and species richness varied with patch area in mountain forest fragments, however, this was not true for total bird abundance (which did not appear to be related to patch size). It appears then, that bird species richness and abundance in forested ecosystems are related to habitat variables and patch size, although the exact mechanisms are still unclear.

Habitat size effects have been less studied in grassland environments than in forests (Herkert 1994; Vickery et al. 1994). A study in Maine by Vickery et al. (1994) examined the effects of habitat area on grassland birds and found that the abundances of seven species were positively correlated with increasing area and that grassland birds respond to vegetation characteristics such as vegetative cover, patchiness, and structure of a site. In addition, Vickery et al. (1994) found the greatest species richness in the small size classes and the largest size class of grasslands. This result was probably caused by the greater amounts of edge in the small habitats, which attracted edge species, and the increase in the area-dependent grassland species in the largest size class. Herkert (1994) demonstrated that species richness increased with grassland area and that larger area positively influenced the probability of finding certain species in a grassland. Herkert (1994) also concluded that vegetation structure has a strong influence on grassland bird distribution patterns, and that the responses by individual species varied (e.g., some species preferred standing dead plant material and others preferred live vegetation). Several other studies have found that grassland birds responded to vegetation elements such as foliage height diversity, shrub cover, herbaceous cover, litter cover, etc. (Wiens 1969; Wiens 1974; Cody 1985; Patterson and Best 1986; McAdoo et al. 1989; McCoy 1996; Estades 1997).

We studied montane meadows in the Greater Yellowstone Ecosystem (GYE) surrounding Yellowstone National Park, in the states of Montana and Wyoming, USA. We examined landscape effects on bird communities, incorporating both fine-scale landscape and habitat data and the coarse-scale component of remotely sensed data. We measured fine-scale data of habitat variables and vegetation composition in the field, and we investigated the relationship between meadow patches and the surrounding landscape through the use of satellite imagery. In 1997 and 1998, we collected bird and plant community data in montane meadows in two regions of the GYE; Grand Teton National Park and Bridger-Teton National Forest, WyoMing (Tetons, Figure 1) and the Gallatin National Forest and northwestern corner of Yellowstone National Park, Montana (Gallatins, Figure 2).

We used satellite imagery to catagorize the non-forested landscape into six different meadow types representing a hydric-to-xeric gradient from willow-dominated (*Salix* spp.) wetlands to sagebrush (*Artemisia* spp.) flats (Saveraid 1999). Previous analyses suggest that it is not possible to accurately predict bird species occurrences in the meadow types based on currently available 20–30 m spatial resolution multispectral satellite data alone (Saveraid 1999). Our goal for this study was to build better predictive models of species occurrences in the meadow types using landscape and habitat variables. Spectral reflectance

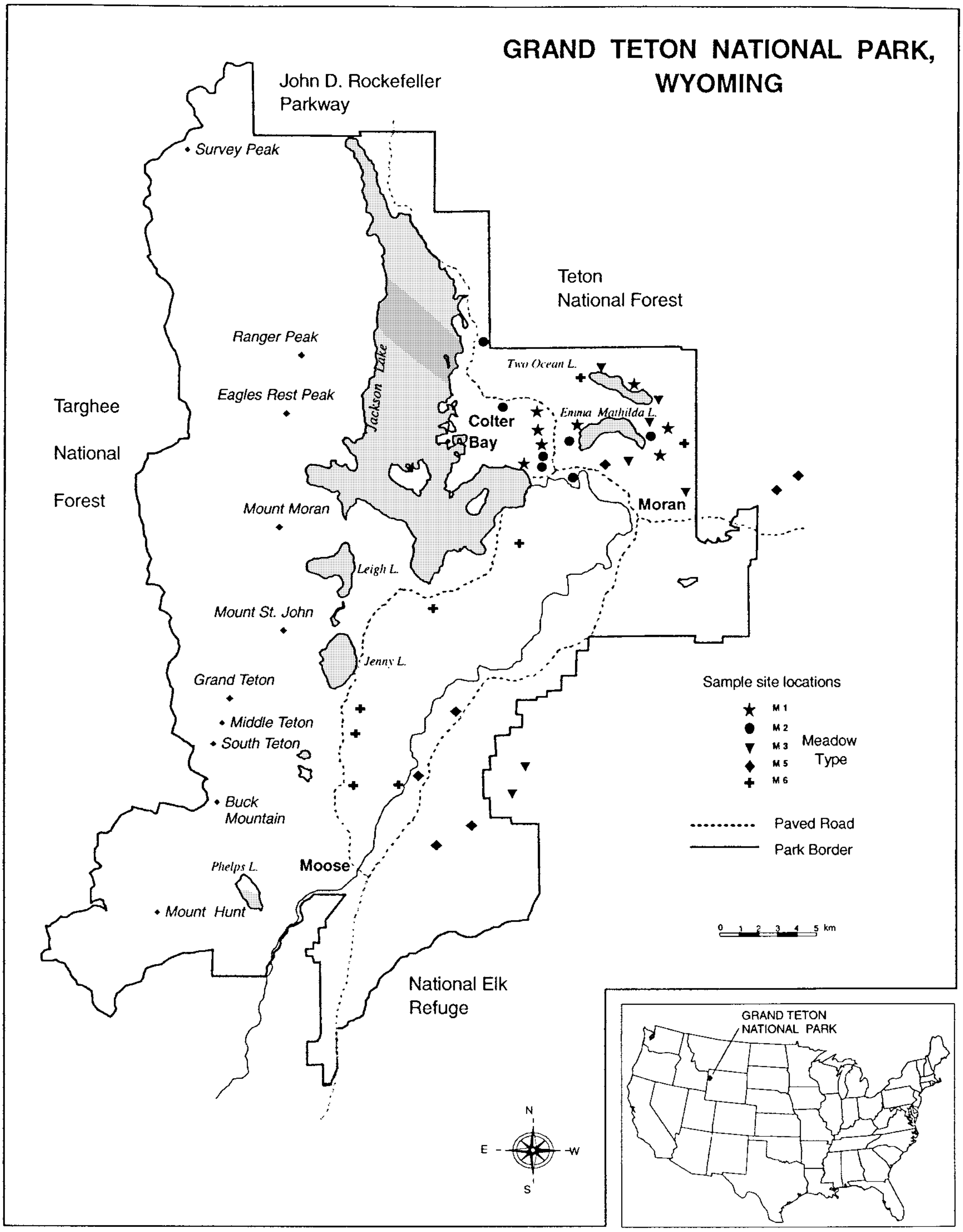

Figure 1. Map of study site locations in Grand Teton National Park and Bridger-Teton National Forest, Wyoming, USA.

values of montane meadow, as recorded in satellite multispectral imagery, are a product of the vegetation composition and state of the different meadows. Satellite data alone, however, do not provide sufficient information to enable accurate predictions of the bird species composition and abundances. Landscape and habitat variables incorporate information about the habitat structure of a meadow, its area, single or small groups of trees located within the meadow, and other data which cannot be determined from currently available satellite data, but may be important for bird species in the selection of breeding habitat.

Methods

We used an unsupervised computer classification of multitemporal SPOT satellite imagery to produce maps of spectrally distinct meadow classes within the Gallatin and Teton study areas to guide selection of meadow sample sites. The SPOT multispectral scanner records reflected light in three spectral bands (green, red, and near-infrared) with a spatial resolution of 20 m. A summer and fall date of SPOT multispectral imagery were selected for each study area; 25 May and 6 September 1994 (Gallatin study area), 17 June and 3 September 1996 (Teton study area). Selection of these dates was a function of orbital revisit dates, cloud cover, and availability. All data were converted from brightness values to units of radiance (mW/cm^2/sr/um) and then reflectance. Maps of six non-forested meadow classes (labeled M1-M6) representing a distinct xeric-to-hydric gradient ranged from moist willow bogs (M1) to dry sagebrush with grasses (M6) were created for each study area (Gallatin and Teton) by classification of the combined six-band data set (two dates, three spectral bands per date) (Debinski et al. 1999; Jakubauskas et al. 1998; Kindscher et al. 1998).

Selection of sampling sites

Because class polygons smaller than 1 ha are difficult to locate with confidence in the field, the minimum mapping unit of the final vegetation map was 25 pixels (1 ha). Generalization was accomplished using the Arc/Info (ESRI, Redlands, CA, USA) ELIMINATE command to remove polygons smaller than the minimum area. Final maps were plotted on translucent paper at a scale of 1:24,000 for overlay onto topographic maps of the study area. Maps and field surveys were used to identify five spatially distinct examples of each meadow type. Sample sites were located in the field with the aid of global positioning devices, aerial photography, topographic maps, and compass readings from identifiable landmarks. Field investigations indicated that the M4 meadow types in the Teton study area represented groves of aspen (*Populus tremuloides*) with a dense herbaceous understory. Aspens are virtually absent in the Gallatins, so the M4 classifications are not analogous between the two regions. Because the focus of this research was on non-forested montane meadows, and there is no close corollary to these groves in the Gallatins, the M4 type was eliminated from use in the Tetons, and sampling proceeded in the remaining five meadow types.

Sampling within sites

For each of the fifty sites, we established a point within the classified meadow which served as the center for 50 m-radius point-count bird surveys, and the northwest corner of a 20 × 20 m plot used for vegetation biomass sampling. The point was permanently marked with a 1.25 m steel or wooden post driven into the ground, and flags were used to mark the edges of the 50 m-radius circle. In some cases, the center point for the point-count survey was off-set slightly from the steel or wooden post to avoid trampling the vegetation in the botanical plot. For these cases, a white flag was placed at the center and the distance and direction from the northwest corner was recorded. This allowed us to relocate the center points for surveys in the summer of 1998.

Bird surveys

Abundance data were collected for birds using 50 m-radius point-count surveys. These surveys were performed three times from 0530–1030 h for each study site from 1 June–17 July in 1997 and 1998. Each survey involved two people recording and observing for 15 min. Three of the four people performing point-counts were the same for both years of the study. All researchers were trained in identifying birds by sight and sound, and we randomized any biases by alternating team members and rotating the sites visited by the teams. Birds were not surveyed if it was snowing or raining, but surveys were conducted if there was light mist or snow/frost on the ground, because bird activity was observed not to be reduced under these conditions. During a survey, each individual bird seen and/or heard within the 50 m-radius circle was recorded,

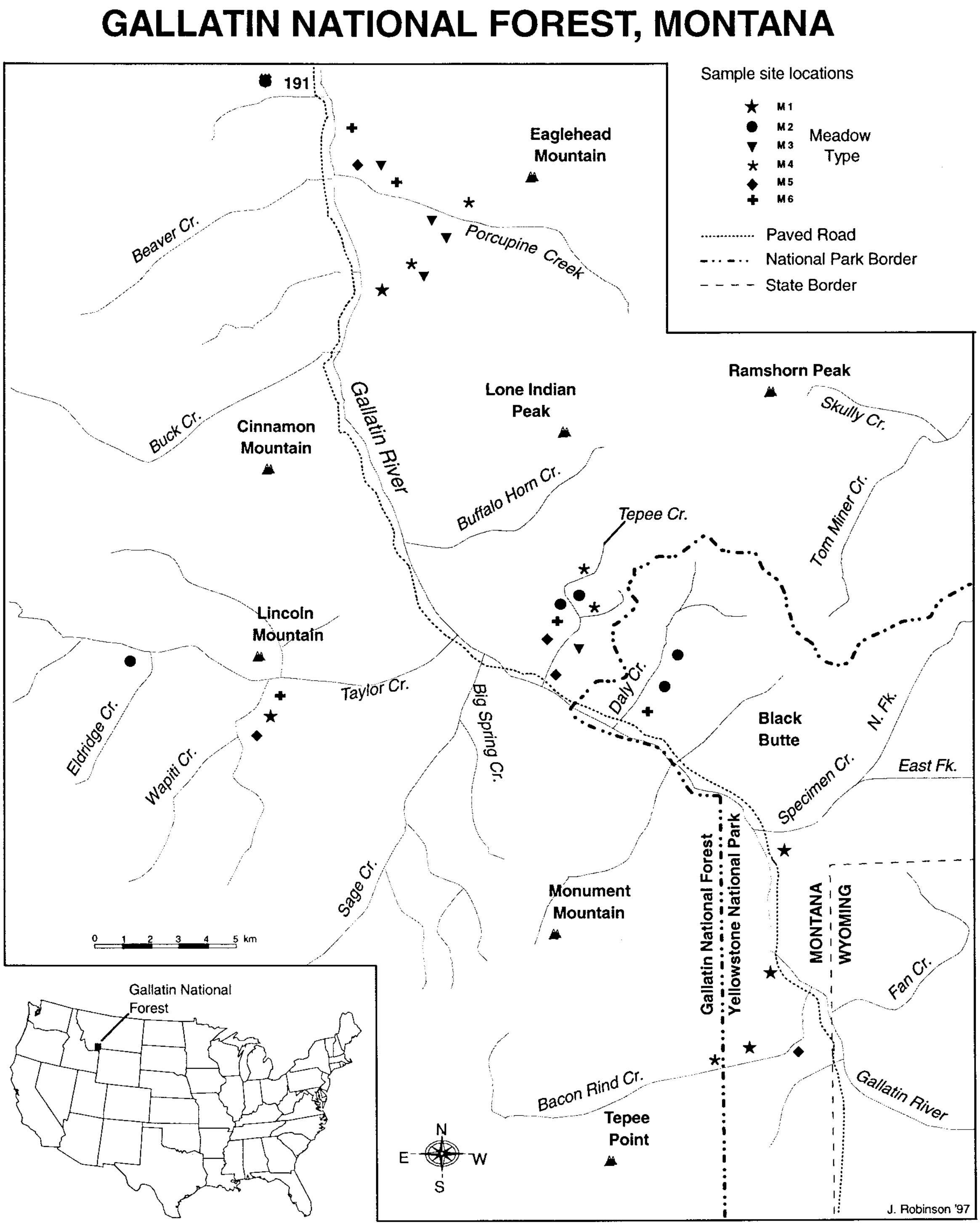

Figure 2. Map of study site locations in Gallatin National Forest and Yellowstone National Park, Montana, USA.

and its location and distance from the observer was mapped. Flyovers were not included in the analysis. Behaviours such as singing, agitated chipping, carrying nesting material, and feeding fledglings were also recorded because birds exhibiting these behaviours are likely to be nesting (Vickery et al. 1992; Gill 1995). The sum of all the counts for each bird species by site over the season was used in the statistical analyses.

Biophysical and spectral field sampling

Measurements of vegetation biomass were made in July 1997 and 1998 for both the Teton and Gallatin regions. For each site, three 0.20×0.50 m (0.1 m^2) quadrats were spaced at 10.0 m intervals along the northern edge of each 20×20 m vegetation plot. All aboveground green photosynthetically-active vegetation within each quadrat was clipped, sorted by life form (graminoids, forbs, and shrubs), placed in paper bags, and immediately weighed in the field using spring scales to the nearest 1.0 g to determine 'wet' weight. In the lab, bags were dried in a laboratory oven at 100 °C for 48 hours, and weighed again to determine 'dry' weight and percent moisture by life form.

Spectral reflectance readings were taken using an Analytical Spectral Devices (ASD) spectroradiometer, recording electromagnetic energy reflected by the surface over the range 0.326–1.055 μm (visible and near-infrared) in 512 discrete spectral bands. Measurements were taken in twenty 1×1 m quadrats within the 20×20 m plot. The 1×1 m quadrats were spaced 4 m apart with the first plot starting at the center point post. Ten spectroradiometer scans per quadrat were acquired and internally averaged by the system to determine spectral reflectance.

All sites were sampled between 0900 and 1550 hours local solar time. A white reference calibration reading was made at the start of each plot to normalize all reflectance values to a common standard. Leaf Area Index (LAI) was determined in 1997 using a Li-Cor LAI-2000. Sites in the Tetons were sampled during the period of 2–7 July and 20–23 July for the Gallatins.

Treeline and tree density surveys

A modified point-quarter sampling technique (e.g., Bower et al. 1990) was developed to measure distance from the bird survey point to the closest treeline and tree density. A rangefinder (Ranging 1000 Rangematic) was used to measure the distance to the closest treelines for each site. Each site was divided into four quadrants, based on the cardinal directions, and the nearest treeline distance (±10 m) was recorded for each quadrant (NW, NE, SW, SE). An average treeline distance was calculated for each site. The treeline type was recorded as conifer, aspen, or mixed. In addition, we counted the number of tree stems (trees greater than 0.5 m in height) within a 50 m-radius to determine a relative density measure for all of the sites.

Vegetation surveys

Using the 20×20 m biomass plot as the center, a 100×100 m vegetation plot was established for each site and the areal percent cover of all plant species was estimated during a July sampling period to derive a measure of plant species composition. The cover of plant species and combined cover of litter and bare ground were estimated to the nearest percent using Daubenmire's (1959) principles of sampling.

Statistical analysis

Eleven birds species were selected for the analysis: American Robin (*Turdus migratorius*), Brewer's Blackbird (*Euphagus cyanocephalus*), Chipping Sparrow (*Spizella passerina*), Dark-eyed Junco (*Junco hyemalis*), Lincoln's Sparrow (*Melospiza lincolnii*), Common Yellowthroat (*Geothlypis trichas*), Yellow Warbler (*Dendroica petechia*), Savannah Sparrow (*Passerculus sandwichensis*), Common Snipe (*Gallinago gallinago*), Vesper Sparrow (*Pooecetes gramineus*), and White-crowned Sparrow (*Zonotrichia leucophrys*). The selection criterion for the birds used in the analysis was an overall total abundance greater than or equal to 12 in each year of the study, excluding swallow species. This criteria was chosen to restrict the analysis to those birds with abundances large enough for the statistical analysis.

The FRAGSTATS (McGarigal and Marks 1994) statistical analysis program was applied to the ArcInfo GIS coverage of meadow habitat classifications to calculate two of the landscape parameters: nearest neighbor of the same meadow type, and meadow size (area). These parameters were selected *a priori* because they were likely to be the most related to bird habitat preferences.

A correlation analysis was performed (SAS, proc corr, v. 6.12) to determine whether any of the percent cover variables (willows, sagebrush, forbs, graminoids, woody vegetation) or the biomass vari-

Table 1. Species abundances for 11 birds across all meadow types in two regions of the Greater Yellowstone Ecosystem: Gallatin National Forest/Yellowstone National Park (Gallatins) and Grand Teton National Park/Bridger Teton National Forest (Tetons). Abundances are summed across five spatial replicates per meadow type (M1-M3, M5-M6) and three temporal replicates per site.

Species	1997		1998	
	Gallatins	Tetons	Gallatins	Tetons
American Robin	14	18	19	10
Brewer's Blackbird	14	16	7	18
Chipping Sparrow	12	7	19	7
Common Snipe	2	10	8	9
Common Yellowthroat	3	29	5	24
Dark-eyed Junco	11	2	19	3
Lincoln's Sparrow	34	35	53	31
Savannah Sparrow	10	26	10	17
Vesper Sparrow	24	58	26	24
White-crowned Sparrow	14	46	13	21
Yellow Warbler	0	53	1	39

ables (woody vegetation, forbs, graminoids) were highly correlated.

Three multiple regression models were developed for each species using continuous, discrete, and a combination of these two types of variables. First, a multiple linear regression was performed using all of the variables in a stepwise selection method (SAS, proc reg, v. 6.12) to determine the most important variables in predicting abundances of each bird species. This method selects a subset of the variables that are the most highly correlated with abundance for each species. A variable was selected for the model if the p value was less than 0.20 (in order to obtain at least one variable for most of the species). The landscape and habitat variables used included distance to the nearest treeline, stem density per site, distance to the nearest neighboring meadow of the same type, meadow area, percent cover of woody vegetation, forbs, graminoids, sagebrush, and willows, biomass of woody vegetation, forbs, and graminoids, Leaf Area Index (LAI-1997 only), and Normalized Difference Vegetative Index (NDVI).

The second step of the analysis was a multiple regression (SAS, proc glm, v. 6.12) of two variables, region (Tetons or Gallatins) and meadow type (M1-M6), on species abundance. Region was used in the regression, because several bird species (Common Yellowthroat, Yellow Warbler, and Vesper Sparrow) showed large differences in abundances between the Tetons and the Gallatins (Table 1). The results from the multiple regression analyses indicate which of the two variables was significantly correlated to bird abundance. This test of discrete variables was used to determine whether the variables produced as high a correlation to bird abundances as the landscape and habitat variables. It was necessary to perform the analysis in this way, because the stepwise statistical program (SAS, proc reg, v. 6.12) does not test discrete variables.

We ran a final analysis to determine whether the addition of the variable *meadow type* improved the results from the first multiple regression analysis of the landscape and habitat data. We included the meadow type variable in a multiple regression analysis (SAS, proc glm, v. 6.12) with the significant landscape and habitat variables which were selected from the stepwise regression for each bird species. This method allowed us to compare the results from the first two analyses to a multiple regression analysis which included the significant landscape and habitat variables as well as the variable *meadow type*.

Results

Abundances of the 11 bird species for the Gallatins and Tetons in 1997 and 1998 show dramatic differences in abundance between regions for general species (Table 1).

Table 2. Results from correlation analyses of percent cover variables from montane meadows in the Greater Yellowstone Ecosystem.

	Graminoids	Sagebrush	Willow	Woody
		1997		
Forbs	−0.213	0.193	−0.150	−0.031
Graminoids		−0.441*	0.124	0.109
Sagebrush			−0.334	−0.219
Willow				0.169
		1998		
Forbs	−0.141	−0.067	−0.056	−0.013
Graminoids		−0.512**	−0.0001	0.148
Sagebrush			−0.389*	−0.224
Willow				0.145

* Indicates significance at $p < 0.01$.
** Indicates significance at $p < 0.001$.

The results from the correlation analysis (SAS, proc corr, v. 6.12) indicated that the percent covers of graminoids and sagebrush were significantly negatively correlated ($p < 0.001$) so these two variables were not used together in the multiple regression analysis (Table 2). Percent cover of sagebrush and willows were also negatively correlated ($p < 0.01$) and were not used together. Percent cover of sagebrush was not included in the regressions for birds typically found in wetter habitats (American Robin, Lincoln's Sparrow, Common Yellowthroat, Yellow Warbler, Savannah Sparrow, and Common Snipe) and percent cover of graminoids and willows were not included in the regressions for the birds typically found in dry habitats (Chipping Sparrow, Dark-eyed Junco, Vesper Sparrow, and White-crowned Sparrow). No biomass variables were correlated.

In the multiple regression of the discrete variables, meadow type was a significant predictor variable for six of the 11 species (Lincoln's Sparrow, Common Snipe, Common Yellowthroat, Savannah Sparrow, Vesper Sparrow, and Yellow Warbler) for both years of the study (Table 3). Region was a significant predictor variable for the Yellow Warbler and Common Yellowthroat in both years, and for the Vesper Sparrow in 1997 only. The remaining five species (Dark-eyed Junco, Chipping Sparrow, Brewer's Blackbird, American Robin, and White-crowned Sparrow) did not show significant correlations with region or meadow type in either year.

Table 4 shows the results from the stepwise multiple regression of the landscape and habitat variables on abundances for the 11 bird species, as well as the results from the final multiple regression analysis using the significant predictor variables for each species and the classification variable *meadow type*. The stepwise technique selected the variables which are the best fit to the model for each bird species. Different variables were selected as significant predictor variables in 1997 and 1998 for nearly all of the bird species. The species could be considered more generalist (Salt 1957), open-canopy species (American Robin, Dark-eyed Junco, White-crowned Sparrow, Brewer's Blackbird, and Chipping Sparrow) did not have high R^2 values using the landscape and habitat variables ($R^2 = 0 - 0.311$), with the exception of the multivariate regression of the Dark-eyed Junco in 1997 ($R^2 = 0.725$).

Common Yellowthroat, Lincoln's Sparrow, and Yellow Warbler, species we observed to be associated with shrubby habitat and willows (Salt 1957; Cody 1985; Cicero 1997), had higher R^2 values than the open-canopy generalists and were highly significant ($R^2 = 0.450$–0.811; $p < 0.0001$). For each of these species, at least one of the habitat variables (percent willow, graminoid biomass, and shrub biomass) was a significant predictor variable in the multiple regression in both years. The regression for Common Snipe and Savannah Sparrow, species which are typically associated with sedges and some willows (Salt 1957; Cody 1985), had high R^2 values ($R^2 = 0.370$–0.530; $p < 0.001$) and were significantly correlated in both years to at least one of the habitat variables of percent graminoid, percent willows, or graminoid biomass. The regression analysis for Vesper Sparrow, which is associated with sagebrush habitat (Cody 1985) also had greater R^2 values than those for the open-canopy generalists ($R^2 = 0.538$, 0.558; $p < 0.001$), and had percent sagebrush as one of the significant predictor variables in both years. Meadow area was a significant predictor variable in at least one year for six species: Common Yellowthroat, Dark-eyed Junco, Vesper Sparrow, American Robin, Chipping Sparrow, Yellow Warbler. Distance to treeline was a significant predictor for several species: Chipping Sparrow, Common Snipe, Common Yellowthroat, Lincoln's Sparrow, Savannah Sparrow in 1997 and Common Snipe, Common Yellowthroat, Savannah Sparrow in 1998.

Table 3. Results from a multivariate regression analysis of the classification variables *region* (Gallatin National Forest/Yellowstone National Park versus Grand Teton National Park Bridger-Teton National Forest) and *meadow type* (hydric to xeric gradient M1-M6) on abundance of 11 bird species in the Greater Yellowstone Ecosystem. R^2 values include both region and meadow type.

Species	Region (df=1)		Meadow type (df=4)		R^2	
	1997	1998	1997	1998	1997	1998
American Robin	NS	NS	NS	NS	0.153	0.112
Brewer's Blackbird	NS	NS	NS	NS	0.054	0.154
Chipping Sparrow	NS	NS	NS	NS	0.154	0.154
Common Snipe	NS	NS	$p < 0.05$	$p < 0.001$	0.275	0.365
Common Yellowthroat	$p < 0.05$	$p < 0.05$	$p < 0.001$	$p < 0.001$	0.441	0.422
Dark-eyed Junco	NS	NS	NS	NS	0.157	0.093
Lincoln's Sparrow	NS	NS	$p < 0.001$	$p < 0.001$	0.380	0.435
Savannah Sparrow	NS	NS	$p < 0.01$	$p < 0.001$	0.295	0.357
Vesper Sparrow	$p < 0.05$	NS	$p < 0.001$	$p < 0.001$	0.489	0.471
White-crowned Sparrow	NS	NS	NS	NS	0.121	0.048
Yellow Warbler	$p < 0.005$	$p < 0.001$	$p < 0.005$	$p < 0.001$	0.414	0.481

NS= not significant.

Results from the multiple regression of the significant landscape variables and meadow type improved R^2 values generally (10 of the 11 species in 1997 and 11 of 11 in 1998) (Table 4).

Discussion

As expected, combining data on landscape metrics, habitat variables, and meadow type improved the R^2 values for most of the bird species tested. Species that breed in specific habitat types were highly correlated with variables characterizing that habitat. For example, the Common Yellowthroat, Yellow Warbler, and Lincoln's Sparrow, species that prefer shrubby willow habitat, were all correlated with percent willow coverage. The abundances of these three species were also frequently correlated with shrub biomass, and percent woody vegetation. The abundances of the Common Snipe and Savannah Sparrow were correlated with the percent willow variable, as well as the percent and biomass graminoid variables. These two species are typically found in sedge meadows, which are surrounded by willow habitat. The Vesper Sparrow, known to prefer sagebrush habitat for breeding, was correlated to the percent sagebrush variable. The five other species used in the multiple regression analyses (American Robin, Brewer's Blackbird, Chipping Sparrow, Dark-eyed Junco, and White-crowned Sparrow) are not necessarily considered 'meadow species' and can be found in a variety of habitats. All of these species (except Dark-eyed Juncos in 1997) had low R^2 values and inconsistent predictor variables in both years of the study.

There were several landscape and habitat variables that were strong predictors for some of the species. Stem density and distance to treeline were important variables in predicting species that were both avoiding the edge and edge-associated species. Meadow area was also a significant predictor for some species ($n = 6$).

Saveraid (1999) suggests that it may not be possible to use satellite data alone in the prediction of bird species occurrences in montane meadows. Satellite data are useful for identifying potential areas where certain species may be located, but more detailed vegetative and habitat data are necessary to more accurately determine nesting and breeding habitats. Our results indicate that the overall habitat structure of the meadows is an important factor in the selection of habitat by the bird species, and the required detail cannot be gleaned from coarse resolution satellite data. Field surveys were necessary to measure landscape and habitat variables such as stem density, distance to the treeline, vegetation biomass and percent cover, which provide more detailed information about the structure of the meadows. In addition, we found that there were some differences between the two regions which could not be detected by the satellite data. Meadow types were similar in plant species composition between the two regions, but there were some important vertical structure differences, particularly

Table 4. Results from stepwise multiple regression (stepwise) and multiple regression (multiple) analyses of 11 bird species in the Greater Yellowstone Ecosystem. Significant predictor variables were selected from the stepwise regression and used in a multiple regression which also included the variable *meadow type*. Variables included in the stepwise regression: nearest treeline, stem density per site, nearest neighboring meadow of the same type, meadow area, percent cover of woody vegetation, forbs, graminoids, sagebrush, and willow, biomass of woody vegetation, forbs, and graminoids, Leaf Area Index (LAI-1997 only), and Normalized Difference Vegetative Index (NDVI).

Species	1997					1998				
	Significant predictor variables	Parameter estimate	P value	Stepwise R^2	Multiple R^2	Significant predictor variables	Parameter estimate	P value	Stepwise R^2	Multiple R^2
American Robin	Shrub biomass	0.0313	0.004	0.240*	0.334	Meadow area	-3.0×10^{-8}	0.009	0.311*	0.324
						NDVI	−4.5143	0.034		
	% Forb	0.3326	0.104			Stems/Plot	0.0177	0.077		
	% Willow	1.5754	0.162			Graminoid biomass	0.0234	0.102		
Brewer's Blackbird	none	–	–	–	0.349	none	–	–	–	0.266
Chipping Sparrow	Treeline	−0.0005	0.228	0.030	0.154	Stems/plot	0.0340	0.031	0.225*	0.345
						% Sage	4.9287	0.042		
						Meadow area	-3.0×10^{-8}	0.077		
Common Snipe	% Willow	1.8396	0.002	0.384**	0.459**	% Willow	104783	0.002	0.530**	0.617**
	Shrub biomass	−0.0230	0.016			Shrub biomass	−0.0281	0.067		
	Treeline	0.0004	0.050			Treeline	−0.0005	0.058		
	Graminoid	0.0085	0.067			%Forb	−1.1417	0.0005		
						Forb biomass	−0.0353	0.062		
						NDVI	1.3857	0.152		
Common Yellowthroat	% Willow	4.2570	0.0001	0.811**	0.820**	%Willow	3.5629	0.0001	0.638**	0.654**
	Nearest neighbor	5.95×10^{-6}	0.0001			Nearest neighbor	1.7×10^{-6}	0.072		
	Meadow area	-1.0×10^{-7}	0.0001			Meadow area	-3.0×10^{-8}	0.089		
	Treeline	0.0011	0.002			Treeline	0.0011	0.001		
	Shrub biomass	−0.0331	0.125			Schrub biomass	−0.350	0.066		
						% Forb	−0.9389	0.020		
						% Woody	3.7347	0.118		
Dark-eyed Junco	Stems/plot	0.0599	0.0001	0.725**	0.740**	Stems/plot	0.0276	0.087	0.060	0.130
	Meadow area	2.0×10^{-8}	0.049							
	Nearest neighbor	-1.06×10^{-6}	0.062							
	Shrub biomass	0.0171	0.092							
Lincoln's Sparrow	% Willow	4.8651	0.0001	0.450**	0.580**	% Willow	6.8188	0.0001	0.545**	0.576**
	LAI	0.88105	0.031			NDVI	3.9236	0.023		
	Treeline	0.0010	0.173			% Woody	8.6694	0.130		
	Graminoid biomass	−0.0313	0.185							
Savannah Sparrow	Treeline	0.0030	0.0001	0.522**	0.623**	Treeline	0.0014	0.009	0.370**	0.485**
	Graminoid biomass	0.0367	0.001			% Graminoid	2.0650	0.0003		
						% Woody	−5.6790	0.130		
	% Willow	1.2186	0.13							
Vesper Sparrow	Meadow area	8.0×10^{-8}	0.003	0.558**	0.626**	Meadow area	2.0×10^{-8}	0.163	0.538**	0.590**
	% Forb	0.6238	0.004			Forb biomass	−0.0600	0.050		
	% Sage	5.1927	0.153			% Sage	8.0526	0.0001		
	LAI	−0.3164	0.186							
White-crowned Sparrow	NDVI	10.4442	0.026	0.189*	0.189*	% Sage	2.7830	0.143	0.116	0.129
	LAI	−1.1455	0.081			Forb biomass	0.1117	0.177		
						%Forb	−1.3980	0.185		
Yellow Warbler	% Willow	11.8600	0.0001	0.560**	0.568**	% Willow	5.8250	0.0001	0.601**	0.605**
	Shrub biomass	−0.1086	0.031			Meadow area	-5.0×10^{-8}	0.063		
			0.078			Nearest neighbor	2.9×10^{-6}	0.078		
	% Woody	−8.8320				Stems/plot	−0.0211	0.142		

*Indicates significance at $p < 0.01$.
**Indicates significance at $p < 0.001$.

the height of willows, which need to be surveyed in the field. Although we estimated percent cover of willows and measured willow biomass, in the future we suggest that willow height also be included in such an analysis, because it appears to have a strong effect on Yellow Warbler and Common Yellowthroat abundances.

Predicting abundances for fine-scale montane meadow communities from coarse resolution satellite imagery is difficult, as demonstrated here, and predictive abilities may be affected by the spatial heterogeneity of the landscape, which limits the translation of information between scales (Turner et al. 1989). An integrated approach using Geographic Information Systems (GIS) techniques to classify habitat based on vegetation, along with information from remotely sensed data and species-specific vegetation type preferences, is likely to produce more accurate results in the prediction of species distributions (Stoms and Estes 1993). However, these techniques are still lacking information regarding detailed structural characteristics of the habitat, and it may still be difficult to make accurate predictions for certain organisms, such as birds. Birds respond to habitat structure in the selection of suitable breeding habitat (MacArthur and MacArthur 1961; Willson 1974; May 1982; Cody 1985), so in this case coarse resolution satellite data do not contain enough information to accurately predict their occurrence.

Other studies have been successful at using satellite imagery to map and characterize species habitats (Haney 1986; Frank 1988; Pearce 1991; Aspinall and Veitch 1993; Scott et al. 1993, 1996; Hepinstall and Sader 1997; Tucker et al. 1997; Beard et al. 1999; Dettmers and Bart 1999). Pearce (1991) was successful in mapping sedge-meadow habitat for musk ox, but cautioned that vegetation types classified by satellite data need to be confirmed through studies in the field. These studies identified and mapped potential habitats for a particular species, however, and except for Aspinall and Veitch (1993), most were not trying to predict species occurrences on a fine scale (1 ha).

Studies such as ours, which have attempted to use satellite imagery for predicting species occurrences at a high resolution, have had less success than those mapping potential habitats for a species (Jorgensen and Nohr 1996; Mack et al. 1997). Jorgensen and Nohr (1996) could explain only 40–50% of the variation in bird populations in the Sahel from satellite images measuring landscape diversity and biomass production. In a study area with high heterogeneity, it is difficult to use satellite imagery to classify different vegetation types on the ground (Jorgensen and Nohr 1996). Mack et al. (1997) found that bird species richness was better described using ground-based data than the remotely sensed data, but that the remotely sensed data were sufficient at coarse-scales. These studies both found that the resolution of the satellite data was not at a scale that could be used for accurate predictions. Mack et al. (1997) could not identify woodlots smaller than 2 ha from the remotely sensed data. Jorgensen and Nohr (1996) could not detect several vertically separated habitats in the dense forest cover. The inability to detect structure and smaller habitat patches reduces the correlation between the bird species and the satellite imagery. In our study differences in patch sizes between the two regions may have contributed to the differences in abundances for the bird species which were correlated to meadow area (Debinski, unpublished data). Because we had greater heterogeneity within our meadows than depicted on the remotely sensed image, and we could not determine habitat structure, it is not surprising that we had difficulty predicting bird species in our study using meadow type alone. However, we were able to make better predictions from the satellite data with the addition of landscape and habitat data.

Our results indicate that satellite imagery is applicable for the estimation of potential habitats and bird species distributions in the different types of montane meadows. However, the remotely sensed imagery was not suitable for fine scale information about birds in specific sites or areas. For future studies using satellite data to predict bird occurrences, we recommend the use of additional landscape and habitat data collected in the field. The combination of remotely sensed and ground-based data provides a researcher with more complete information and the ability to determine species occurrences.

Acknowledgements

This research was supported by a grant from the U.S. Environmental Protection Agency (EPA) through their Ecological Assessment and Restoration program. Although the research described in this article has been funded by the U.S. EPA (through grant 96-NCERQA-1A to Debinski et al.), it has not been subjected to the Agency's peer review and therefore does not necessarily reflect the views of the Agency and no official endorsement should be inferred. We thank T. Saveraid,

J. Pritchard, D. Friedrick, J. Auckland, B. Norris, J. Clark, and T. Hanks for the collection of the bird data, A. Fraser, D. Hurlburt, H. Loring, C. Morse, T. Aschenbach, I. Jordan, J. Hanlon, and S. Ashworth for collection of the botanical data, M. Micozzi, D. Kurtz, J. Robinson, T. Searls, C. Blodgett, A. Repinsky for the collection of the biophysical and satellite data, K. Jovaag for assistance with data analysis, and K. Moloney, J. Dinsmore, J. Heppinstall for comments on previous versions of the manuscript, and the ELVIS labgroup for comments on the research as it progressed. This is Journal Paper No. J-18564 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa, Project 3377, and supported by U.S. Hatch Act and State of Iowa Funds.

References

Aspinall, R. and Veitch, N. 1993. Habitat mapping from satellite imagery and wildlife survey data using a Bayesian modeling procedure in a GIS. Photogr Eng Remote Sensing 59: 537–543.

Beard, K.H., Hengartner, N. and Skelly, D.K. 1999. Effectiveness of predicting breeding bird distributions using probabilistic models. Cons Biol 13: 1108–1116.

Blake, J.G. and Karr, J.R. 1987. Breeding birds of isolated woodlots: area and habitat relationships. Ecology 68: 1724–1734.

Bower, J.E., Zar, J.H. and von Ende, C.N. 1990. Field and laboratory methods for general ecology, 3rd Edition. William Brown Publishers, Dubuque, IA, USA.

Cicero, C. 1997. Boggy meadows, livestock grazing, and interspecific interactions: influences on the insular distribution of montane Lincoln's Sparrows (*Melospiza Lincolnii alticola*). Great Basin Nat 57: 104–115.

Cody, M.L. 1985. Habitat selection in birds. Edited by M.L. Cody. Academic Press, Inc., San Diego, CA, USA.

Daubenmire, R.F. 1959. A canopy coverage method of vegetation analysis. Northwest Sci 33: 43–64.

Debinski, D.M., Kindscher, K. and Jakubauskas, M.E. 1999. A remote sensing and GIS-based model of habitats and biodiversity in the Greater Yellowstone Ecosystem. Int J Remote Sensing 20: 3281–3291.

Dettmers, R. and Bart, J. 1999. A GIS modeling method applied to predict forest songbird habitat. Ecol Appl 9: 152–163.

Dunning, J.B., Danielson, B.J. and Pulliam, H.R. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65: 169–175.

Estades, C.F. 1997. Bird-habitat relationships in a vegetational gradient in the Andes of central Chile. Condor 99: 719–727.

Fahrig, L. and Merriam, H.G. 1994. Conservation of fragmented populations. Cons Biol 8: 50–59.

Frank, T.D. 1988. Mapping dominant vegetation communities in the Colorado Rocky Mountain Front Range with Landsat Thematic Mapper and digital terrain data. Photogr Eng Remote Sensing 54: 1727–1734.

Freemark, K.E. and Merriam, H.G. 1986. Importance of area and habitat heterogeneity to bird assemblages on temperate forest fragments. Biol Cons 36: 115–141.

Gill, F.B. 1995. Ornithology, 2nd edition. W.H. Freeman and Company, New York, NY, USA.

Hagan, J.M., vader Haegen, W.M. and McKinly, P.S. 1996. The early development of forest fragmentation effects on birds. Cons Biol 10: 188–202.

Haila, Y., Hanski, I.K. and Raivio, S. 1993. Turnover of breeding birds in small forest fragments: the 'sampling' colonization hypothesis corroborated. Ecology 74: 714–725.

Haney, J.C. 1986. Remote sensing of seabird environments. Am Birds 40: 396–400.

Hepinstall, J.A., and Sader, S.A. 1997. Using Bayesian statistics, Thematic Mapper satellite imagery, and Breeding Bird Survey data to model bird species probability of occurrence in Maine. Photogr Eng Remote Sensing 63: 1231–1237.

Herkert, J.R. 1994. The effects of habitat fragmentation on Midwestern grassland bird communities. Ecol Appl 4: 461–471.

Jakubauskas, M.E., Kindscher, K. and Debinski, D.M. 1998. Multitemporal characterization and mapping of montane sagebrush communities using Indian IRS LISS-II imagery. Geocarto Int 13: 65–74.

Jorgensen, A.F. and Nohr, H. 1996. The use of satellite images for mapping of landscape and biological diversity in the Sahel. Int J Remote Sensing 17: 91–109.

Kindscher, K., Fraser, A., Jakubauskas, M.E. and Debinski, D.M. 1998. Identifying wetland meadows in Grand Teton National Park using remote sensing and average wetland values. Wetlands Ecol Manag 5: 265–273.

Lescourret, F. and Genard, M. 1994. Habitat, landscape, and bird composition in mountain forest fragments. J Environ Manag 58: 249–254.

MacArthur, R.H. and MacArthur, J.W. 1961. On bird species diversity. Ecology 42: 594–598.

Mack, E.L., Firbank, L.G., Bellamy, P.E., Hinsley, S.A. and Veitch, N. 1997. The comparison of remotely sensed and ground-based habitat area data using species-area models. J Appl Ecol 34: 1222–1228.

May, P.G. 1982. Secondary succession and breeding bird community structure: patterns of resource utilization. Oecologia 55: 208–216.

McAdoo, J.K., Longland, W.S. and Evans, R.A. 1989. Nongame bird community responses to sagebrush invasion of crested wheatgrass seedings. J Wildlife Manag 53: 494–502.

McCoy, T. 1996. Predictive models for grassland bird abundance and species richness in Missouri Conservation Reserve Program fields. Master's Thesis, University of Missouri, Columbia, MO.

McGarigal, K. and Marks, B.J. 1994. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. Version 2.0.

Patterson, M.P. and Best, L.B. 1996. Bird abundance and nesting success in Iowa CRP fields: The importance of vegetation structure and composition. Am Midland Nat 135: 153–167.

Pearce, C.M. 1991. Mapping muskox habitat in the Canadian high arctic with SPOT satellite data. Arctic 44 (suppl. 1): 49–57.

Pearson, S.M. 1993. The spatial extent and relative influence of landscape-level factors on wintering bird populations. Landsc Ecol 8: 3–18.

Salt, G.W. 1957. An analysis of avifaunas in the Teton mountains and Jackson Hole, Wyoming. Condor 59: 373–393.

SAS Institute Inc.1990. SAS/STAT User's Guide, Version 6, Fourth Edition, Volume 1 and 2, Cary: North Carolina SAS Institute Inc.

Saveraid, E.H. 1999. Using satellite imagery and landscape variables to predict bird communities in montane meadows of the Greater Yellowstone Ecosystem. Master's Thesis, Iowa State University. Ames, IA, USA.

Scott, J.M., Tear, T.H. and Davis, F.. (eds). 1996. Gap analysis: a landscape approach to biodiversity planning. American Society for Photogrammetry and Remote Sensing, Bethesda, MD, USA.

Scott, J.M., Davis, F.W., Csuti, B., Noss, R., Butterfield, B., Groves, C., Anderson, H., Caicco, S., D'Erchia, F., Edwards, T.C. Jr., Ulliman, J. and Wright, R.G. 1993. Gap analysis: a geographic approach to the protection of biological diversity. Wildlife Monogr 123: 1–41.

Stoms, D.M. and Estes, J. E. 1993. A remote sensing research agenda for mapping and monitoring biodiversity. Int J Remote Sensing 14: 1839–1860.

Tucker, K., Rushton, S.P., Sanderson, R.A., Martin, E.B. and Blaiklock, J. 1997. Modelling bird distributions–a combined GIS and Bayesian rule-based approach. Landsc Ecol 12: 77–93.

Turner, M.G. 1989. Landscape ecology: the effect of pattern on process. Ann Rev Ecol Syst 20: 171–197.

Turner, M.G., Dale, V.G. and Gardner, R.H. 1989. Predicting across scales: theory development and testing. Landsc Ecol 3: 245–252.

van Dorp, D. and Opdam, P.F.M. 1987. Effects of patch size, isolation, and regional abundance on forest bird communities. Landsc Ecol 1: 59–73.

Vickery, P.D., Hunter, M.L. Jr. and Wells, J.V. 1992. Use of a new reproductive index to evaluate the relationship between habitat quality and breeding success. Auk 109: 697–705.

Vickery, P.D., Hunter, M.L. Jr. and Melvin, S.M. 1994. Effects of habitat area on the distribution of grassland birds in Maine. Cons Biol 8: 1087–1097.

Wiens, J.A. 1969. An approach to the study of ecological relationships among grassland birds. Ornithol Monogr 8: 1–93.

Wiens, J.A. 1974. Habitat heterogeneity and avian community structure in North American grasslands. Am Midland Nat 91: 195–213.

Wiens, J.A. 1995. Habitat fragmentation: island versus landscape perspectives on bird conservation. Ibis 137: s97–s104.

Wiens, J.A., Crawford, C.S. and Gosz, J.R. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. Oikos 45: 421–427.

Willson, M.F. 1974. Avian community organization and habitat structure. Ecology 55: 1017–1029.