A LANDSCAPE APPROACH TO GRASSLAND BIRD CONSERVATION IN THE PRAIRIE POTHOLE REGION OF THE NORTHERN GREAT PLAINS

By

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A Landscape Approach to Grassland Bird Conservation in the Prairie Pothole Region of the Northern Great Plains

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Prairie is one of the most imperiled ecosystems, and grassland birds have experienced steeper and more consistent declines than any other group of birds in North America. Habitat-based planning tools are a cornerstone of conservation in forested ecosystems, but remain a novel approach in grasslands. In Chapter 2, I developed spatially-explicit habitat models as decision support tools for conservation. I surveyed birds, measured local vegetation and quantified landscape features at 952 sites in western Minnesota and northwest Iowa. Findings indicated that cropland provided little habitat for grassland songbirds and that hayland did not compensate for loss of grasslands. Multiscale models showed that conservation actions that integrate management at local and landscape scales have the greatest chance of success. At landscape scales, conserving and creating grasslands, removing trees from the landscape, or both will increase songbird density. Density of many species was positively related to amount of grassland at the smallest scale evaluated ($0.5km^2$), but large grasslands were vital for others whose density was related to grassland abundance at large scales ($32km^2$). At local scales, managing for a mosaic of vegetation that varies in structure and composition will increase bird diversity. Model validation showed that planning maps can be used reliably ($r^2 \geq 0.90$) to establish a regional conservation strategy. I used spatially-explicit maps to identify five landscapes capable of attracting the highest densities of the greatest number of songbirds, and showed that most of this habitat is unprotected from risk of conversion to other land uses. Models in Chapter 2 confirmed that woody edges exacerbated effects of habitat loss, so in Chapter 3 I tested whether birds used otherwise suitable habitats by experimentally removing trees in a before-after/control-impact design. This is the first study to experimentally show that songbirds avoid woody edges in otherwise suitable habitat. Avoidance of trees was apparent as far away from woody edges as surveys were conducted (240 m). The spring following tree removal, the four most common species redistributed themselves ubiquitously in grasslands where trees were removed. I recommend that managers remove trees from grasslands and avoid planting trees in grasslands where conservation of songbirds is the management goal.

‘The subtlety and serenity of grasslands defines their character,

but those same traits engender a lack of focus

compared with jagged peaks and cascading waters.

Grasslands require familiarity before appreciation, not the other way around. Unfortunately we never had a chance to develop that familiarity. Therefore, restoring and protecting grassland ecosystems remains considerably more difficult than doing so for other natural resources.’

-from Ecology and Economics of the Great Plains

(Daniel Licht 1997)

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The USFWS Regions 3 and 6 HAPET offices contributed greatly to the planning and implementation of this project, and were integral to its success. Mike Estey and Diane Granfors provided extensive GIS technical support and assisted with our sampling strategy. Neal Niemuth provided extensive statistical and field methodology advice. Resultant planning maps in this document were created by the HAPET offices using the models derived from this research.

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My pilot field season was conducted in cooperation with Lostwood National Wildlife Refuge and Wetland Management District and the Morris Wetland Management District. Shane Patterson collected all data at the Minnesota sites. Todd Frerichs, Bob Murphy and Karen Smith provided valuable support and hospitality. Elizabeth Madden and Todd Grant offered study design and vegetation sampling advice. My months spent on the prairies in the Lostwood area deepened my appreciation for the grassland landscape.

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I also recognize my committee: Joe Ball, Dick Hutto, Jon Graham, and Tom Martin – all giants in their fields in my opinion. They were patient with me throughout this academic process and provided insightful edit suggestions to this document. Jon Graham, as well as Mark Hebblewhite, offered extensive and much-needed statistical advice and were overly-generous with their office hours.

My advisor, Dave Naugle was integral in making this project a success. Without his skills in procuring funding and his talent for eloquently editing scientific writing, this project never would have come full circle. I thank Dave and his family for their friendship, as well as the many other folks in Missoula who befriended me over the years.

Finally, I sincerely thank my parents, Royce and Peg Quamen, my brothers Jeremy, Brady, and Shannon, sisters Shawn and Chelsie, and nieces Kelbi, Hannah, and Lucie, as well as the rest of my extended family. I could never have finished this degree without their love and support. They are, and will always be, my motivation to succeed in life.

For Rudy

1997-2005

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CHAPTER I

A MULTI-SCALE APPROACH

TO PLANNING FOR

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JUSTIFICATION, METHODS AND PARTNERSHIPS

Introduction

Prairie was once the most common ecosystem in North America, but today loss of prairie habitats now exceeds that of most other major ecosystems in North America (Samson and Knopf 1994, Noss et al. 1995). Consequently, grassland birds have experienced steeper, more consistent, and more widespread population declines than any other group of North American birds (Herkert 1995, Igl and Johnson 1997, Peterjohn and Sauer 1999). Declines are attributed to severe habitat loss (e.g., Herkert 1994) and degradation of remaining prairie remnants (Herkert et al. 2003). Although evidence suggests that grassland birds require large tracts of treeless grasslands (Cunningham and Johnson 2006, Kelsey et al. 2006), how fragmented landscapes function as habitat for birds is poorly understood. An understanding of how local and landscape features influence habitat suitability for grassland birds is vital to our ability to protect and restore habitats that maintain grassland bird populations. Insights into how birds perceive grassland habitats at multiple scales will enhance our ability to direct grassland conservation over broad geographic regions.

Integration of Scale into Research on Grassland Birds

Structure and composition of local vegetation (Wiens 1969, Whitmore 1979, Rotenberry and Wiens 1980, Madden et al. 2000, Grant et al. 2004) have long been known to affect habitat use by grassland birds, whereas more recent research has shown that landscape attributes also influence local species abundance and diversity (Bakker et al. 2002, Fletcher and Koford 2002, Cunningham and Johnson 2006, Winter et al. 2006).

Multiscale habitat modeling is likely an appropriate research approach because grassland birds respond to habitat features at a variety of scales. Studies that conducted multiscale analyses report that grassland birds respond to landscape attributes at scales from 12.5 ha to 804 ha (Bergin et al. 2000, Soderstrom and Part 2000, Ribic and Sample 2001). In native and restored grasslands in Iowa, local vegetation variables explained variation in density of 8 common bird species, and landscape attributes improved models for 4 of 8 species considered, explaining an additional 10-20% of variation (Fletcher and Koford 2002). In North Dakota's Sheyenne National Grassland, the largest remaining expanse of publicly-owned tallgrass prairie in the U.S., Cunningham and Johnson (2006) report that models with local and landscape attributes best explained habitat requirements for 17 of 19 birds species. And in eastern South Dakota, Bakker et al. (2002) found that occupancy rates for two species were higher in small patches within landscapes with high grassland abundance than in large patches within low grassland landscapes. Most importantly, nest predation rates in small (78-84%) versus large prairie remnants (54-68%) suggest a link between productivity and habitat fragmentation (Herkert et al. 2003), and further indicate that maintaining grassland bird populations in the Mid-continent may depend on protection and restoration of large grassland landscapes.

Regional Conservation Planning

Resource managers confronted with conserving grassland landscapes require large-scale studies that direct conservation over broad geographic regions to complement what has been learned at local scales. Landscape-level research is used in forested ecosystems to direct large-scale conservation efforts and design nature reserves (Askins et al. 1987, Flather and Sauer 1996, Ferraz et al. 2007, Thogmartin and Knutson 2007). Still, managers in grassland ecosystems continue to extrapolate recommendations from local studies to regional conservation plans because few studies have investigated the relative importance of local and landscape factors, and even fewer have identified the appropriate scales at which different species respond to habitat features in the landscape.

Technological advances such as remote sensing and geographic information systems (GIS) enable researchers to turn spatially implicit habitat models into spatially explicit maps that are useful in conservation planning over large geographic areas. Habitat-based maps depicting bird densities are crucial for decision-makers responsible for implementing on-the-ground habitat actions to conserve and restore bird populations. Despite this capability, predicting bird densities by linking habitat models to landscape attributes in a GIS remains a novel approach in grassland ecosystems.

Multiscale Approach to Implementing Conservation

Spatially-explicit habitat models are essential for establishing regional strategies as context for implementation of conservation actions locally. Equally important is feedback from local-scale management to inform regional conservation strategies. This interaction of regional strategies with local scale management fits the concept of "top-down" and "bottom-up" processes. Conservation planning maps created as a result of this study will serve as tools for conservation and restoration of grasslands at regional scales. Land managers can use maps depicting priority grasslands to identify which landscapes are capable of providing habitat for species of interest. Once priority landscapes are identified, then local vegetative attributes in our best habitat models can be managed to meet requirements of desired species. In fragmented landscapes where restoration is the management goal, characteristics of existing priority landscapes can be used to reconstruct additional grassland landscapes that mimic those known to attract priority species.

Study Region and Species of Interest

The study region for this research is the Prairie Pothole Region of western Minnesota, northwest Iowa, and the Dakotas. In the Midwest United States, >99% of native tallgrass prairie has been converted to row crop agriculture and associated uses (Samson and Knopf 1994). And in Iowa, for example, where tallgrass prairie once covered >79% of the state, <1% remains (Smith 1998). Regional grassland abundance occurs along a gradient from few remaining grasslands (<2% of land area) in the eastern tallgrass prairie region of western Minnesota and northwest Iowa to an abundance of grasslands (~40% remaining) in the mixed grass prairie region of eastern and central North and South Dakota. As a result, habitat conservation in the tallgrass prairie region is aimed at protecting remnant grasslands from tillage and restoring grasslands to enhance songbird populations.

I developed habitat models for 9 species, 5 of which are listed as priority species of management concern by the U.S. Fish and Wildlife Service, Partners-In-Flight or both (Table 1). Species of management concern that were not evaluated using point counts in this study include large-bodied species such as burrowing owl (*Athene cunicularia*), greater prairie chicken (*Tympanuchus cupido*) and others.

Table 1. Nine species of grassland birds for which I developed habitat models. Five species are Priority Grassland Species as listed by the U.S. Fish and Wildlife Service (USFWS 2002), Partners-in-Flight (PIF) conservation plans for Bird Conservation Region 11 (BCR 11) and PIF Physiographic Areas 40 (Northern Tallgrass Prairie) (Rich et al. 2004). The last 4 species are abundant throughout most of the study area.

Species	USFWS PPR	PIF Tier 1 BCR 11	PIF Tier 1 Phys 40	Other Species
LeConte's sparrow (*Ammodramus leconteii*)	X	X	X	
grasshopper sparrow (*Ammodramus savannarum*)	X	X		
bobolink (*Dolichonyx oryzivorus*)			X	
dickcissel (*Spiza americana*)			X	
sedge wren (*Cistothorus platensis*)			X	
clay-colored sparrow (*Spizella pallida*)				X
savannah sparrow (*Passerculus sandwichensis*)				X
western meadowlark (*Sturnella neglecta*)				X
horned lark (*Erempohila alpestris*)				X

Partnerships and Applied Context of this Research

The conceptual framework for our approach to this research follows the template set forth by the North American Waterfowl Management Plan for comprehensive planning and delivery of habitat objectives critical to meeting population goals. In 1989, the Management Board of the Prairie Pothole Joint Venture created two Habitat and Population Evaluation Teams, commonly referred to as HAPET offices, to assist in planning and evaluation of joint venture activities. Since then, HAPET offices have developed powerful landscape models that serve as decision support tools to help meet the waterfowl objective of the Prairie Pothole Joint Venture Implementation Plan. These landscape models are breeding duck pair distribution maps that predict the capacity of a landscape to attract breeding waterfowl (Reynolds et al. 2006). In the 1995 Prairie Pothole Joint Venture Implementation Plan Update (Rich et al. 2004), the Management Board approved a second objective to "*stabilize or increase populations of declining wetland/grassland-associated wildlife species in the PPR, with special emphasis on non-waterfowl migratory birds*".

To guide this new objective, the Technical Committee of Prairie Pothole Joint Venture, HAPET offices and grassland bird experts from the U.S. and Canada met in 1999 to develop criteria for mapping of grassland bird habitat in the U.S. Prairie Pothole Region. In meetings that followed, participants agreed on a conceptual approach to identifying priority landscapes for grassland birds. The HAPET offices adopted the conceptual framework to develop a rule-based model known as the Grassland Bird Conservation Area concept. Rules are based on four implicit assumptions: 1) large grasslands support more species or higher densities of birds than small grasslands, 2) less edge is better than more edge in grasslands of similar area, 3) more grassland is better than less grassland in the surrounding landscape and 4) trees reduce use of otherwise suitable habitats for some species. In 2000, HAPET interfaced the conceptual model with digital land cover in a GIS to identify locations that met the criteria in the U.S. portion of the Prairie Pothole Region. Response to this effort has been overwhelmingly positive as federal, state and private land managers and conservation planners voice their need for regional grassland bird planning tools. Development of the conceptual model was a critical step in understanding the data necessary to construct empirically based planning tools for grassland bird conservation.

In Chapter 2, I move beyond the conceptual model to develop empirically-based landscape models that can be used as decision support tools for grassland bird habitat conservation across regional scales. Specific objectives were to: 1) empirically identify local and landscape attributes that influence density of grassland songbirds in the Prairie Pothole Region of western Minnesota and northwest Iowa, 2) assess the relative importance of local versus landscape attributes in determining habitat suitability, 3) develop a regional conservation planning tool by linking species-specific habitat models to landscape attributes in a GIS, and to 4) cross-validate the predictive capability of grassland bird models to quantify how well they perform. In chapter 3, I evaluate effects of woody edges on grassland birds by experimentally removing trees in a before-after/control-impact design. My landscape models confirm that woody edges exacerbate effects of habitat loss, but the linear shape of planted treebelts makes them difficult to map using satellite imagery, so I conducted a field experiment to quantify the extent to which birds avoid trees in otherwise suitable grassland habitats. I predicted that grassland birds would avoid woody edges, and that birds would use otherwise suitable habitats after edges were removed.

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CHAPTER II

A LANDSCAPE APPROACH

TO GRASSLAND BIRD CONSERVATION

IN THE PRAIRIE POTHOLE REGION

OF MINNESOTA AND IOWA

Abstract

Prairie is one of the most imperiled ecosystems in North America and, in response to habitat loss, grassland birds have experienced steeper and more consistent and widespread population declines than any other group of birds. My objectives were to identify local and landscape features related to density of songbirds, assess the relative importance of local versus landscape features, develop a regional planning tool by linking habitat models to landscape features in a GIS, and to cross-validate the predictive capability of resulting maps. I surveyed birds at 952 point-count locations during the summers of 2003 – 2005 throughout western Minnesota and northwest Iowa. I measured structure and composition of local vegetation at each survey location and quantified features of the surrounding landscape at 3 spatial scales. I adjusted estimates of bird density for detection probability using Program DISTANCE, accounted for zero inflation in counts using mixture models and modeled out spatial dependency in data with an autologistic term. My findings showed the fundamental dependence of grassland passerines on grassland habitats and the resulting influence of agricultural tillage on songbird populations. Species-specific habitat models showed that conservation actions that focus on both local and landscape scales have the greatest chance for success because improvements in fit in multiscale models (ΔBIC = -59 to -17) largely precluded interpretation of models that contain only either local or landscape variables. At landscape scales, models indicated that conserving and creating grasslands, removing trees from the landscape or a combination of both will increase songbird density. At local scales, managing for a mosaic of vegetation that varies in structure and composition will increase songbird diversity. Model validation showed that spatially-explicit habitat models can be used reliably (r^2 = 0.90 – 0.99) to establish a regional strategy for grassland bird conservation. I used planning maps to identify 5 landscapes capable of attracting the highest densities of songbirds, and showed that most of the habitat in these landscapes remains unprotected from risk of conversion to other land uses.

Introduction

Loss of grasslands now exceeds that of most other major ecosystems in North America (Samson and Knopf 1994, Noss et al. 1995), and grassland birds have experienced steeper, more consistent, and more widespread population declines than any other group of North American birds (Herkert 1995, Igl and Johnson 1997, Peterjohn and Sauer 1999). Tallgrass prairie once covered >79% of Iowa, but <1% remains (Smith 1998). Although evidence suggests that grassland birds require large tracts of treeless grasslands (Cunningham and Johnson 2006, Kelsey et al. 2006), how fragmented landscapes function as habitat for birds is poorly understood. Local species abundance and diversity is influenced by both local (Wiens 1969, Whitmore 1979, Rotenberry and Wiens 1980, Madden et al. 2000, Grant et al. 2004) and landscape variables (Bakker et al. 2002, Fletcher and Koford 2002, Winter et al. 2006). Insights into grassland bird settlement patterns at multiple scales will enhance our ability to apply grassland conservation over broad geographic regions.

The purpose of this study was to 1) empirically identify local and landscape attributes that influence density of grassland songbirds in the Prairie Pothole Region of western Minnesota and northwest Iowa, 2) assess the relative importance of local versus landscape attributes in determining habitat suitability for grassland birds, 3) develop a conservation planning tool by linking species-specific habitat models to landscape attributes in a GIS to depict landscape suitability for birds across the entire study region, and 4) cross-validate the predictive capability of grassland bird models to quantify how well they perform.

Study Region

The study region for this research was the Prairie Pothole Region of western Minnesota and northwest Iowa (Figure 1). In the Midwest U.S., >99% of native tallgrass prairie has been converted to row crop agriculture and associated uses (Samson and Knopf 1994). Regional grassland abundance occurs along a gradient from few remaining grasslands (<2% of land area) in the eastern tallgrass prairie region of western Minnesota and northwest Iowa to a relative abundance of grasslands (~40% remains) in the mixed grass prairie region of eastern and central North and South Dakota.

Methods

GIS Land Cover Data

Land cover and GIS support for this project was provided by the U.S. Fish and Wildlife Service's Region 3 Habitat and Population Evaluation Team (HAPET) in Fergus Falls, Minnesota. Land cover was constructed using 2001-2003 Landsat Thematic Mapper (TM) Imagery (30 × 30 resolution; 900-m^2) covering western Minnesota and northwest Iowa (Figure 1). Land cover was classified into 4 general habitats: cropland, grassland, hayland and woodland. Cropland included tilled lands, small grain fields, and annually fallowed sites. Grassland represented both annually grazed native or introduced grassland cover (pasture) and undisturbed grasslands that were typically Conservation

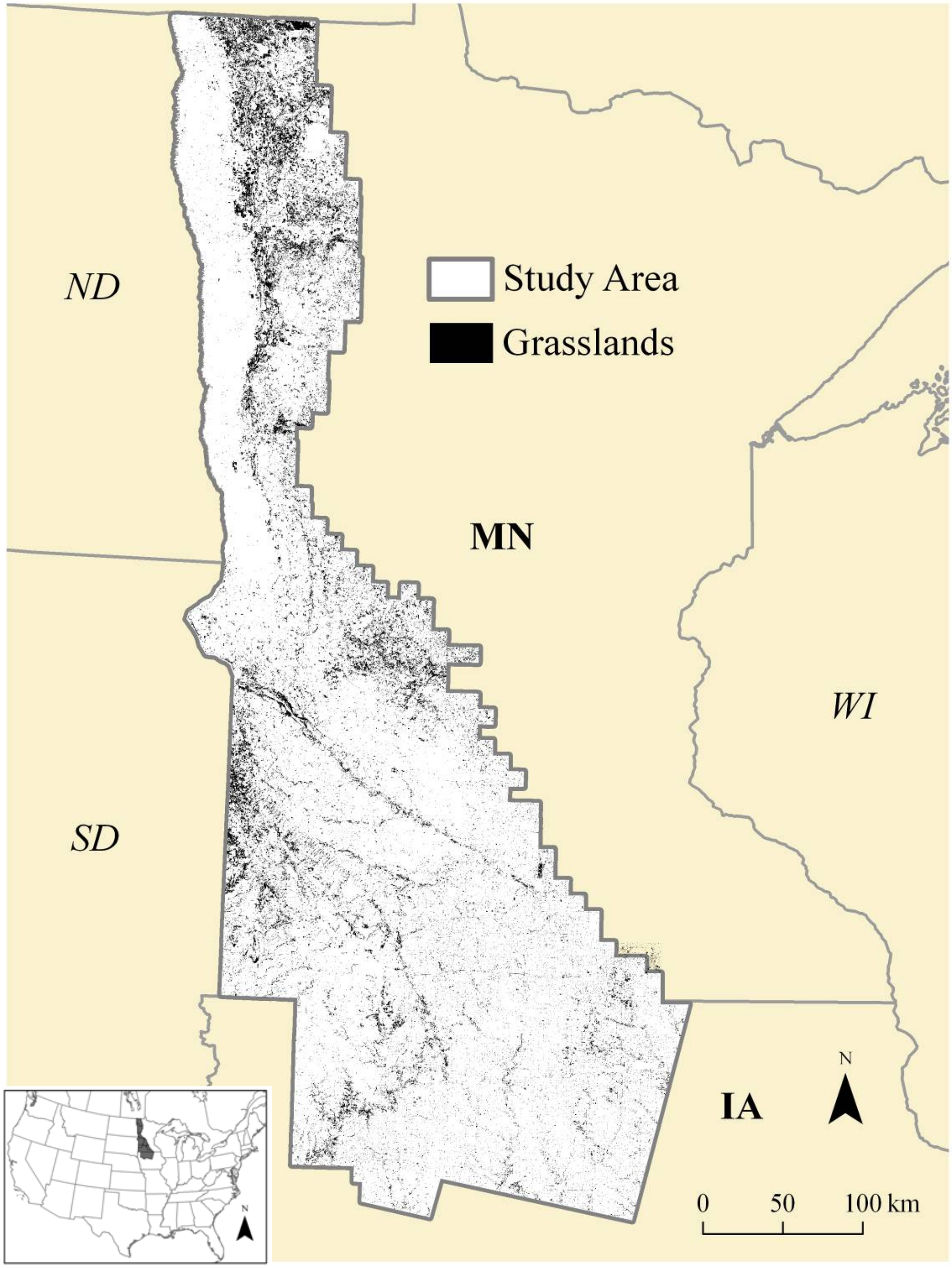

Figure 1. Study area of the Prairie Pothole Region of Minnesota and Iowa.

Reserve Program (CRP) fields and other idled grasslands. Hayland was predominantly composed of alfalfa or alfalfa mixed with cool-season grasses and was hayed one to three times annually. Woodland was a mixture of planted tree belts in upland habitats, natural woodlands in the prairie-woodland interface of Minnesota, and woody cover in riparian lowlands. Overall accuracy for the land cover classification from an independent dataset was 78% (76% for Grassland, 79% for Cropland, and 75% for Woodland). Urban areas were removed from analyses. Detailed imagery classification protocol and accuracy assessment information can be obtained from the USFWS Region 3 HAPET Office, 18965 County Hwy 82 S, Fergus Falls, MN 56537 (http://www.fws.gov/midwest/hapet/index.htm).

Study Design for Bird Surveys

I used stratified random sampling to select 952 survey locations throughout the study region. I stratified by USFWS Wetland Management District, land cover type, and grassland abundance in the landscape (Figure 2). I stratified survey locations by area of 9 management districts to approximate equal allocation of points across the region. I stratified by land cover type using unequal allocation to minimize variation in bird density estimates among land cover types. I allocated 15% of points to cropland (n = 148), 70% to grassland (n = 658), and 15% to hayland (n=146). Bird density and variation in estimates were low in cropland, and hayland is a rare habitat that covered <5% of the study region. I designed this study to assess the relative importance of local versus landscape attributes in determining habitat suitability, and predicted

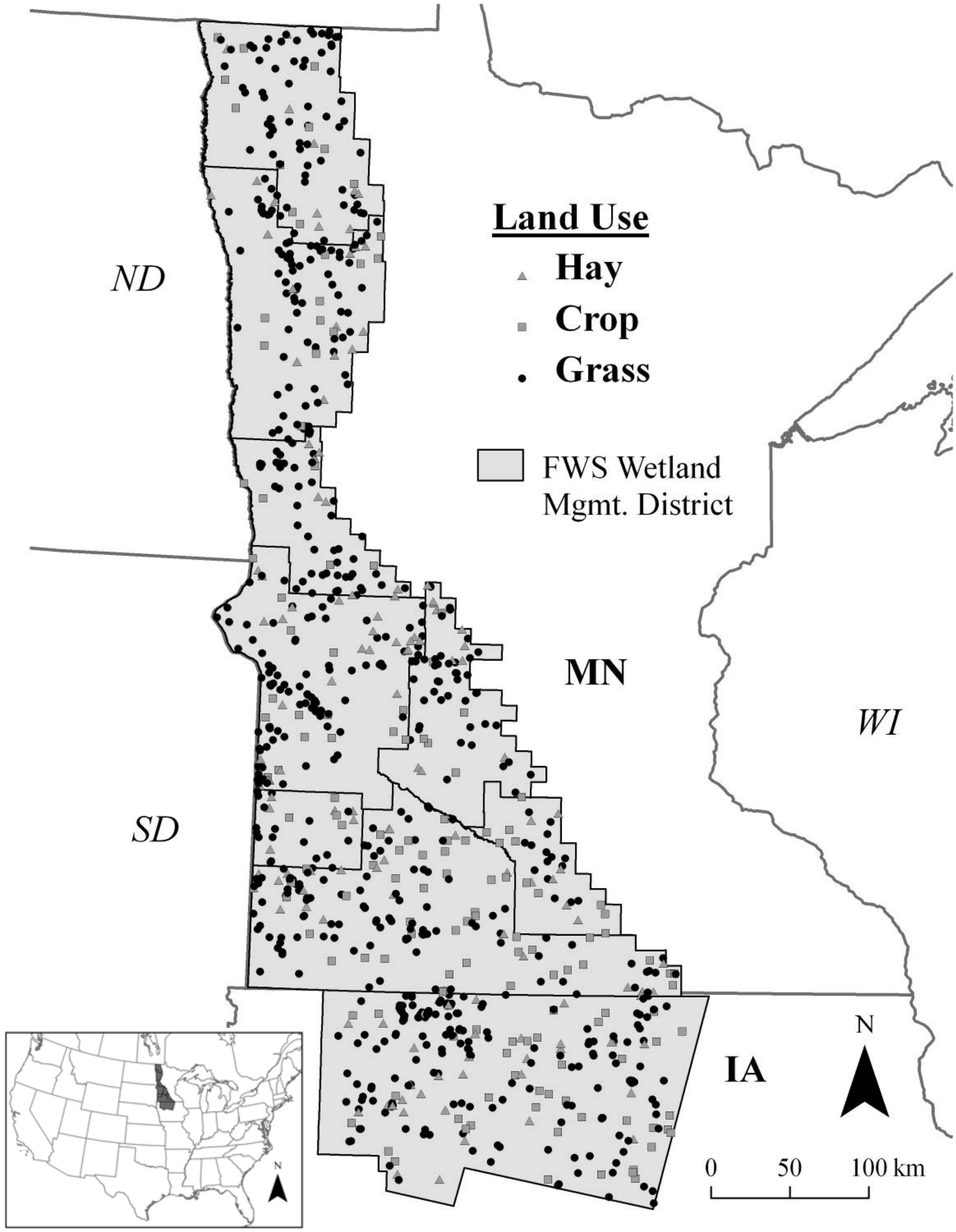

Figure 2. Locations of a stratified random sample of 952 survey sites throughout the study region. Sites were stratified by management district, land cover type and grassland abundance in the landscape.

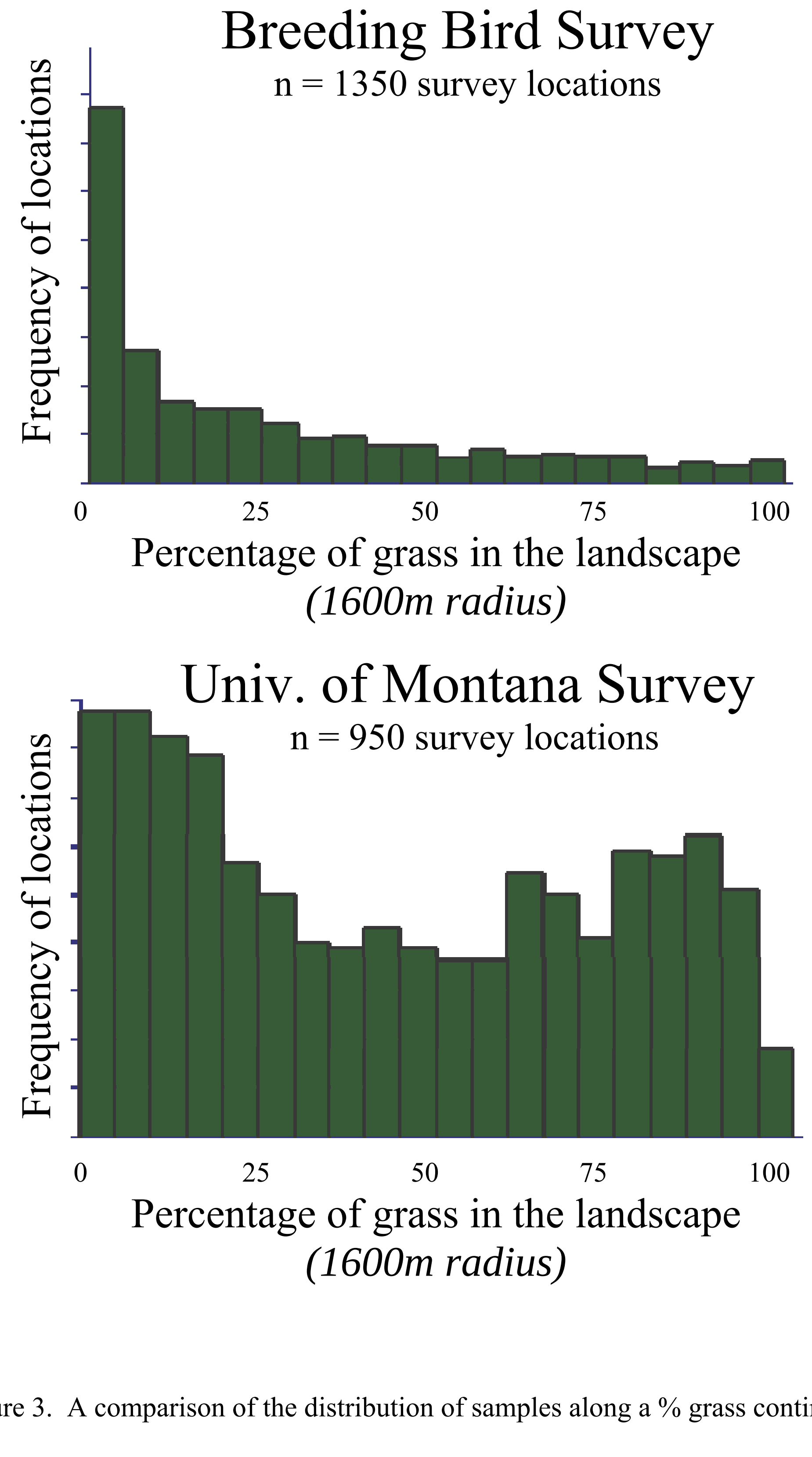

Figure 3. A comparison of the distribution of samples along a % grass continuum between our sampling design and that of the Breeding Bird Survey.

that grassland abundance in the landscape may be an important determinant. Thus, I stratified by grassland abundance to ensure that survey locations were equally allocated across the range of variation within each management district. I calculated the amount of grassland within 8 km^2 of each 900-m^2 cell in the GIS and assigned survey locations to categories of high, medium, or low grassland abundance. Stratification marks an improvement over the simple random sampling design employed by the United States Geological Survey Breeding Bird Survey (BBS; http://www.pwrc.usgs.gov/BBS/; Figure 3) by decreasing standard errors along the regression line, making better inference for this landscape attribute possible. Each survey location was >1.6 km from neighboring locations to minimize spatial autocorrelation (i.e., similarity in sample points that are near one another; Legendre 1993) and to maximize independence of observations (Hurlbert 1984). I telephoned landowners to ask for access to private lands because 95% of survey locations fell outside of public ownership. Alternate survey locations replaced those that were misclassified in land cover data or where private landowners denied access.

Number of visits to each site

To evaluate how many times to visit individual points, I recorded number of singing males within a 100-m fixed-radius point count at 21 points in Minnesota 5 times from 15 May – 4 July 2002 between sunrise and 1000 hrs CST. I then conducted Monte Carlo simulations on the data to ask the question "Is it better to survey a few points many times or should I sample more points once?" This is a key question in estimating sample sizes, evaluating whether I could adequately sample the study area with survey sites and still detect enough individuals to construct landscape models for a suite of 9 species (Table 1).

Bird Surveys

I surveyed birds for 10 min within 100-m fixed-radius point counts. Surveys were conducted from sunrise to 1000 hrs CST 19 May – 30 June 2003, 23 May – 29 June 2004 and 23 May – 22 June 2005. I recorded number of singing males for each species except bobolink for which all males were counted regardless of whether they were singing. I used plat books, maps derived from GIS land cover data, and global positioning units (±10 m accuracy) to navigate to survey locations. Observers wore drab rather clothing to minimize the likelihood of reactions from birds (Gutzwiller and Marcum 1997). I monitored individual bird movements to avoid double counting. Surveys were conducted only on mornings when weather conditions did not impede detection of birds (no rain, fog, or wind >24 km/h; Ralph et al. 1995).

Observers recorded the distance to each bird detected (Rotella et al. 1999, Rosenstock et al. 2002) as well as the cover type in which they were located so that I could use detection probabilities to adjust density estimates using Program DISTANCE (Buckland et al. 1993, Laake et al. 1993). Distance to each bird when first detected was estimated to the nearest 5 m. To address assumptions of distance sampling (Buckland et al. 1993), I trained observers in bird identification by song, point count techniques, and distance estimation, with particular emphasis on estimating distances to aurally detected birds (Rotella et al. 1999). Observers used flagging to learn how to accurately estimate distance, and when assignment to a distance category was uncertain, would confirm the estimate by pacing to the observed location after the count was completed (Rotella et al. 1999). I used equal area sampling (i.e., one point count per location) to avoid passive sampling issues (Vickery et al. 1994, Horn et al. 2000). I surveyed each point once. A new sample of locations was selected annually to obtain a large sample over an extensive geographic region. I did not relocate point count areas that fell within divided land use to account for edge avoidance and/or attraction.

Structure and Composition of Local Vegetation

I quantified structure of vegetation with three attributes measured at 10-m intervals along a transect within point count locations (Grant et al. 2002; Figure 4): height-density or visual obstruction readings, effective leaf height, and litter depth (Table 1). I assessed visual obstruction by obtaining a reading in a random direction 4 m from the pole at a height of 1 m horizontal to the Robel pole (Robel et al. 1970, Higgins and Barker 1982). I estimated effective leaf height at the average height of the tallest grass leaves within 4 m of the pole. I measured litter depth to the nearest millimeter with a ruler inserted into the detritus until it made contact with the soil.

I quantified composition of vegetation with 10 attributes measured at 10-m intervals along a transect within each point count (Table 1, Figure 4). I estimated a 1-m^2 area at each of 10 stops using the Robel pole. Dominant vegetation type within this area was recorded as: shrub, forb, small grain crop, row crop, exotic grass, native warm season grass, native cool season grass, alfalfa, wetland vegetation or noxious weed.

I visually estimated percent area of each cover type within the 100-m radius point count as percent cropland (CROPCOVER), grassland (GRASSCOVER), hayland

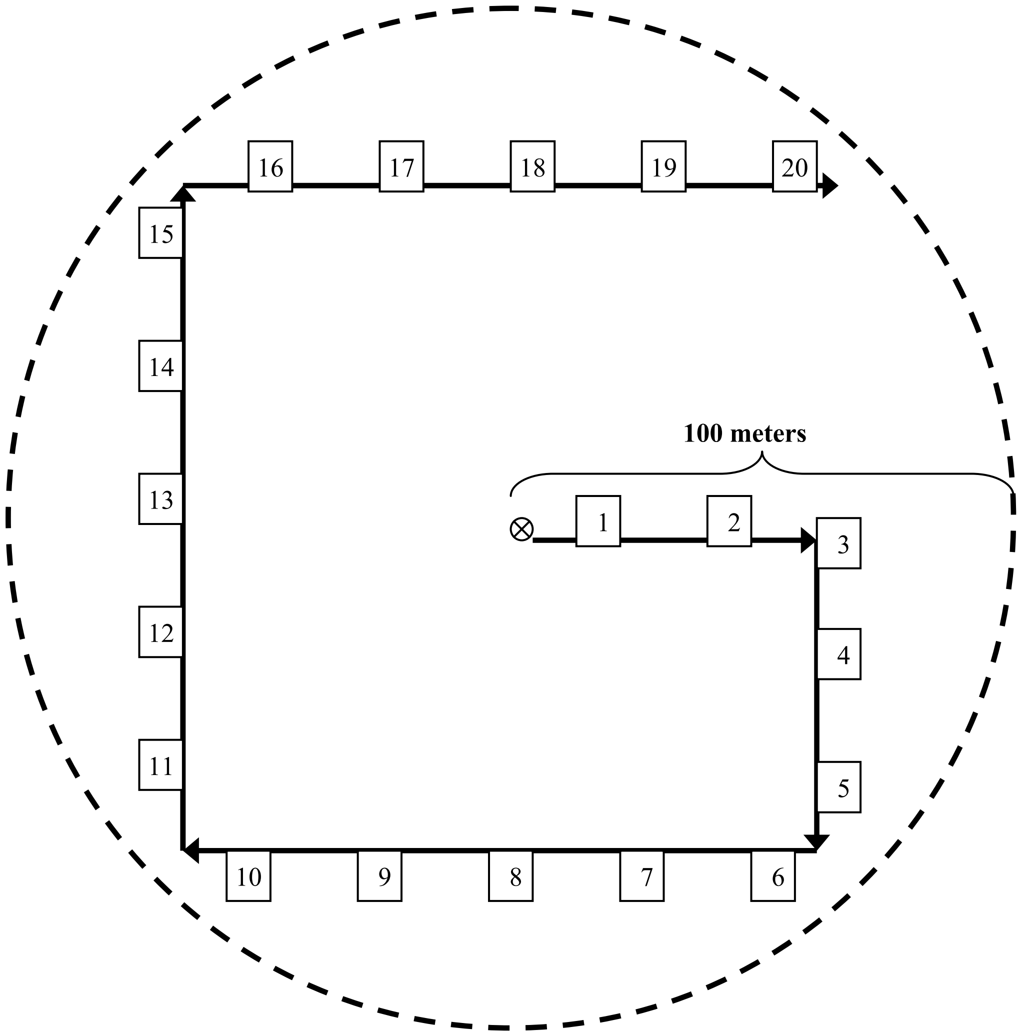

Figure 4. Vegetation sampling design within the 100-m fixed-radius point count.

Table 1. Vegetation, landscape, and Breeding Bird Survey (BBS) parameter definitions.

Class	Variable	Definition
Cover Type	Cropcover**	Visual estimate of percent cropland covering 100m count area
	Grasscover**	Visual estimate of percent grassland covering 100m count area
	Haycover	Visual estimate of percent hayland covering 100m count area
	Treecover	Visual estimate of percent woodland covering 100m count area
	Wetcover	Visual estimate of percent wetland covering 100m count area
Structure	VOR	Average visual obstruction reading (dm) at 20 stops
	Leaf	Average leaf height (cm) at 20 stops
	Litter	Average litter depth reading (dm) at 20 stops
Composition	Grasses	% of stops where dominant vegetation was grasses
	Shrubs	% of stops where dominant vegetation was shrubs
	Forbs	% of stops where dominant vegetation was forbs
	SmallGrain*	% of stops where dominant vegetation was small grain
	RowCrop*	% of stops where dominant vegetation was row crop
	ExoticGrass*	% of stops where dominant vegetation was exotic grasses
	CoolNativeGrass*	% of stops where dom. vegetation was cool season native grass
	WarmNativeGrass*	% of stops where dom. vegetation was warm season native grass
	Alfalfa	% of stops where dominant vegetation was alfalfa
	WetMeadow*	% of stops where dominant vegetation was wet meadow
	Weeds*	% of stops where dominant vegetation were weeds
Landscape	Crop400**	% of landscape (400m radius) in cropland
	Crop800**	% of landscape (800m radius) in cropland
	Crop1600**	% of landscape (1600m radius) in cropland
	Crop3200**	% of landscape (3200m radius) in cropland
	Grass400	% of landscape (400m radius) in grassland
	Grass800	% of landscape (800m radius) in grassland
	Grass1600	% of landscape (1600m radius) in grassland
	Grass3200	% of landscape (3200m radius) in grassland
	Hay400	% of landscape (400m radius) in hayland
	Hay800	% of landscape (800m radius) in hayland
	Hay1600	% of landscape (1600m radius) in hayland
	Hay3200	% of landscape (3200m radius) in hayland
	Trees400	% of landscape (400m radius) in woodland
	Trees800	% of landscape (800m radius) in woodland
	Trees1600	% of landscape (1600m radius) in woodland
	Trees3200	% of landscape (3200m radius) in woodland
BBS	(BOBO)	Relative abundance of bobolinks (1992-2003 BBS)
	(CCSP)	Relative abundance of clay-colored sparrows (1992-2003 BBS)
	(DICK)	Relative abundance of dickcissels (1992-2003 BBS)
	(GRSP)	Relative abundance of grasshopper sparrows (1992-2003 BBS)
	(HOLA)	Relative abundance of horned larks (1992-2003 BBS)
	(LCSP)	Relative abundance of LeConte's sparrows (1992-2003 BBS)
	(SAVS)	Relative abundance of savannah sparrows (1992-2003 BBS)
	(SEWR)	Relative abundance of sedgw wrens (1992-2003 BBS)
	(WEME)	Relative abundance of western meadowlarks (1992-2003 BBS)

**not used in analysis due to low sample size*

***not used in analyses due to correlation with other variables*

(HAYCOVER), woodland (TREECOVER) and wetland (WETCOVER). Only bird counts on the cover type of interest were used, and these counts were adjusted to the percentage of cover type within the 100-m point count area. Lastly, I estimated distance (m) to the nearest electrical line, road, fence, wetland, building and tree >6 m in height.

Landscape Attributes

Using a GIS constructed from TM imagery, I quantified landscape attributes from the center of each point count area at four spatial scales: 0.5 km^2 (400-m radius), 2 km^2 (800-m radius), 8 km^2 (1600-m radius) and 32 km^2 (3200-m radius). I calculated percentage of area in grassland, cropland, hayland and woodland to describe composition of the landscape surrounding each survey location (Table 1). I analyzed spatial data using the Arc/Info GRID module (Environmental Systems Research Institute, Redlands, California, USA).

An Autologistic Term to Account for Spatial Dependency

Autocorrelation in spatial distribution and abundance of grassland birds may result from behavioral or demographic processes such as territoriality or philopatry (Wintle and Bardos 2006) and when environmental variables influencing the niche of a species are themselves spatially structured (Legendre 1993). Failure to account for spatial structuring when constructing species-habitat models violates the assumption of independence, a basic tenant of most statistical approaches, which leads to biased standard errors, and ultimately results in lower predictive power (Legendre 1993).

I used estimates of grassland bird abundance from Breeding Bird Survey data (BBS; Sauer et al. 2005) as a term in our models used to account for variation in bird abundance outside, inside and on the edge of each species range. Resulting residuals were used to identify important habitat attributes after accounting for autocorrelation in the abundance of each species across their range. The BBS collects data on roadside bird populations and provides broad-scale digital summaries of abundance for 1993-2002 across our study region (Appendix 1). I intersected study locations from this study with those from BBS using GIS. Grid cell size for BBS summaries is 461 km^2.

Statistical Analyses

Distance Sampling.

Point count methodologies provide a foundation for estimating relative bird abundances and habitat associations (Norvell et al. 2003). Still, unadjusted point counts often fail to account for unequal detection probabilities that may vary across distances, habitat types, species and environmental conditions, yielding biased density estimates (Rotella et al. 1999), and ultimately leading to spurious inferences about species-habitat relationships. Distance sampling (Rosenstock et al. 2002) reduces bias in estimates of population density (Somershoe et al. 2006) by adding an analytical component to point counts that models variation in species' detectability, thus yielding more reliable information for habitat assessments and conservation planning and implementation. It is gaining popularity over alternative approaches, such as double-observer (Nichols et al.

2000, Alldredge et al. 2006) or removal methods (Farnsworth et al. 2002), which are generally regarded as expensive, time consuming, and logistically challenging in large-scale field studies.

I used program DISTANCE (Buckland et al. 2001, Thomas et al. 2005) to estimate densities of grassland birds using detection probabilities estimated from observer-to-bird distance data (Appendix 2). I plotted frequency histograms of raw detection data by habitat type to evaluate overall detection patterns and to look for evidence of evasive bird movements, heaping, and outliers (Buckland et al. 2003). I stratified detection data by land cover types in which birds were surveyed to improve precision and reduce bias of estimates when detection patterns vary substantially among cover types (i.e., grassland versus cropland; Buckland et al. 2003). I fit detection functions for models with cosine and simple polynomial expansions, and half-normal and hazard-rate model forms with cosine expansions (Appendix 2). I used Akaike's Information Criteria (AIC) values to select among competing candidate models. The model with the lowest AIC value for each species was considered the most parsimonious and best approximation of information contained in the data (Burnham and Anderson 2002). I used the AIC "best" model to adjust raw count data to make valid estimates of density for use as a dependent variable in modeling species-habitat relationships. Lastly, I calculated occupancy rates by land cover type as number of survey locations in which a species was detected divided by total number of survey locations. I compared occupancy rates with adjusted densities to evaluate whether the habitats most commonly occupied also contained the highest densities of birds.

<u>Accounting for Zero-Inflation in Choice of Modeling Approach</u>.

Many datasets used to estimate occurrence rate or abundance of organisms contain a large proportion of zero values due to no occurrences (Welsh et al. 1996, Hall 2000). When the number of zeros is so large that the data do not fit standard distributions (e.g., normal, Poisson, negative binomial), the data set is referred to as 'zero-inflated' (Martin et al. 2005). Zero inflation is often due to a large number of 'true' zeros that reflect the real ecological effect of interest (Barry and Welsh 2002). Failure to account for zero inflation when choosing a modeling approach leads to bias in parameter estimates and their associated measures of uncertainty (e.g., inappropriately small confidence intervals; MacKenzie et al. 2002). Under a scientific framework that relies on model-based inference (Burnham and Anderson 2002, Link and Barker 2006), bias in parameter estimates and their confidence intervals ultimately results in poor inference (Barry and Welsh 2002) and may misdirect conservation actions (Martin et al. 2005).

I explicitly account for zeros in our modeling approach because examination of frequency of counts showed that data were zero-inflated for each of nine species in this study (Figure 5). My heuristic approach is to model grassland bird count data in three steps (Heilbron 1994, Welsch et al. 1996). First, I model the presence / absence component of the data as a binary logistic regression (LOGIT) with habitat variables. Second, I model density as a negative binomial regression (NBREG) to account for overdispersion in count data (Figure 6; Cheung 2002). Third, I combine in a zero-inflated negative binomial model (ZINB) the habitat variables identified as important in steps one and two of model development. The ZINB provides a mixing parameter (Martin et al. 2005) that often times provides better model fit by assigning a probability

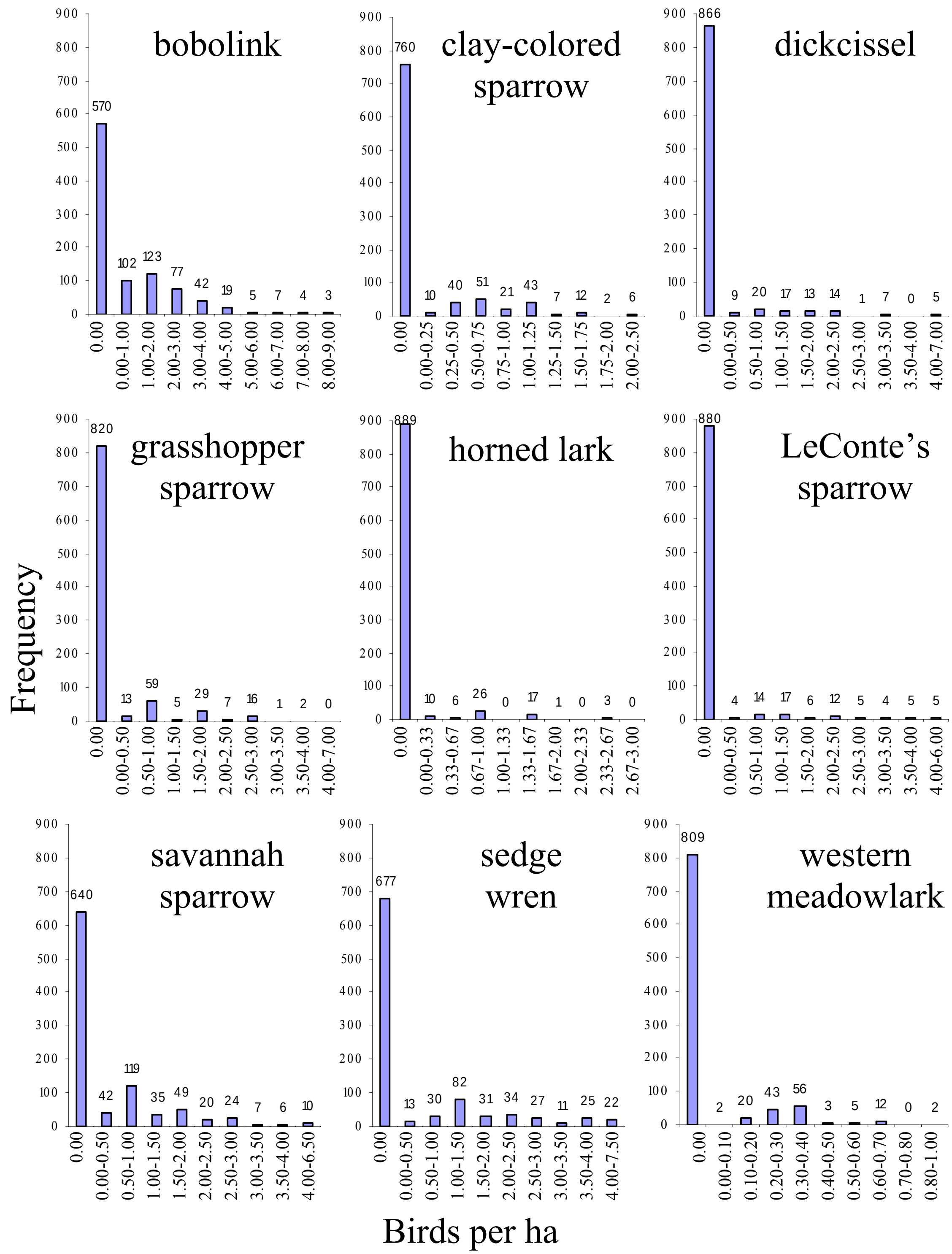

Figure 5. Histograms showing zero-inflation in data sets. Zero counts make up 40-92% of data, which is more than expected if a Poisson distribution is assumed.

(P) to zeros and $1 - P$ to the negative binomial portion of the equation (Guisan et al. 2002, Lewsey and Thompson 2004). I evaluated LOGIT and NBREG models before combining output in a ZINB because no multi-scale studies involving occurrence and density data exist upon which to base a priori models (Burnham and Anderson 2002).

Variable Selection for Species-Habitat Relationships.

I selected variables for consideration in LOGIT and NBREG models within each of five categories: cover type, structure, composition, landscape or BBS (Table 1). I identified all correlated variables ($r \geq |0.7|$). When ≥2 variables were correlated, I chose the variable with the greatest biological meaning according to known characteristics of grassland bird habitat from published studies. I tested all variables individually and retained those with confidence intervals that did not overlap zero. For each landscape variable, I retained the scale that best explained either the occurrence or density of birds based on log-likelihood values.

I then allowed cover type, structure, composition, and BBS variables, as well as the best scale for each landscape variable to compete with all combinations of other variables within the same category to identify the most parsimonious model. I checked again for highly correlated variables ($r \geq |0.7|$) and assessed stability and consistency of estimates of regression coefficients. If a coefficient switched direction or if its standard error increased substantially when a correlated variable was in the same model, I removed one variable from analysis if the other was an important predictor. Statistical analyses were conducted using Stata 7.0 (Stata Corporation, College Station Texas, USA).

Model Selection.

After identifying the top model(s) within categories of cover type, structure, composition, landscape and BBS, I allowed models to compete across categories to see if the additional information increased model fit. I use information-theoretic methods to choose between competing models to identify the "best" LOGIT and NBREG models. I chose the "best" models by converting log-likelihood values to Bayesian Information Criterion (BIC) because BIC has been shown to yield conservative models that are adequately penalized for additional variables (Hastie et al. 2001, Link and Barker 2006). I also calculated Akaike's Information Criterion (AIC; Akaike 1973, Burnham and Anderson 2002). Both BIC and AIC are based on the principle of parsimony and help to identify the model that explains the most variation with the fewest variables. However, I primarily used BIC for multimodel inference because AIC tends to select models with too many variables when sample sizes are large (Boyce et al. 2002). Lastly, I assigned variables identified as important in LOGIT and NBREG models to the inflation and density components of the ZINB equation to assess whether model fit increased. I compared model fit for LOGIT, NBREG and ZINB using BIC.

I constructed a second set of models containing only landscape and BBS variables that could be mapped in a GIS for use in regional conservation planning. Variables that could not be mapped (i.e., structure and composition of vegetation) or that were poorly mapped (i.e., land cover within 100 m of the point count location) using TM satellite imagery were omitted from this model set. I constructed this set of models using the same variable and model selection criteria and evaluated model fit for LOGIT, NBREG and ZINB using BIC.

<u>Cross-validating Models</u>.

I partitioned bird surveys into model-training and model-testing sets by withholding 20% of the data using a *k*-fold partitioning of the original samples (Fielding and Bell 1997), where *k* represents the five partitions (Boyce et al. 2002, Nielson et al. 2002). I used the BIC "best" model to estimate bird density for each of five datasets containing 80% of the original information. I used resulting models to estimate density for each of five model-testing datasets containing 20% of the original data that were not used to construct models. After re-assembling the five model-testing datasets, I categorized observed bird densities into five ordinal 20% quintile bins representing progressively selected habitats based on predicted densities. I tested the relatedness of observed bird density in each bin against predicted density to evaluate model fit. Observed and predicted bird densities should be highly correlated if the model is a good one, indicating that indeed the model is predicting density of grassland birds on the landscape (Boyce et al. 2002, Johnson et al. 2006). I evaluated model fit according to Johnson et al. (2006). Good model fit should have a high Spearman Rank Coefficient (i.e., r^2) value, a slope not different from 1.0, and an intercept not different from zero. Using these same procedures, I validated separately the BIC "best" models for the initial model set containing all five categories of variables and for the model set containing only landscape and BBS variables.

<u>Comparing the Relative Importance of Local and Landscape Variables</u>.

I compare the relative importance of local versus landscape variables in predicting bird abundance to understand the relative importance of management decisions at multiple scales. I define local vegetation variables as those habitat attributes within a nesting territory that can be managed at a field level including structure and composition of grassland vegetation. I defined landscape variables as those that extend beyond a nesting territory at multiple scales to describe the quantity, composition and juxtaposition of adjacent cover types. I use delta BIC and the difference in r^2 from k-fold validations for BIC "best" models to compare the role of local versus landscape variables in describing habitat suitability for grassland birds and to evaluate whether regional maps provide a useful tool for conservation planning.

Linking Bird Densities with Landscape and BBS Variables to Make Regional Planning Tools.

I constructed regional planning maps for each of nine species investigated. I used BIC "best" landscape and BBS models to make maps that show spatial relationships between bird density and habitat variables in GIS. I used variables identified as important predictors at appropriate scales to run models. I also constructed two maps that spatially depict landscapes capable of supporting the highest species richness of obligate grassland birds. I used estimates of density for individual species to scale richness maps for all species but western meadowlark. For meadowlark, I used estimates of probability of occurrence since models using abundance did not converge. In the first map, a species was included in richness at each 900-m^2 cell in the landscape where its predicted density was in the upper two-thirds of the estimate. In a second and more restrictive map, a species was included in richness when its predicted density was within the upper one-third of the estimate. Western meadowlark was included in the richness maps when it had a >0.33 and >0.67 maximum probability of occurrence, respectively. Horned lark was excluded from calculations of species richness because the BIC "best" model shows that this species prefers agricultural landscapes**.** Clay-colored sparrow was also excluded because k-fold validation of the landscape model for this species would not converge.

Results

Monte Carlo simulations using data collected in a pilot year in 2002 indicate that on average, detection rates increased <5% for rare species when sites were visited twice instead of once (Figure 6). For more abundant species (e.g., savannah sparrow, bobolink, clay-colored sparrow), detection rates on average increased 9-11% when sites were visited twice. A large number of sites should be visited to ensure enough detections to construct models for rare species of conservation interest. Consequently, I maximized sample size in 2003-2005 by surveying a large number of sites once.

In three field seasons, I surveyed 952 points and detected nine species of grassland passerines for which densities and occupancies were estimated and habitat relationships investigated (Figures 5, 7 and 8). Of point counts surveyed, 52% were grassland, 27% cropland, 11% hayland and 5% woodland (Table 2). Visual obstruction in grassland survey points averaged 2.4 dm, effective leaf height was 43.6 cm and litter depth was 36.8 mm (Table 2). On average, composition of grasslands was 81.8% grasses, 4.3% forbs and 2.9% shrubs (Table 2). I excluded from analyses composition of warm- versus cool-season native grasses because most grasslands surveyed were exotic cool seasonbelts (Table 2). Cropland dominated the landscape at each scale investigated,

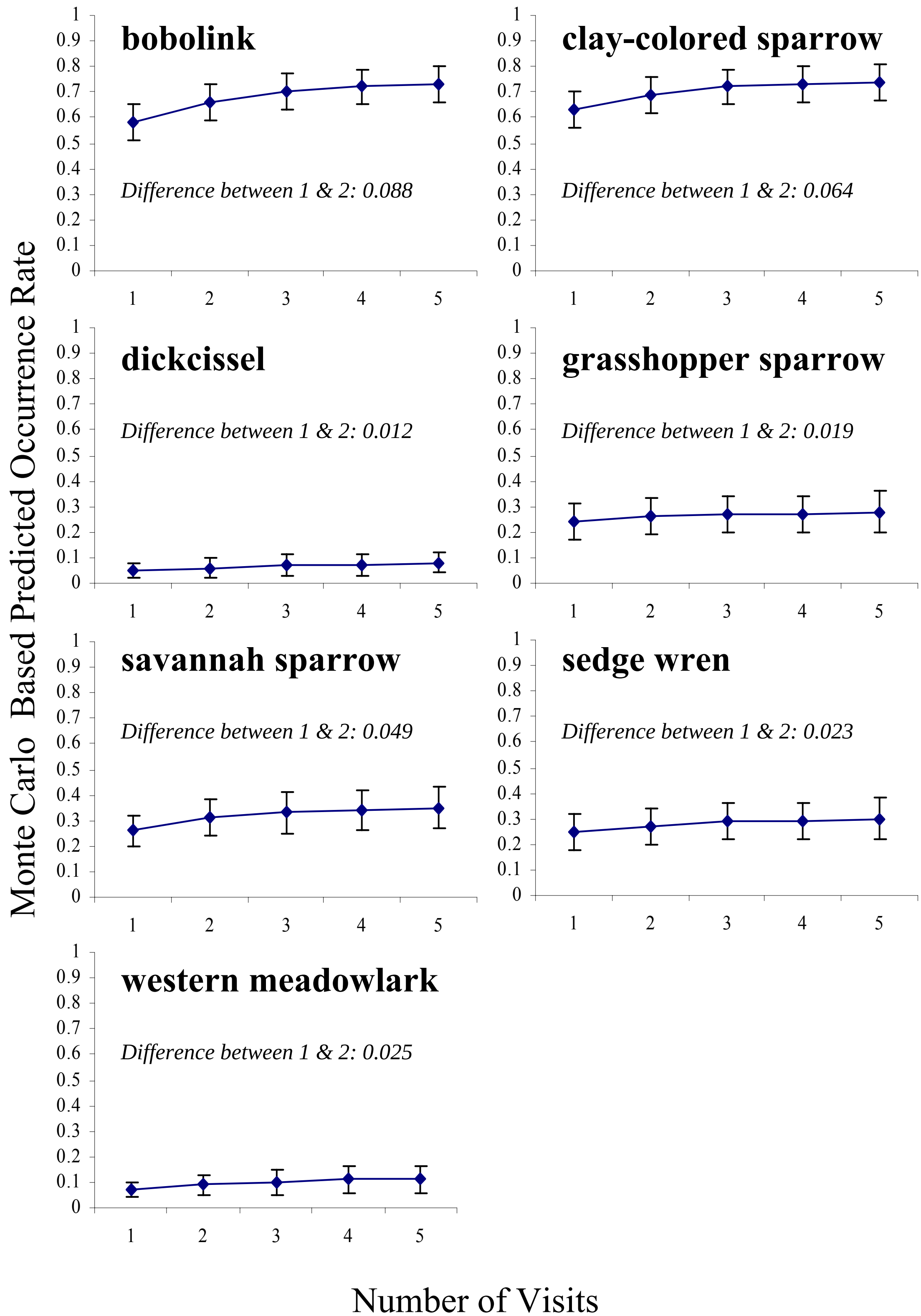

Figure 6. Monte Carlo based predicted occurrence rates determined by 1-5 visits.

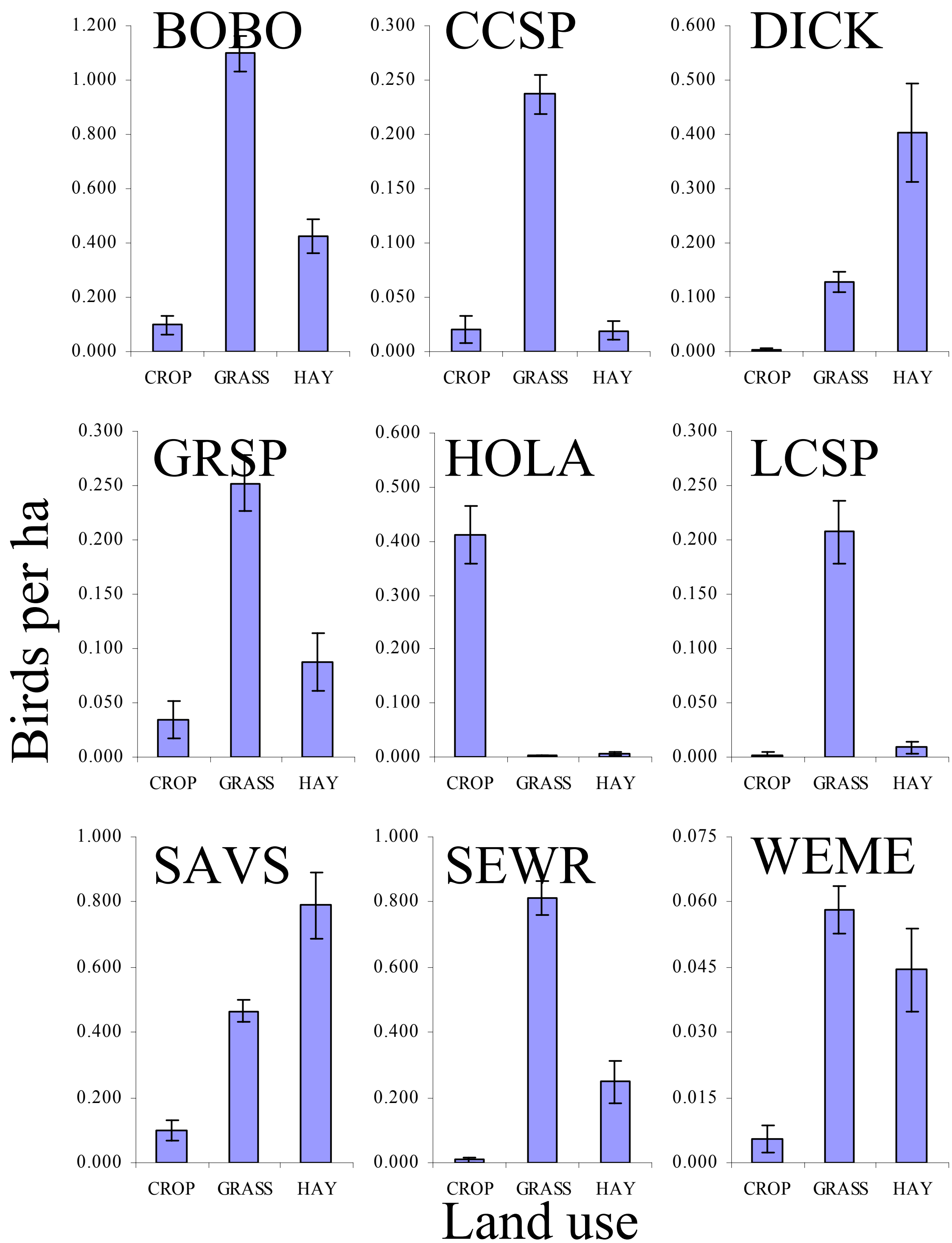

Figure 7. Average densities of grassland birds in croplands (n = 148), grasslands (n = 657), and haylands (n = 146) in the Prairie Pothole Region of MN and IA (2003-2005).

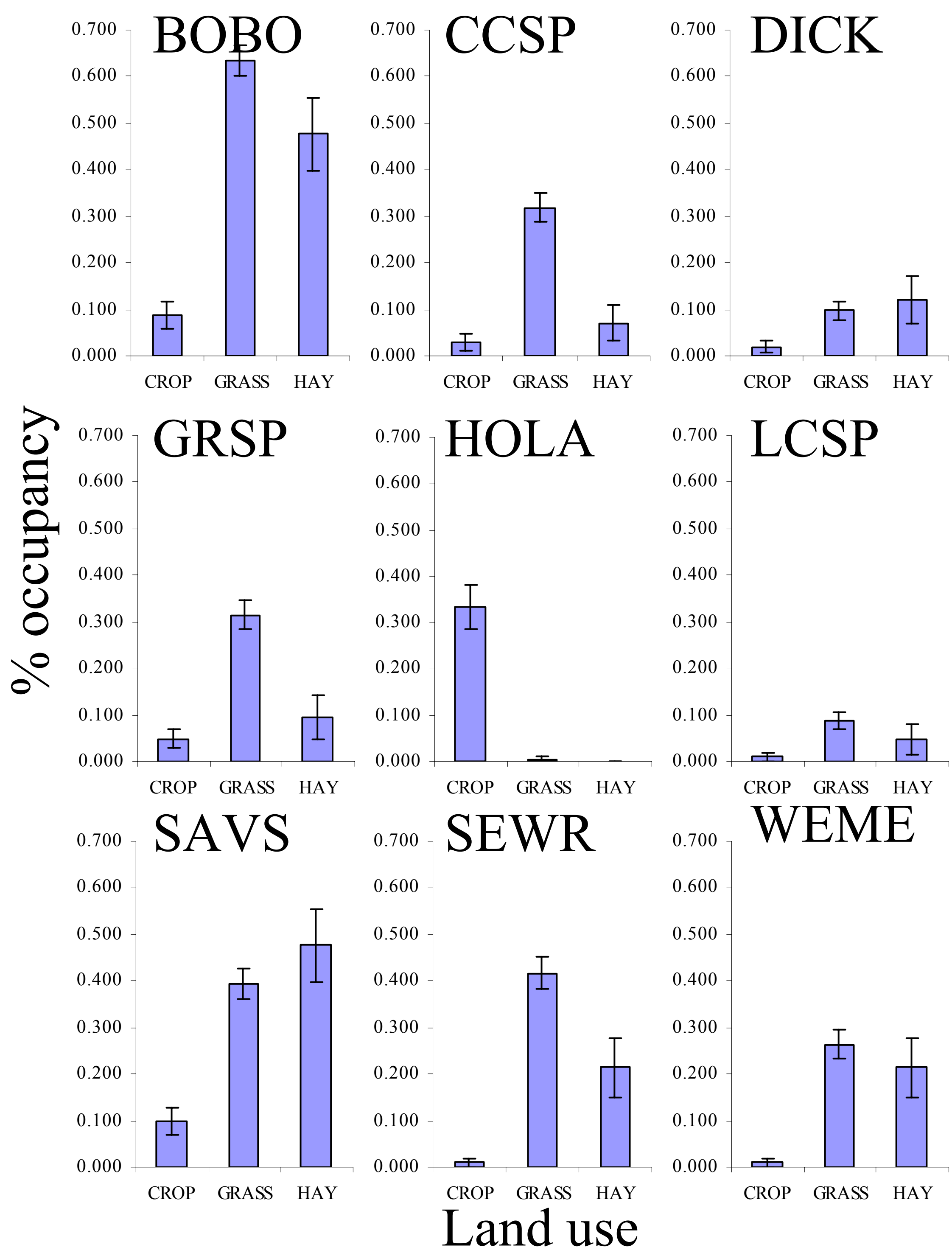

Figure 8. Average occupancy rates of grassland birds in croplands (n = 102), grasslands (n = 216), and haylands (n = 42) in the Prairie pothole Region of MN and IA (2003-2005). Only survey areas with >95% of one land use were used in calculations.

Table 2. Average vegetation structure, composition, landscape and BBS measurements.

Class		Variable	Average		SE	Min	Max
Cover Type		Cropcover	27.132	%	1.175	0.000	100.000
		Grasscover	52.180	%	1.266	0.000	100.000
		Haycover	11.507	%	0.898	0.000	100.000
		Treecover	5.693	%	0.369	0.000	90.000
		Wetcover	2.925	%	0.279	0.000	80.000
Structure	***in grasslands***	VOR	2.385	dm	0.060	0.000	13.350
		Leaf	43.641	cm	0.764	0.000	160.000
		Litter	36.830	mm	1.188	0.000	163.000
	in haylands	VOR	2.357	dm	0.147	0.000	9.300
		Leaf	36.444	cm	1.755	0.000	90.000
		Litter	13.789	mm	2.054	0.000	142.000
	in croplands	VOR	0.525	dm	0.113	0.000	7.450
		Leaf	10.136	cm	1.416	0.000	76.500
		Litter	2.176	mm	0.91	0.000	80.000
Composition	***in grasslands***	Grasses	81.106	%	1.022	0.000	100.000
		Shrubs	2.964	%	0.387	0.000	100.000
		Forbs	4.339	%	0.408	0.000	100.000
		ExoticGrass	69.767	%	0.160	0.000	100.000
		CoolNativeGrass	2.058	%	0.428	0.000	100.000
		WarmNativeGrass	9.281	%	0.884	0.000	100.000
		WetMeadow	6.272	%	0.675	0.000	100.000
		Weeds	2.359	%	0.387	0.000	100.000
	in haylands	Grasses	27.870	%	2.978	0.000	100.000
		Forbs (Alfalfa)	63.377	%	3.303	0.000	100.000
	in croplands	SmallGrain	7.432	%	2.163	0.000	100.000
		RowCrop	42.527	%	4.047	0.000	100.000
Landscape		Crop400	43.138	%	1.015	0.000	96.000
		Crop800	51.303	%	1.003	0.000	99.000
		Crop1600	57.535	%	0.914	0.000	99.000
		Crop3200	63.772	%	0.786	0.000	98.000
		Grass400	31.498	%	0.901	0.000	96.000
		Grass800	26.998	%	0.807	0.000	95.000
		Grass1600	21.688	%	0.656	0.000	77.000
		Grass3200	17.021	%	0.496	0.000	67.000
		Hay400	6.446	%	0.397	0.000	75.000
		Hay800	3.923	%	0.234	0.000	56.000
		Hay1600	2.402	%	0.137	0.000	31.000
		Hay3200	4.330	%	0.189	0.000	39.000
		Trees400	2.324	%	0.195	0.000	53.000
		Trees800	2.366	%	0.174	0.000	58.000
		Trees1600	2.463	%	0.155	0.000	40.000
		Trees3200	2.875	%	0.148	0.000	34.000
BBS		BOBO	14.899		0.478	2.201	63.592
		CCSP	6.893		0.223	0.000	24.962
		DICK	6.067		0.212	0.000	32.957
		GRSP	2.470		0.068	0.214	17.799
		HOLA	17.918		0.367	3.312	50.448
		LCSP	0.737		0.067	0.016	12.309
		SAVS	13.601		0.621	0.689	81.177
		SEWR	4.909		0.158	0.344	23.861
		WEME	9.593		0.311	3.420	48.283

and its area increased at larger scales, indicating that remaining grasslands are typically small and isolated (Table 2). I used percentage of area in grassland rather than cropland because these variables were highly correlated (r = 0.786 – 0.835) at each of four scales (Table 2). Hayland and woodland each comprised <7% of area at each scale evaluated (Table 2).

To account for bird movement away from the observers, I combined the first two 10-m distance intervals (i.e., 0-20 m, 30, 40…100 m) to estimate detectability using program DISTANCE. For each of nine species, half-normal or hazard-rate functions with no adjustments best fit the data, indicating that detectability either declined markedly from the center of fixed-radius point counts (half-normal) or remained high out to an inflection point and declined thereafter towards the perimeter of the point (hazard-rate) (Table 3; Appendix 2). Across species, probability of detection in grasslands varied from 0.690 to 0.967 (Table 3) and adjusted densities were 2.5 – 9.6 times larger than their standard errors (Table 3). Differences between raw and adjusted densities were usually greatest in grasslands (Table 3) where dense vegetation had the greatest chance of masking our ability to hear or see birds.

Density estimates and occupancy rates differed among species, but generally were similar within cover types for a particular species, indicating that habitats most frequented also contained the most individuals (Figures 7, 8). The two exceptions include dickcissel and LeConte's sparrow where occupancy rates were similar in grassland and hayland (Figures 7, 8), but density of dickcissel was 3-5 times greater in hayland than grassland, and density of LeConte's sparrow was 8-12 times higher in grassland than hayland (Table 3). Discrepancies may reflect differences in range

Table 3. Program DISTANCE models and detection probabilities.

Species	Land Use	Raw Density	Distance Density	Standard Error	Best Model	Detection Percentage
Bobolink						
	Crop	0.910	1.626	0.647	Half-normal	65.200
	Grass	0.795	3.106	0.371	Half-normal	84.900
	Hay	0.915	1.626	0.647	Half-normal	70.200
Clay-colored sparrow						
	Crop	0.637	0.800	0.316	Hazard-Rate	20.100
	Grass	0.613	1.123	0.126	Hazard-Rate	78.500
	Hay	0.318	0.318	0.322	Half-normal	100.000
Dickcissel						
	Crop			*na*		
	Grass	0.531	1.882	0.707	Half-normal	93.800
	Hay	1.234	4.292	1.105	Half-normal	66.100
Grasshopper sparrow						
	Crop	0.318	1.555	0.360	Half-normal	100.000
	Grass	0.582	1.727	0.278	Hazard-Rate	86.100
	Hay	0.398	1.248	0.715	Half-normal	87.800
Horned lark						
	Crop	0.525	1.375	0.232	Half-normal	85.800
	Grass			*na*		
	Hay			*na*		
LeConte's sparrow						
	Crop	0.477	0.478	0.508	Half-normal	90.200
	Grass	0.732	2.906	0.872	Hazard-Rate	90.800
	Hay			*na*		
Savannah sparrow						
	Crop	0.663	1.226	0.407	Half-normal	73.200
	Grass	0.645	1.781	0.177	Half-normal	69.000
	Hay	0.712	2.525	0.928	Half-normal	84.600
Sedge wren						
	Crop	0.955	0.965	1.120	Half-normal	75.200
	Grass	0.692	2.800	0.745	Hazard-Rate	96.700
	Hay			*na*		
Western meadowlark						
	Crop			*na*		
	Grass	0.402	0.402	0.082	Half-normal	94.400
	Hay	0.318	0.318	0.197	Half-normal	100.000

distributions where dickcissel is restricted to hayland in southwest Minnesota and Iowa where grassland habitat loss is greatest, whereas LeConte's sparrow occurred almost exclusively in grassland habitat, was the rarest of species surveyed, but was widespread and abundant (0.200 birds/ha) within its range in northwest Minnesota. Bobolink was the most common species surveyed with an average density of 1.1 birds/ha in grassland habitat (Table 3), followed by savannah sparrow in hayland and sedge wren in grassland with densities of 0.8 birds/ha (Table 3). Grasshopper sparrow and clay-colored sparrow occurred most often in grasslands at moderate average densities (0.200 - 0.250 birds/ha). Western meadowlark was the least abundant of species surveyed (Table 3) and occurred at low densities (0.030 - 0.060 birds/ha) in grassland and hayland habitats (Table 3). Horned lark was the only passerine surveyed that used cropland almost exclusively (Table 3).

Selection in univariate space yielded a diverse set of 5-10 uncorrelated ($r < |0.7|$) variables with corresponding parameter confidence intervals that did not overlap zero (Appendix 2). Variables retained for further consideration in LOGIT and NBREG models represented up to 4 of 5 possible categories of attributes for 8 of 9 species investigated (Appendix 2). In all but two instances, I retained landscape variables at 0.5- and 32-km^2 scales because they best explained either the presence or density of each species (Appendix 2). Combining categories of uncorrelated variables explained more variation than any single category of variables in each BIC "best" model for every species (Table 4). The autologistic BBS term improved model fit for 5 species with range distributions that only partially overlapped the study area (Table 4). Patterns in the presence / absence component of our datasets differed from those of non-zero count data.

Table 4a. Negative binominal regression (NBREG) and zero-inflated negative binomial (ZINB) models (BOBO, CCSP, DICK).

Model		Parameters	LL	K	AIC	BIC	ΔBIC
Bobolink							
ZINB	**land+local**	Grass400+Grasses-Treecover; (inflate) Leaf+Litter	-1059.984	8	2135.969	2174.837	0.000
ZINB	**local only**	(-)Treecover+Litter+Grasses; (inflate) Leaf+Litter	-1077.590	8	2171.181	2210.049	-35.212
NBREG	**land+local**	Grass400+Forbs+Grasses+Litter+Leaf-Treecover	-1086.994	8	2189.989	2228.857	-54.020
NBREG	**local only**	(-)Treecover+Leaf+Litter+Grasses	-1110.468	6	2232.936	2262.087	-87.250
NBREG	**land only**	Grass400	-1146.484	3	2298.967	2313.543	-138.706
ZINB	**land only**	Grass400-Trees400; (inflate) Grass400	-1137.591	6	2287.182	2316.333	-141.496
Clay-colored sparrow							
ZINB	**land+local**	Grass400+Grasses+Shrub; (inflate) BBS+Grass400	-389.798	8	693.141	732.010	0.000
ZINB	**land only**	BBS+Grass400; (inflate) BBS+Grass400-Hay400	-347.319	8	710.637	749.506	-17.496
NBREG	**land+local**	BBS+Grass400+Grasses+Shrub	-369.355	5	748.709	773.002	-40.992
NBREG	**land only**	BBS+Grass400	-382.476	3	770.951	785.527	-53.517
NBREG	**local only**	Litter+Grasses+Shrubs	-417.633	4	843.267	862.701	-130.691
ZINB	**local only**	Shrubs+Grasses; (inflate) Litter	-412.880	6	837.759	866.911	-134.901
Dickcissel							
ZINB	**land+local**	BBS+Leaf-Wetcover+Forbs; (inflate) BBS	-300.030	8	616.060	654.929	0.000
NBREG	**land+local**	BBS+Forbs+Leaf-Wetcover	-319.300	6	650.599	679.751	-24.822
ZINB	**land only**	Hay400; (inflate) BBS	-330.711	5	671.422	695.715	-40.786
NBREG	**land only**	BBS+Hay400	-339.026	4	686.051	705.486	-50.557
NBREG	**local only**	(-)Wetcover+Forbs	-360.354	4	728.709	748.143	-93.214

Table 4b. Negative binominal regression (NBREG) and zero-inflated negative binomial (ZINB) models (GRSP, HOLA, LCSP).

Model		Parameters	LL	K	AIC	BIC	ΔBIC
Grasshopper sparrow							
NBREG	**land+local**	Grass400-Trees400+Grasses-Treecover-Wetcover	-418.028	7	850.055	884.065	0.000
ZINB	**land+local**	(-)Trees400+Grasses-Treecover-Wetcover; (inflate) Grass400	-423.910	8	863.819	902.688	-18.622
NBREG	**local only**	(-)Treecover-Wetcover+Grasses	-442.048	5	894.095	918.388	-34.323
NBREG	**land only**	Grass400-Trees400	-449.320	4	906.641	926.075	-42.010
ZINB	**land only**	Grass400; (inflate) -Trees400	-453.827	5	917.654	941.947	-57.882
Horned lark							
NBREG	**local only**	(-)Leaf-Grasses-Forbs	-140.133	5	290.266	314.559	0.000
NBREG	**land+local**	(-)Grass400-Forbs-Grasses	-144.807	5	299.613	323.906	-9.347
ZINB	**land+local**	(-)Grass400-Forbs; (inflate) (-)Grasses-Leaf	-162.215	7	338.430	372.440	-57.881
NBREG	**land only**	(-)Grass400	-203.497	3	412.994	427.570	-113.011
LeConte's sparrow							
ZINB	**land only**	Grass3200; (inflate) BBS	-242.594	5	495.189	519.482	0.000
ZINB	**land+local**	Grass3200; (inflate) BBS	-242.594	5	495.189	519.482	0.000
NBREG	**land+local**	BBS+Grass3200+Leaf+Litter	-279.474	6	570.947	600.098	-80.616
NBREG	**land only**	BBS+Grass3200	-286.623	4	581.247	600.681	-81.199
NBREG	**local only**	Leaf+Litter	-335.773	4	679.547	698.981	-179.499

Table 4c. Negative binominal regression (NBREG) and zero-inflated negative binomial (ZINB) models (SAVS, SEWR, WEME).

Model		Parameters	LL	K	AIC	BIC	ΔBIC
Savannah sparrow							
NBREG	**land+local**	BBS+GRASS3200+Forbs-Treecover	-762.027	6	1536.055	1565.206	0.000
NBREG	**land only**	BBS+Grass3200+Hay3200	-795.046	5	1600.092	1624.385	-59.179
ZINB	**land+local**	Grass3200+Forbs-Treecover; (inflate) BBS	-799.675	7	1613.349	1647.359	-82.153
ZINB	**land only**	Grass3200+Hay3200; (inflate) BBS	-820.444	6	1652.888	1682.039	-116.833
NBREG	**local only**	(-)Treecover+Leaf+Forbs	-835.011	5	1680.022	1704.315	-139.109
Sedge wren							
ZINB	**land+local**	Grass400+Leaf; (inflate) Grass400+Leaf+Litter	-827.626	8	1671.253	1710.121	0.000
ZINB	**local only**	(-)Treecover+Leaf+Litter; (inflate) Wetcover+Leaf+Litter+Grasses+Shrub	-834.906	11	1691.811	1745.255	-35.134
NBREG	**land+local**	Grass400+Grasses+Leaf+Litter	-852.979	6	1717.959	1747.110	-36.989
NBREG	**local only**	(-)Treecover+Leaf+Litter+Grasses	-873.915	6	1759.830	1788.982	-78.861
ZINB	**land only**	Grass400; (inflate) Grass400	-911.544	6	1835.089	1864.240	-154.119
NBREG	**land only**	BBS+Grass400	-922.366	4	1852.732	1872.167	-162.046
Western Meadowlark							
LOGIT	**land+local**	BBS+Grass800+Hay800-Trees400+Grasses+VOR	-346.232	7	706.465	740.474	0.000
LOGIT	**land only**	BBS+Grass800+Hay800-Trees400	-363.328	5	736.657	760.950	-20.476
LOGIT	**local only**	(-)Treecover-VOR+Grasses	-375.808	4	759.616	779.050	-38.576

Flexibility in modeling approach that accounted for zero-inflation improved predicted capability for some species. For 5 of 8 species, BIC indicated that ZINB model forms best explained the response variable in the dataset, decreasing bias in parameter estimates and their associated confidence intervals. I interpret model output from ZINB rather than NBREG because improvements in fit were substantial for LeConte's sparrow (ΔBIC = -80.616), bobolink (-54.020), clay-colored sparrow (-40.992), sedge wren (-36.989) and dickcissel (-24.822). Despite improvements in model fit, no patterns emerge to explain the types of variables that typically explain variation in the inflation side versus the density side of the ZINB equation (Tables 4 and 5). The NBREG model forms accounted for overdispersion and best fit the information in survey data for savannah sparrow (ΔBIC = -82.153), horned lark (-57.881) and grasshopper sparrow (-18.622; Table 4). I fit a LOGIT model to predict probability of occurrence for western meadowlark because this was the only species for which a model predicting density would not converge (Table 4).

Local vegetative variables inside the area of the point count influence occurrence and density of grassland birds. The BIC "best" models for 8 of 9 species surveyed include one or more predictors related to either the structure or composition of vegetation within the point count. Density of 6 of 8 of those species was positively related to either litter depth, effective leaf height, visual obstruction, composition of local grasses or forbs or some combination thereof (Table 4). Only density of horned lark was negatively associated with local abundance of grasses and forbs, and clay-colored sparrow was the only species whose density was positively related to the local abundance of shrubs (Table 5). In addition, BIC "best" models for 4 species contained a predictor of cover type for

Table 5a. Parameters and coefficients in BIC best models (BOBO, CCSP, DICK).

Species	**Model**	**Parameter**	**Coef**	**Std Err**	**95% CI**	
Bobolink						
	ZINB *(Density)*					
		Grass400	0.0121838	0.0018898	0.0084798	0.0158877
		Grasses	0.0052944	0.0016376	0.0020849	0.0085040
		Treecover	-0.0415056	0.0070764	-0.0553750	-0.0276361
		constant	-0.6566236	0.1521990	-0.9549281	-0.3583191
	(Inflation)					
		Leaf	-0.1562955	0.0393818	-0.2334824	-0.0791085
		Litter	-0.0882785	0.0390674	-0.1648492	-0.0117077
		constant	3.0489120	0.5972976	1.8782300	4.2195940
Clay-colored sparrow						
	ZINB *(Density)*					
		Grass400	0.0100348	0.0031158	0.0039279	0.0161417
		Grasses	0.0117697	0.0029004	0.0060849	0.0174545
		Shrubs	0.0206090	0.0054737	0.0098808	0.0313372
		constant	-2.4461360	0.2771840	-2.9894070	-1.9028650
	(Inflation)					
		BBS	-1.5484690	0.5819326	-2.6890360	-0.4079020
		Grass400	-0.0473538	0.0160703	-0.0788510	-0.0158566
		constant	5.2780400	1.1723310	2.9803140	7.5757660
Dickcissel						
	ZINB *(Density)*					
		BBS	0.0724508	0.0156533	0.0417708	0.1031307
		Leaf	0.0231338	0.0058058	0.0117546	0.0345130
		Wetcover	-0.1012535	0.0510481	-0.2013060	-0.0012010
		Forbs	0.0138872	0.0034759	0.0070746	0.0206997
		constant	-3.3587500	0.3688450	-4.0816730	-2.6358270
	(Inflation)					
		BBS	-2.8736470	1.2855950	-5.3933660	-0.3539274
		VOR	-0.3539846	0.3458328	-1.0318050	0.3238352
		constant	9.9438140	4.1150900	1.8783860	18.0092400

Table 5b. Parameters and coefficients in BIC best models (GRSP, HOLA, LCSP).

Species	Model	Parameter	Coef	Std Err	95% CI	
Grasshopper sparrow						
	Negative Binomial Regression					
		Grass400	0.0254488	0.0030900	0.0193925	0.0315051
		Trees400	-0.0760790	0.0368122	-0.1482297	-0.0039284
		Treecover	-0.0352110	0.0139599	-0.0625718	-0.0078501
		Wetcover	-0.1024090	0.0310330	-0.1632326	-0.0415855
		constant	-2.3499900	0.1755521	-2.6940660	-2.0059140
Horned lark						
	Negative Binomial Regression					
		Grass400	-0.0261462	0.0095343	-0.0448331	-0.0074594
		Forbs	-0.0376666	0.0126688	-0.0624970	-0.0128362
		Grasses	-0.0531123	0.0108386	-0.0743555	-0.0318692
		constant	-0.8344796	0.1459703	-1.1205760	-0.5483831
LeConte's sparrow						
	ZINB *(Density)*					
		Grass3200	0.0244945	0.0077864	0.0092336	0.0397555
		constant	-1.0101900	0.2732811	-1.5458110	-0.4745685
	(Inflation)					
		BBS	-8.3627980	1.8006260	-11.8919600	-4.8336360
		constant	3.8929980	0.4583150	2.9947170	4.7912790

Table 5c. Parameters and coefficients in BIC best models (SAVS, SEWR, WEME).

Species	**Model**	**Parameter**	**Coef**	**Std Err**	**95% CI**	
Savannah sparrow						
	Negative binomial regression					
		BBS	0.0276540	0.0025833	0.0225909	0.0327172
		Grass3200	0.0123122	0.0035682	0.0053186	0.0193058
		Forbs	0.0097904	0.0017528	0.0063549	0.0132258
		Treecover	-0.0454415	0.0081904	-0.0614944	-0.0293886
		constant	-1.5555840	0.1081084	-1.7674730	-1.3436960
Sedge wren						
	ZINB *(Density)*					
		Grass400	0.0111234	0.0026279	0.0059728	0.0162739
		Leaf	0.0093888	0.0043472	0.0008685	0.0179090
		constant	-0.8105553	0.2869527	-1.3729720	-0.2481383
	(Inflation)					
		Grass400	-0.0152605	0.0069589	-0.0288996	-0.0016214
		Litter	-0.0402585	0.0136246	-0.0669622	-0.0135548
		Leaf	-0.0707897	0.0185560	-0.1071587	-0.0344206
		constant	3.5468990	0.5985730	2.3737170	4.7200800
Western meadowlark						
	Logistic Regression					
		BBS	0.0490069	0.0097962	0.0298068	0.0682071
		Grass800	0.0152000	0.0038517	0.0076508	0.0227492
		Hay800	0.0376258	0.0113430	0.0153939	0.0598576
		Trees400	-0.1075312	0.0355328	-0.1771741	-0.0378883
		Grasses	0.0122423	0.0028777	0.0066021	0.0178825
		VOR	-0.2602650	0.0733337	-0.4039965	-0.1165335
		constant	-3.6053850	0.3351922	-4.2623500	-2.9484210

which bird density was negatively related to amount of tree cover, wetland cover or both within the point count (Tables 4 and 5). Landscape variables at multiple scales influence occurrence and density of grassland birds. BIC "best" models for 7 of 9 species include ≥1 predictors related to amount of a particular habitat in the surrounding landscape. The most common landscape variable in BIC "best" models was amount of grassland surrounding survey locations. Densities were positively related to grassland abundance for bobolink, clay-colored sparrow, grasshopper sparrow, and sedge wren at the 0.5 km^2 scale and for LeConte's sparrow and savannah sparrow at 32 km^2 (Table 5). Probability of occurrence for western meadowlark also was positively related to both the amount of grassland and hayland in the landscape at the 8 km^2 scale (Table 5). Density of grasshopper sparrow was negatively related to amount of woodland at 0.5 km^2 and occurrence of western meadowlark was negatively associated with the same variable at the same scale (Table 5).

Local and landscape variables explained more variation than combinations of local or landscape factors alone in BIC "best" models for 7 of 9 species (Table 4). Improvements in fit were substantial for BIC "best" models containing local and landscape variables compared to the next best model containing only local or landscape factors for savannah sparrow (ΔBIC = -59.179), dickcissel (-40.786), bobolink (-35.212), sedge wren (-35.143), grasshopper sparrow (-34.323), western meadowlark (-20.476) and clay-colored sparrow (-17.496). Size of ΔBIC for these 7 species precludes interpretation of models that contain only local or only landscape variables. Still, despite improvements in model fit, no clear pattern emerged to explain the relative importance of local versus landscape factors across species. The next best models below the BIC "best" models contained only landscape variables for 4 species and only local variables for 3 species (Table 4). Only horned lark had a BIC "best" model that contained only local variables (Table 4). LeConte's sparrow was the one species whose density was related to only landscape variables (Tables 4 and 5).

The BIC "best" models containing both local and landscape variables accurately predict density for each of 7 species (k-fold validation $r^2 = 0.70 – 0.99$, Figures 9a-c). The model for western meadowlark accurately predicts occurrence of this species ($r^2 = 0.90$, Figure 9c). Slope of observed versus expected values did not differ from 1.0 for any of the 8 species evaluated and their intercepts did not differ from zero. I predicted that models containing only landscape variables would perform poorly because size of ΔBIC for most models containing only landscape variables was large (ΔBIC -59.179 to -17.496). But separate validations of BIC "best" models containing only landscape and BBS variables did accurately predict density for 8 of 9 species (k-fold validation $r^2 = 0.90 – 0.99$, Figures 9a-c). The only landscape model that performed poorly was that of clay-colored sparrow. I could not complete the k-fold validation because the model failed to converge on one of the folds of data. I exercise great caution in interpretation of the model for clay-colored sparrow that contains only landscape variables. I do not report validation of this model, and although I do present a map constructed from coefficients of this model, clay-colored sparrow is excluded from maps depicting species richness. Problems with the landscape model for clay-colored sparrow likely are related to our inability to map in GIS the prevalence of shrubs, a known variable of importance in the BIC "best" model that cannot be mapped at a landscape scale.

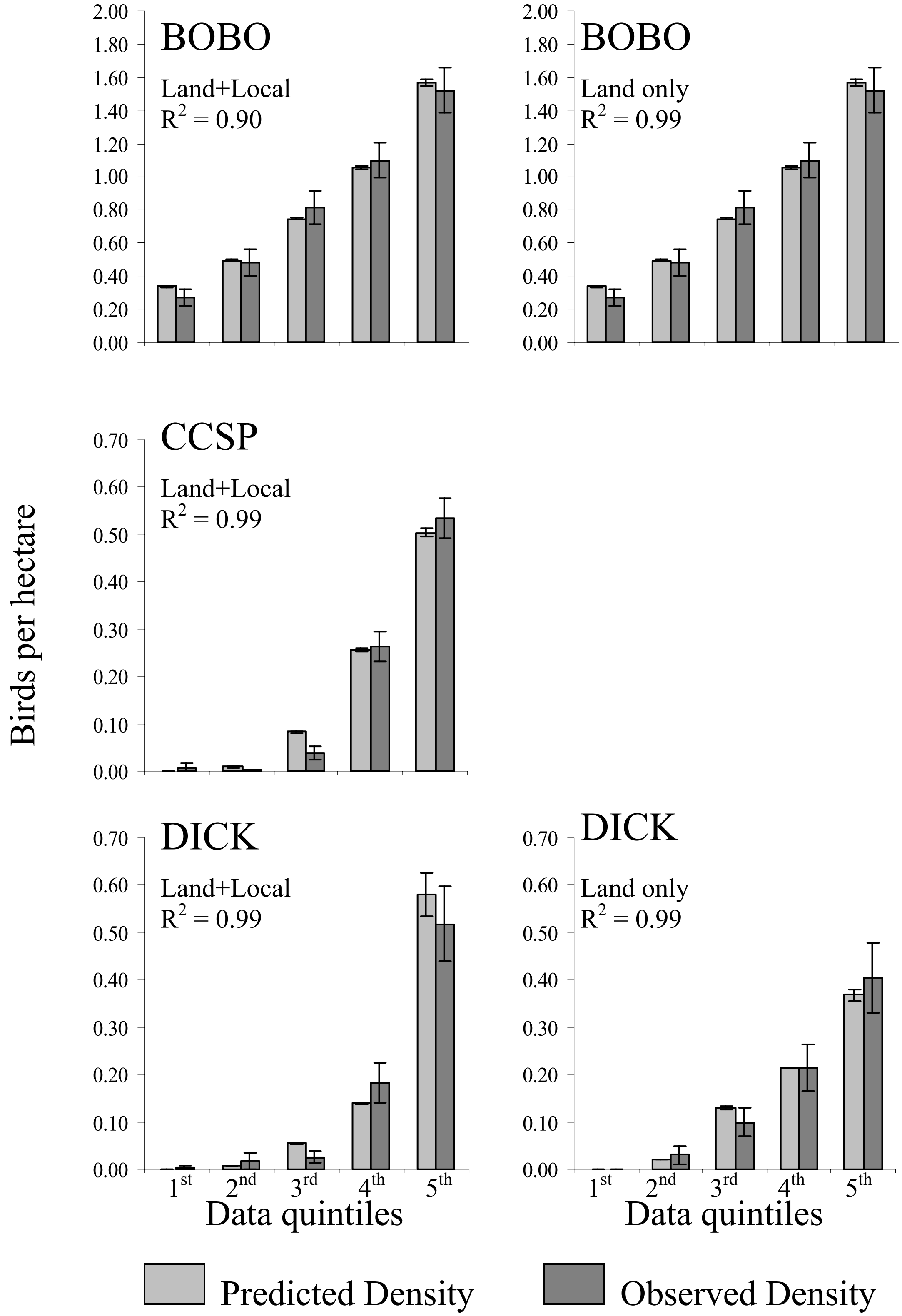

Figure 9a. Quintile histograms of k-fold validation (BOBO, CCSP, DICK).

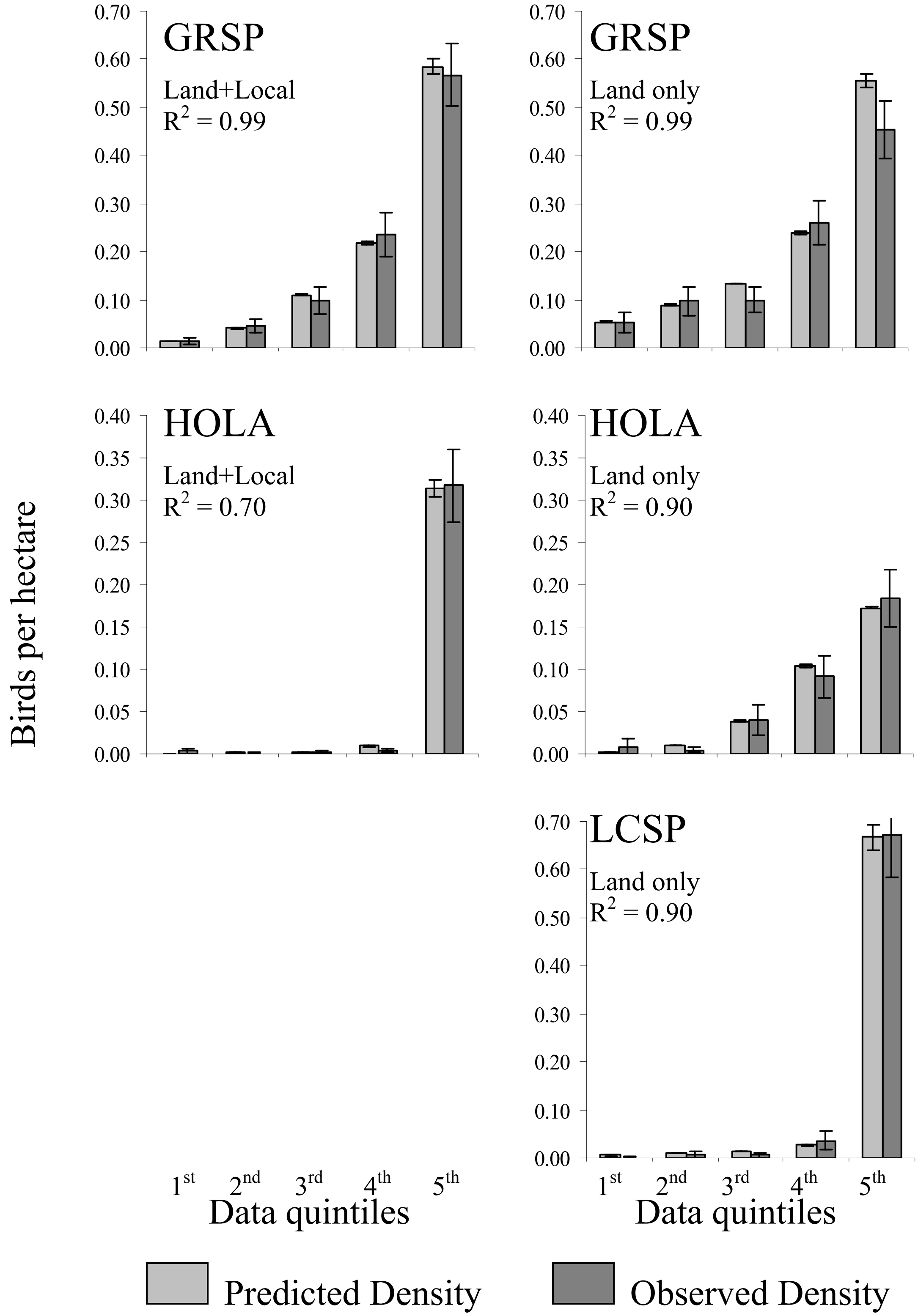

Figure 9b. Quintile histograms of k-fold validation (GRSP, HOLA, LCSP).

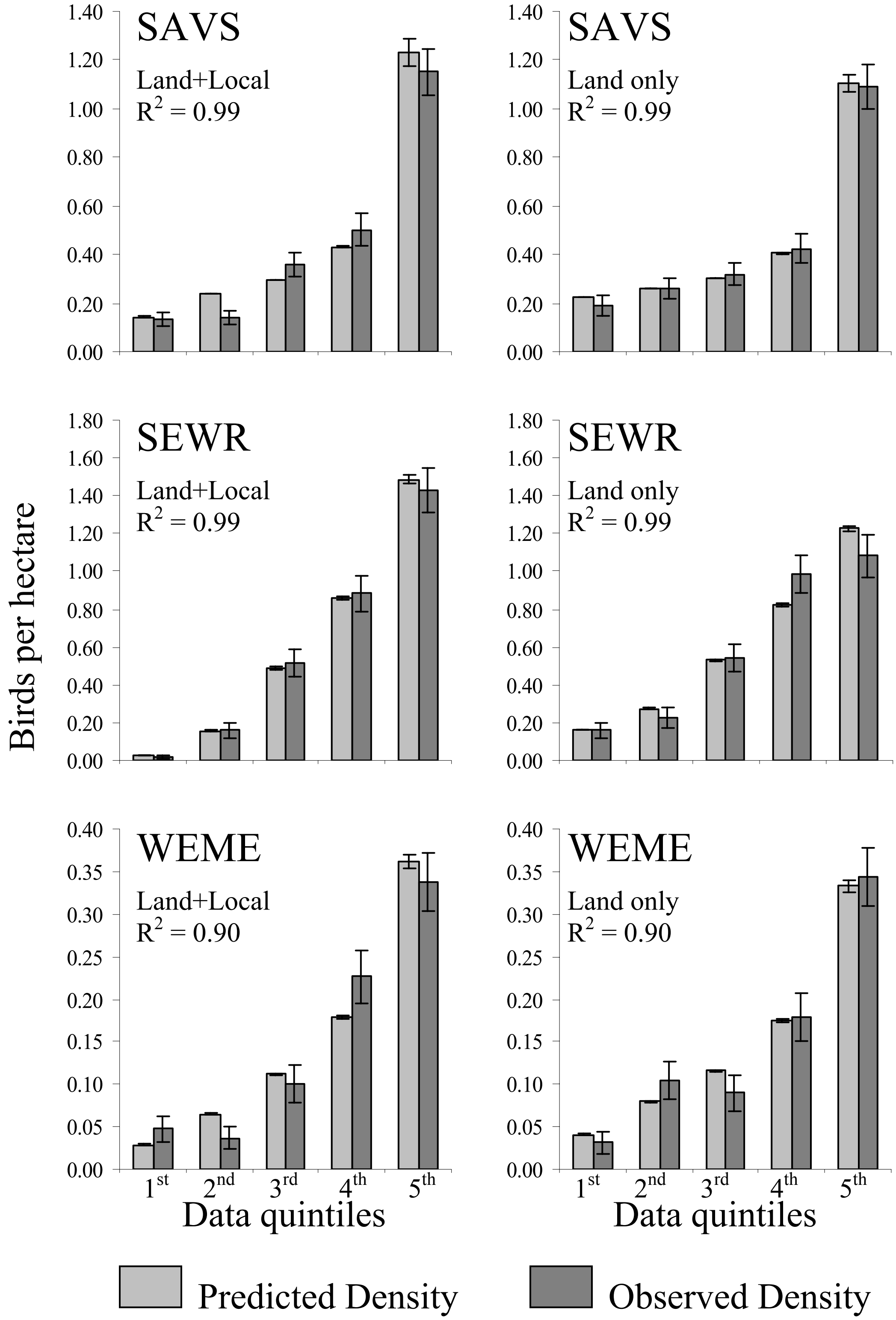

Figure 9c. Quintile histograms of k-fold validation (SAVS, SEWR, WEME).

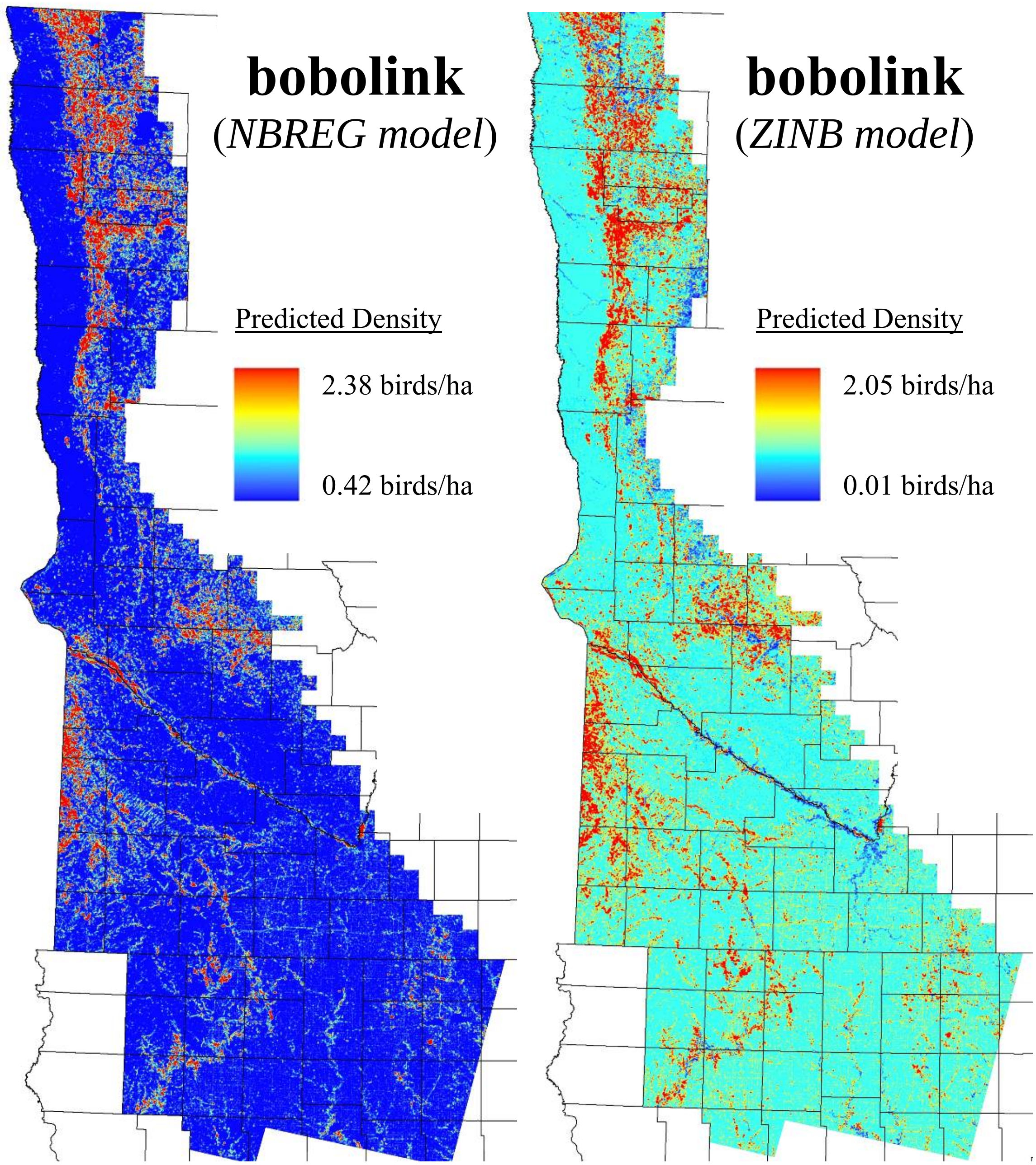

Figure 10a. Predicted densities of bobolink using both NBREG and ZINB models.

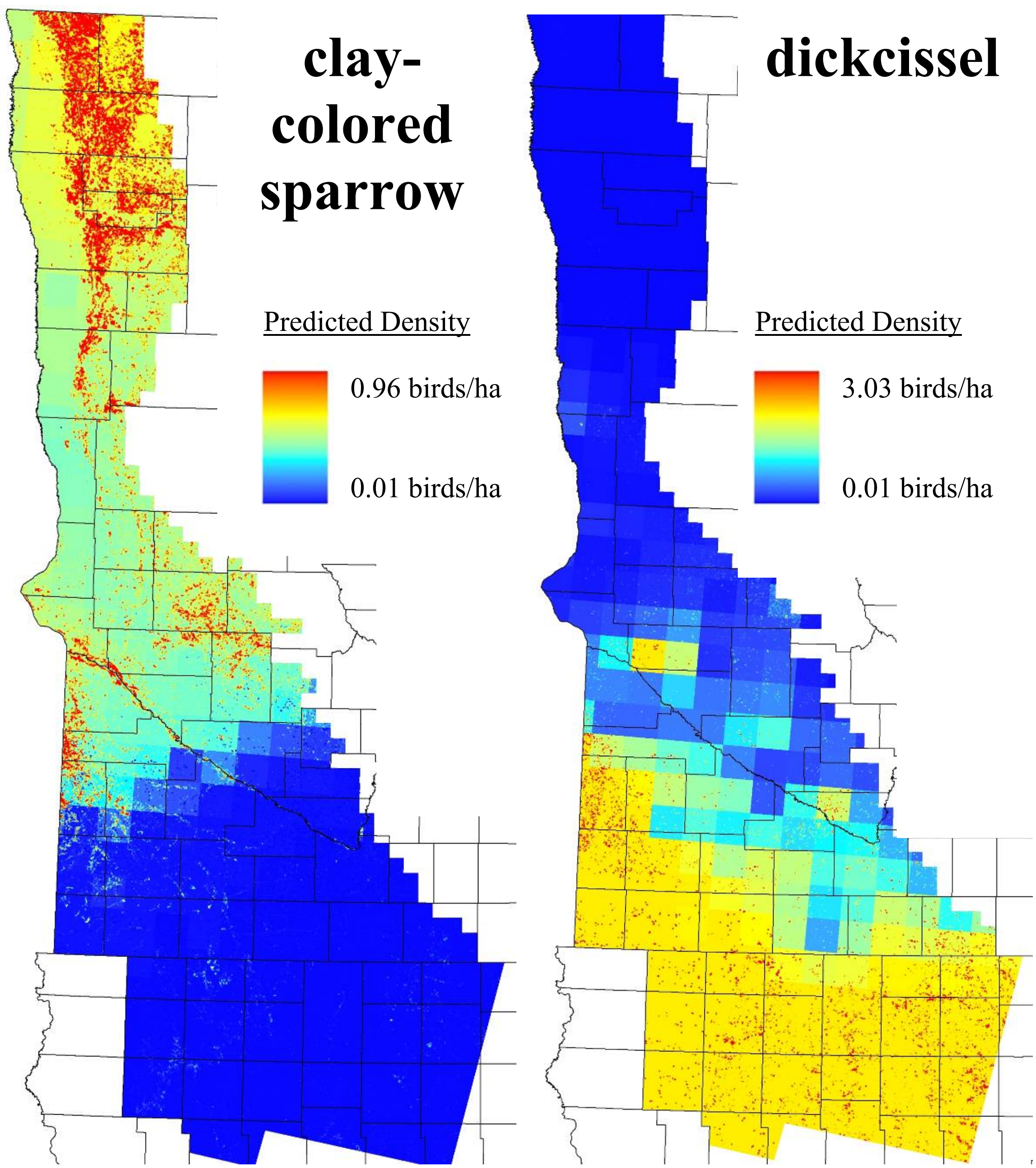

Figure 10b. Predicted densities of clay-colored sparrow and dickcissel.

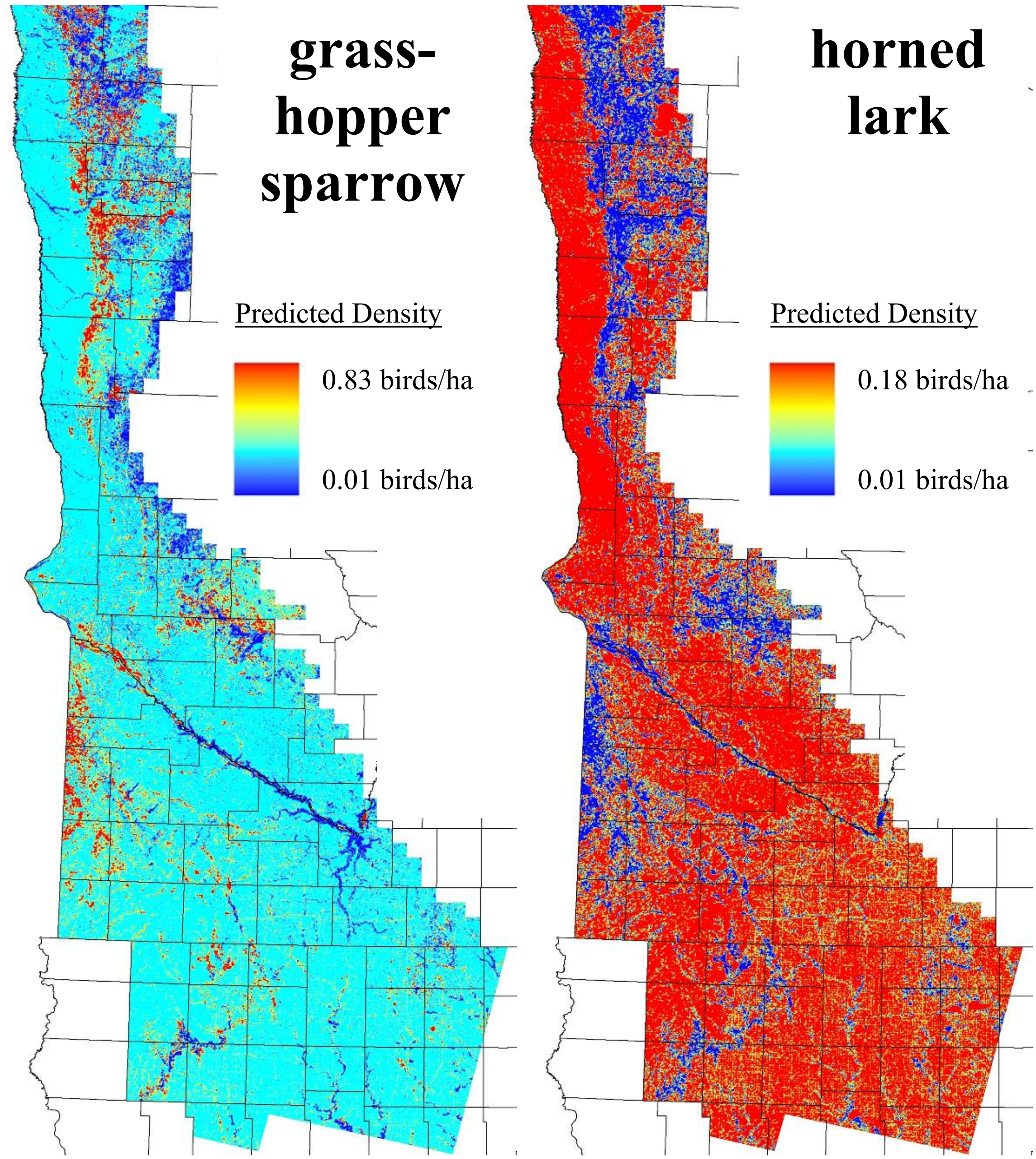

Figure 10c. Predicted densities of grasshopper sparrow and horned lark.

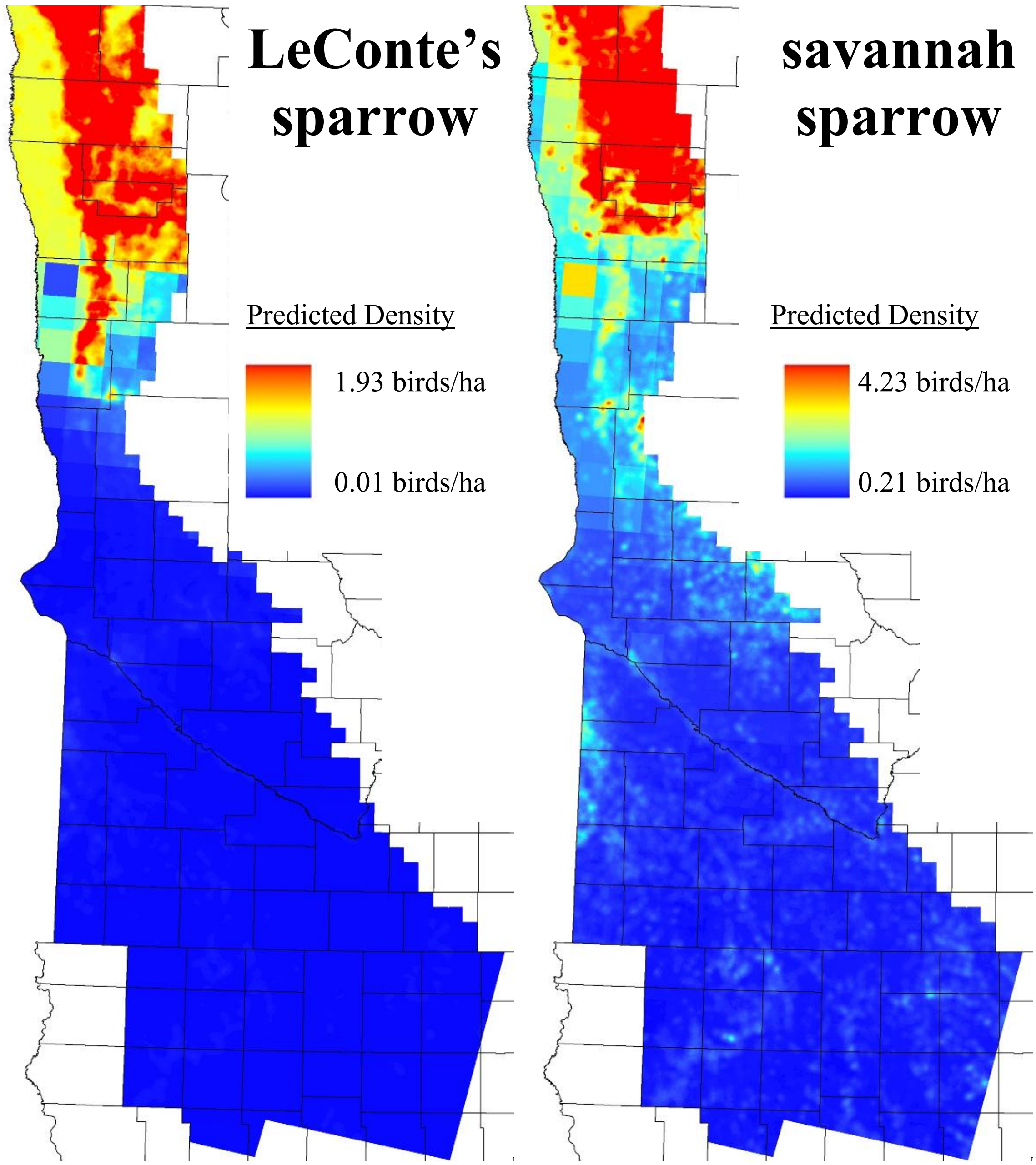

Figure 10d. Predicted densities of LeConte's sparrow and savannah sparrow.

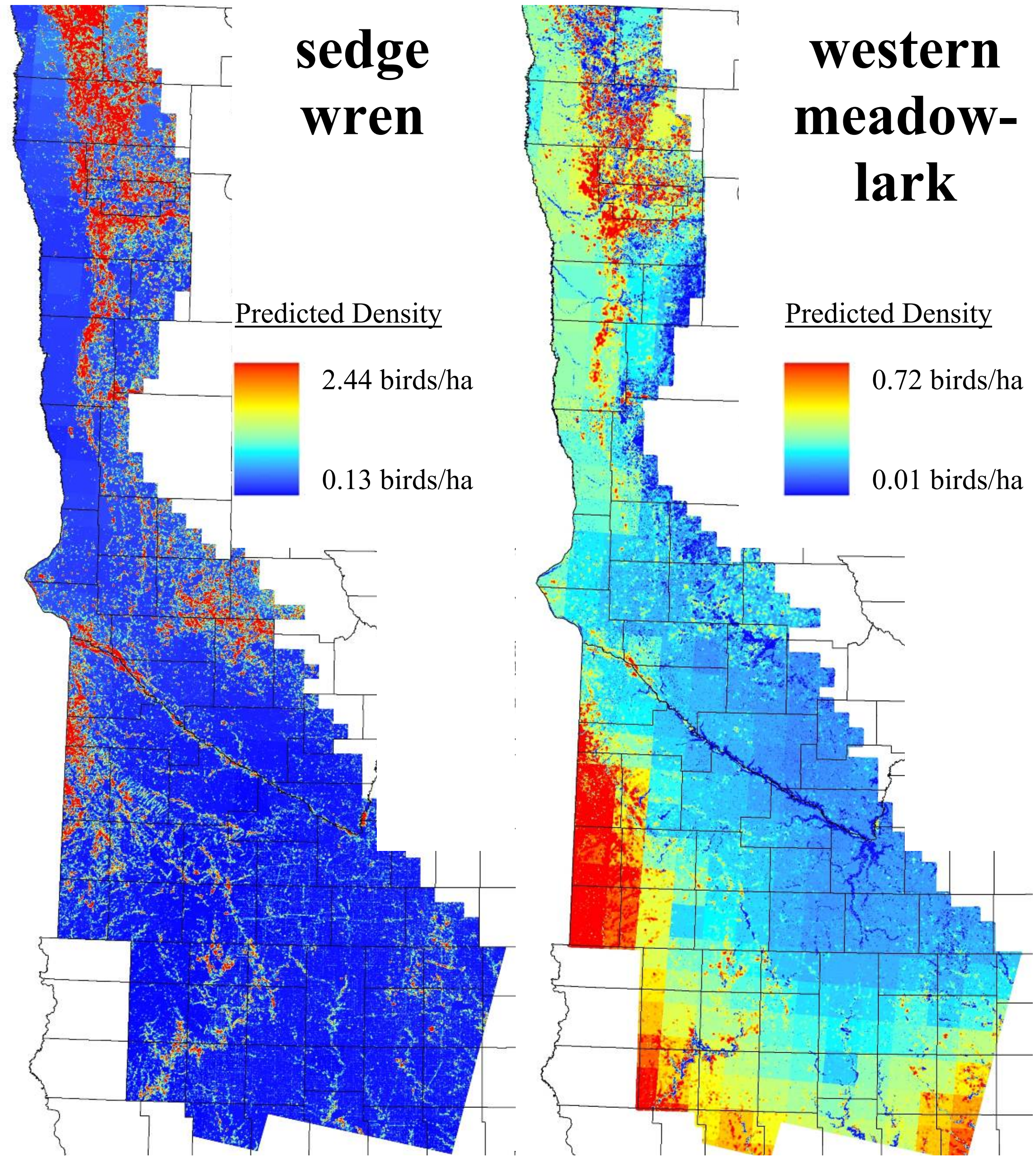

Figure 10e. Predicted densities of sedge wren and western meadowlark.

Discussion

Dependence on Grassland Habitats

Our study illustrates the fundamental dependence of grassland passerines on grassland habitats and the resulting impacts of agricultural tillage on songbird populations. Density estimates indicate that cropland provides little habitat for grassland-dependent species, a finding that matches that of every major synthesis in the published literature (e.g., Herkert et al. 2003, Samson et al. 2004, Brennan and Kuvlesky 2005). Hayland supports higher densities than cropland for several species (Table 4), but the small proportion of the landscape in hayland (<5%) does not compensate for extensive loss of grassland habitats. High forb abundance in hayland is likely the habitat component that attracts high densities of several species, and certainly this is the case for savannah sparrow and dickcissel with BIC "best" models that contain forb abundance as an important determinant. Unfortunately, hayland constitutes an attractive sink to nesting songbirds because timing of cutting alfalfa hay often coincides with nesting and brood rearing (Herkert 1997, McMaster et al. 2005). Delaying cutting until 15 July or later greatly minimizes nest loss and brood mortality, but timing usually is not dictated by wildlife managers because most hay is located on private lands.

A Multiscale Approach to Conservation.

My study shows that conservation actions that focus on both local and landscape scales have the greatest chance for success. Improvements in fit in multiscale models for 7 of 9 species investigated (ΔBIC = -59 to -17) lead to questions of interpretation of models that contain only either local or landscape variables. Still, despite improvements in model fit, I offer no general rules that work for all species because the best single-scale models contained only landscape variables for 4 species and only local variables for 3 species (Table 4). I do suggest that small-scale restorations will attract more birds if they are juxtaposed with existing habitats because half of the species that related to broad-scale factors were positively associated with the amount of grassland in the landscape at the smallest scale evaluated (0.5- km^2; Table 4). I also caution readers that bird productivity can be highly variable among regions and years (Winter et al. 2006), may vary with amount of grassland in the landscape, and that >1000 ha of habitat (~4 mi^2) may be necessary to decrease predation rates (Herkert et al. 2003). Conservation of the largest remaining grasslands is vital for species such as LeConte's sparrow, a species of high conservation concern, whose density is directly related to the amount of grassland in the landscape at the largest scale evaluated (32-km^2; Table 4). Conservation and restoration of large grassland parcels would also benefit large-bodied species, including prairie grouse (*Tympanuchus* spp; Niemuth 2003, Niemuth and Boyce 2004) raptors (e.g., northern harrier [*Circus cyaneus*]; Niemuth et al. 2005) ducks (Ball et al. 1995) and others that were not evaluated as part of this study.

<u>Improving Models with Zero Inflation and Autologistic Terms</u>.

Information criteria showed that I improved predictive models by accounting for zero inflation and spatial autocorrelation in datasets. New model forms such as ZINB that account for zero inflation and decrease bias in parameter estimates improved predictive capability for 5 of 9 in this study (ΔBIC = -80.616 to -24.822). Using BBS data as an autologistic term provided an innovative way to spatially model bird-habitat relationships for 5 species with range distributions that only partially overlapped the study region (Table 4; Figures 10b, d and e). I suggest that mixture models that account for zero inflation and autologistic terms that minimize correlations be considered for use in future studies to increase predictive performance and ecological inference.

Landscape Planning Tools Add Context to Conservation at Local Scales.

Validation indicates that our spatially explicit habitat models can be used reliably ($r^2 = 0.90 – 0.99$) to establish a regional strategy for grassland bird conservation. In the past, managers have been forced to apply findings from local studies to regional scales without knowing the validity of their extrapolations. With a better understanding of the multiple scales at which birds perceive their habitat, and an ability to spatially map those habitats, managers can now integrate across scales to deliver conservation locally in landscapes that will benefit the most birds. Land managers can use maps depicting locations of priority grasslands to identify which landscapes are capable of providing habitat for species of interest. Once priority landscapes are identified, then biologists can use vegetative variables identified in our models to meet local habitat requirements of individual species. In fragmented landscapes where restoration is the management goal, characteristics of existing priority landscapes can be used to reconstruct additional grassland landscapes that mimic those known to attract priority species.

Managing Habitat for a Diverse Assemblage of Species.

Our study shows that conserving and restoring large grasslands, removing trees from the landscape, or a combination of both will increase densities of 7 of 9 species evaluated. At local scales, managing fields within the landscape for a mosaic of vegetation that varies in its structure and composition will benefit the greatest diversity of songbirds. Individual fields that vary in structure and composition of grassland vegetation are likely to attract a diverse array of species. Land managers can vary any of 8 attributes identified as important in our models to enhance habitat for particular species of interest. For example, grasslands that contain a diversity of forbs and little or no tree cover would attract savannah sparrow in northwest Minnesota, and restoring large grasslands in otherwise depauperate landscapes would increase density of this species (Table 4, Figure 10d). Similar landscapes would also attract bobolink if one or more fields were idled to promote higher litter depth and leaf height (Table 4). Clay-colored sparrow will settle in the same landscapes as savannah sparrow and bobolink, and providing a shrub component in part of the mosaic would increase density of this species (Table 4).

Management Implications.

Species richness maps that identify landscapes with the capability of attracting the highest densities of the greatest number of songbirds can be used to prioritize conservation activities (Figure 11). I created two maps that include a species in richness estimates when its predicted density is in the upper 1/3 or upper 2/3 of the estimate, respectively (Figure 11). Both identified the same 5 landscapes as priorities for songbird conservation (Figure 12). I do not target these landscapes as the only places for conservation, but rather identify them as areas where conservation can have a large positive impact. The Inner Coteau and Coteau Moraine (A; Figure 12) and the Aspen Parklands (C) represent the largest remaining intact grasslands that provide habitat for the highest densities and greatest diversity of grassland songbirds in the study region. The Minnesota River Valley (B) is a smaller but important landscape that includes a nucleus of some of the most important remaining habitat for grassland birds (Figure 12). The Northern Minnesota River Prairie (D) is a dissected landscape that contains habitat that attracts high densities of grassland passerines. The best area in northwest Iowa for grassland birds is the NW Iowa Grasslands (E; Figure 12).

A region-wide approach is necessary to conserve the best remaining habitats on which these species depend because no single landscape will conserve the best remaining habitat for each species. A conservation approach that targeted only priority grasslands in the Aspen Parklands (C: Figure 12) would leave dickcissel vulnerable to habitat loss (Figure 10b). Conserving grasslands in only the Northern Minnesota River Prairie (D: Figure 12) would omit dickcissel, LeConte's sparrow, savannah sparrow (Figures 10b, d) and western meadowlark (Figure 10e) with its western distribution from consideration. Limiting conservation to habitats in Iowa would provide for dickcissel (Figure 10b), but would overlook habitat needs for clay-colored sparrow, LeConte's sparrow and savannah sparrow (Figures 10b, d).

Most of the habitat in the best landscapes remains unprotected from risk of conversion to other land uses (Figure 12). When species richness is mapped along with fee-title and easement lands owned by state, federal and private conservation agencies,

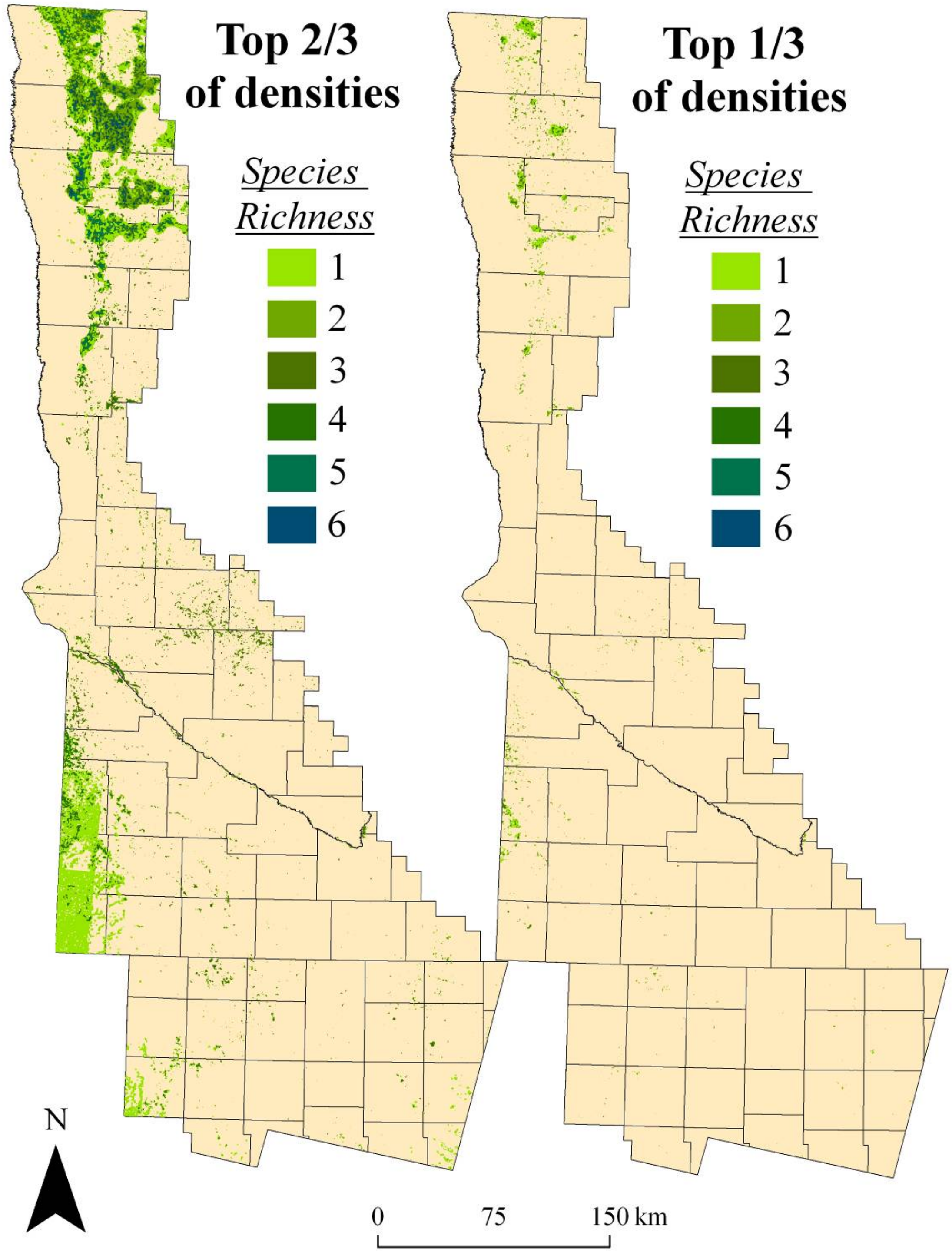

Figure 11. Species richness maps based on the top 1/3 and top 2/3 of predicted densities of bobolink, dickcissel, grasshopper sparrow, LeConte's sparrow, sedge wren, savannah sparrow, and western meadowlark.

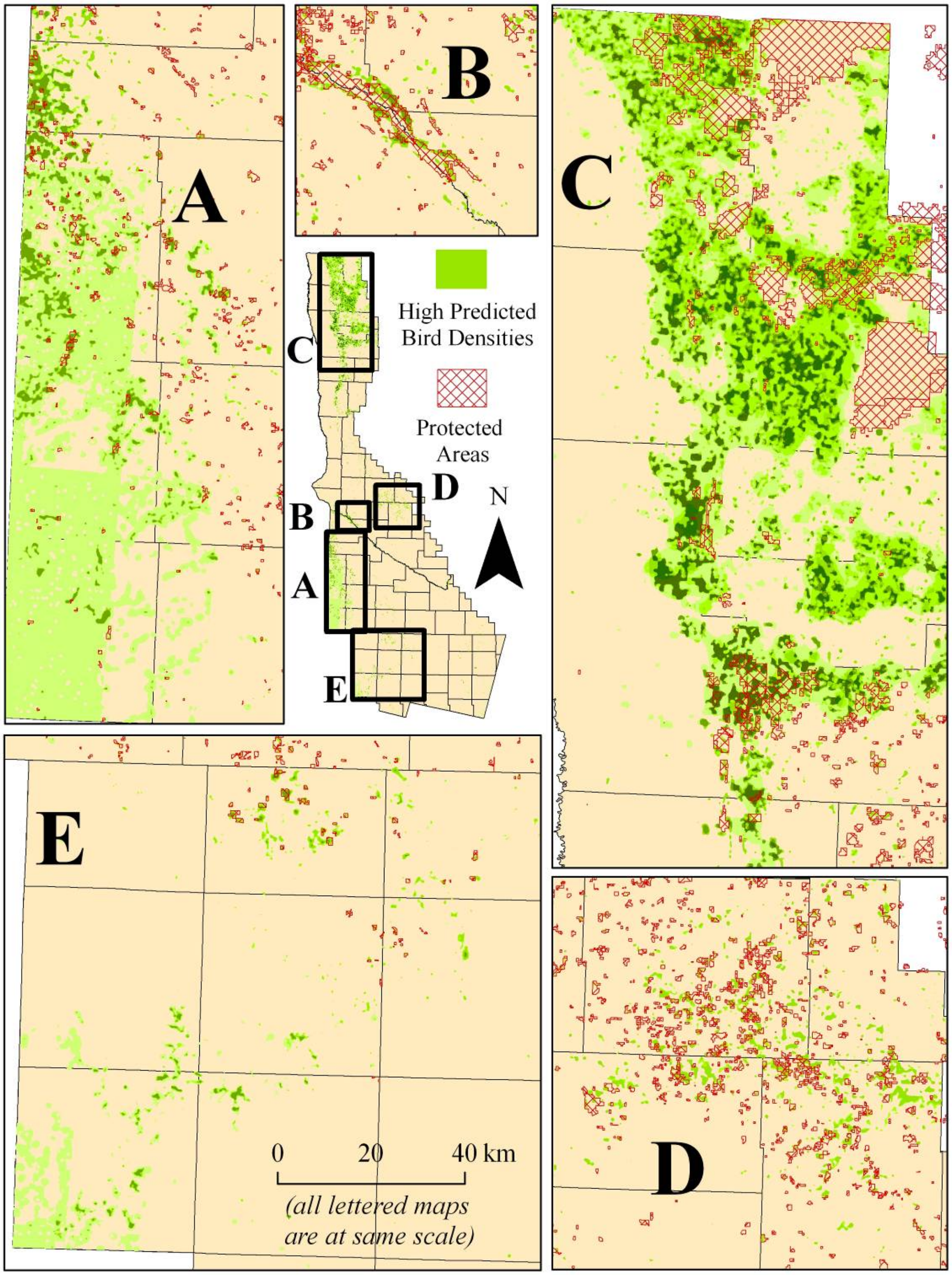

Figure 12. Areas of high predicted bird densities and protection by title or easement in A: Inner Coteau and Coteau Moraine, B: Minnesota River Valley, C: Aspen Parklands, D: Northern Minnesota River Prairie, and E: NW Iowa Grasslands.

the exception to this rule is the Minnesota River Valley (B) that contains Big Stone National Wildlife Refuge and Lac qui Parle State Wildlife Management Area. The Conservation Reserve Program (CRP) as established by the 1985 Food Security Act (Heard 2000) provides temporary habitat for grassland songbirds (Herkert 2007), but few grassland habitats have been protected in perpetuity in The Inner Coteau and Coteau Moraine (A) and NW Iowa Grasslands (E; Figure 12). In the Aspen Parklands (C), the state of Minnesota has acquired numerous large tracts of land for conservation, but few of these tracts overlap priority areas for grassland birds (Figure 12). The CRP has temporarily restored grassland in the Northern Minnesota River Prairie (D), but permanent protection misses most priority areas because efforts are aimed at wetland rather than grassland conservation (Figure 12). Protection of grasslands for songbirds has lagged behind that of wetlands for ducks because non-game birds lack a funding mechanism to pay for conservation for non-hunted species. The newly funded State Wildlife Grants initiative has the potential to at least partially fill this funding gap if some of the funds are spent on implementation rather than research and planning.

Our findings concur with those of Winter et al. (2006) in that conservation actions in treeless landscapes need to focus on composition of habitats at landscape scales and on structure and composition of vegetation at local scales. The concept of patch size, commonly referred to as the habitat area necessary for a bird to occupy a site and to breed successfully, may not be as important as previously proposed (e.g., Herkert 1994). Certainly, large grasslands will almost always be better than small ones because they provide habitat for a greater number of individuals and may serve as core areas for large-bodied species (e.g., prairie grouse). However, I express concern that a conservation strategy that focuses only on large grasslands may miss out on the benefits that clusters of small treeless grasslands provide to numerous species. When juxtaposed in a treeless landscape, several small grasslands may offer conservation values similar to that of a single large grassland for some species. Small grasslands are less expensive and easier to purchase, and therefore more likely to be restored and subsequently protected by local and state conservation organizations, especially in areas like northwest Iowa where habitat losses are greatest.

Conservation planning maps also have the potential to help guide management of new conservation opportunities that can affect large landscapes. Planning maps are ideal for optimizing the benefits of CRP by placing additional grasslands in priority landscapes to benefit the most birds. Once constructed, planning maps can also be used to better understand potential consequences of emerging issues that may be good or bad for birds, but are not yet fully understood. For example, production of switchgrass (*Panicum virgatum*) for biomass energy may be good or bad for birds depending on timing of harvest (Murray and Best 2003, Roth et al. 2005, Adler et al. 2006) and whether switchgrass fields replace cropland or if this technology simply brings even more land into agricultural production. Planning maps can be used to guide placement of switchgrass fields to landscapes where they could add to the habitat base rather than replace existing habitat. Perhaps the best use of regional maps is in planning to minimize the negative effects of unanticipated or new stressors to habitats and their populations. For example, wind power is gaining in popularity as a “green” source of energy, but location of production facilities is critical because poor placement of wind turbines and transmission lines results in either increased mortality (de Lucas et al. 2007), or avoidance of suitable habitats (Leddy et al. 1999). Past habitat loss when coupled with new stressors on populations likely make the future conservation of grassland birds an even a greater challenge. But our conservation planning tools can help land managers to maximize benefits and minimize risks to benefit declining grassland bird populations.

Future Direction.

Bird surveys have been completed, datasets were assembled and analyses are underway to construct habitat models and resulting planning maps for the entire Prairie Pothole Region of eastern North Dakota and South Dakota and northeast Montana. Once models are complete, the vision of a planning tool for grassland songbirds that rivals that for ducks under the North American Waterfowl Management Plan will be made available for implementation. Empirical models and spatially-explicit predictions that I have constructed make future analyses possible that will provide additional inference into both the ecology and management and the policy implications that influence conservation of grassland birds. Now that models have been incorporated into the GIS, priority landscapes for grassland songbirds will be digitally overlaid with those of ducks (Reynolds et al. 2006) to identify where the greatest overlap exists, enabling conservation planners to combine resources in these areas to deliver habitat conservation to areas with the greatest multiple benefits. Next, priority landscapes for grassland songbirds will be digitally overlaid with federal easement and fee-title lands to quantify the extent to which efforts to protect habitats for waterfowl have benefited other non-target species. Using GIS, I will simulate changes in distribution and abundance of grassland habitat to evaluate farm programs (e.g., CRP) and formulate recommendations for future conservation programs (Reynolds et al. 2001, Niemuth et al. 2007). I concur with Winter et al. (2006) in the need for replication of large-scale studies of factors influencing productivity of grassland birds, and suggest that spatially-explicit tools resulting from this study provide a rare opportunity to draw a valid sample of study sites that are stratified by region, cover type and bird density.

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CHAPTER III

AN ASSESSMENT OF THE IMPACTS

OF TREEBELTS

ON NATIVE GRASSLAND BIRDS

Abstract

Grassland habitat loss contributes to declines in grassland bird populations in North America. Anthropogenic edges may further exacerbate effects of habitat loss if edges cause birds to avoid otherwise suitable habitats. Treebelts are striking landscape features characteristic of the northern Great Plains that create abrupt edges in grassland habitats. I compared abundance of grassland birds at increasing distances (1 - 240 m) from treebelts (n = 32) and in treeless grasslands (n = 16) to assess their response to edge. I then experimentally removed treebelts on 15 of 32 sites to evaluate changes in bird abundance at removal sites. I asked whether grassland birds will avoid woody edges, and whether birds will use otherwise suitable habitats after edges were removed. My study is the first to experimentally show that native passerines avoid woody edges in otherwise suitable grassland habitats. Avoidance of trees by the four most common grassland songbirds was apparent as far away from woody edges as surveys were conducted (240 m). The spring following tree removal, bobolink, savannah sparrow, sedge wren and dickcissel distributed themselves ubiquitously in grasslands where trees had been experimentally removed. Although birds re-colonized grasslands following tree removal, their abundance generally remained below that observed in treeless grasslands, indicating that effects of woody edges may extend out beyond our transects such that trees within 240 – 800 m may need to be removed before grasslands attract the abundance of birds observed in treeless grasslands. The abundances of only brown-headed cowbird and clay-colored sparrow were unrelated to the presence or removal of woody edges. I recommend that land managers remove treebelts from grasslands where conservation of native grassland songbirds is the management goal. If managers wish to promote habitat for native grassland birds on privately-owned lands, then discouraging treebelts under the Conservation Reserve Program is advised.

Introduction

Historically the northern Great Plains was a grassland-dominated system where fire and grazing restricted natural tree growth to riparian floodplains, wooded draws, islands within lakes and small patches along leeward wetland edges (Higgins 1986). These patches and corridors of trees and shrubs were the dominant woodland features in the prairie landscape (Rumble et al. 1998). Today, numerous patches of native woodlands still occur in North and South Dakota; however, the once large expanses of nearly treeless prairies are now intermixed with cropland and dotted with small (<2 ha) planted treebelts (synonymous with tree plantings, shelterbelts, or windbreaks; herein "treebelts") that cover ~3% of the land area (Baer 1989).

Grassland bird populations are declining faster and more consistently than any other group of North American birds (Samson and Knopf 1994, Herkert 1995). Primarily implicated in this decline is loss of native grasslands to tillage agriculture (Herkert 1994, Bakker et al. 2002, Herkert et al. 2003). Anthropogenic features can further exacerbate effects of habitat loss if edges cause birds to avoid otherwise suitable habitats (Bevanger 1998, Forman and Alexander 1998). Planting trees in prairie landscapes has been regarded by many as a universally positive land management practice for wildlife in the absence of experimental tests of grassland bird avoidance of trees (Drew 1994). A growing body of literature indicates that trees in prairie landscapes often are associated with negative consequences to numerous avian taxa (Bakker 2003) including ducks (Rumble and Flake 1983, Gazda et al. 2002), wetland birds other than ducks (Naugle et al. 1999), prairie grouse (Hanowski et al. 2000, Niemuth 2000), grassland passerines

(Johnson and Temple 1990, Winter et al. 2000, Bakker et al. 2002, Grant et al. 2004, Cunningham and Johnson 2006, Veech 2006) and ring-necked pheasants (*Phasianus colchicus*; Snyder 1984, Schmitz and Clark 1999; but see Leif 2005).

The objective of this study is to compare abundance of grassland birds at increasing distances (1 – 240 m) from treebelts and in treeless grasslands to assess bird response to edge. Using a before-after control-impact research design, I then experimentally removed treebelts on 15 of 32 sites to evaluate changes in bird abundance at removal sites. I asked whether grassland birds will avoid woody edges, and whether birds will use otherwise suitable habitats after edges are removed.

Study Area and Methods

Study Area

I conducted this study in 14 counties in eastern North and South Dakota (Figure 1) from 2004 to 2006 on public lands owned and managed by the U.S. Fish and Wildlife Service. Dominant grasses on study sites were switchgrass (*Panicum virgatum*), big bluestem (*Andropogon gerardii*) and other native grass species as well as mixtures of exotic grasses such as smooth brome (*Bromus inermis*) and Kentucky bluegrass (*Poa pratensis*). Treebelts included a variety of predominantly deciduous trees including American elm (*Ulmus americana*), green ash (*Fraxinus pennsylvanica*), plains cottonwood (*Populus deltoids*) and Russian olive (*Elaeagnus angustifolia*). Most trees were planted around the perimeter of farmsteads before lands were purchased by the

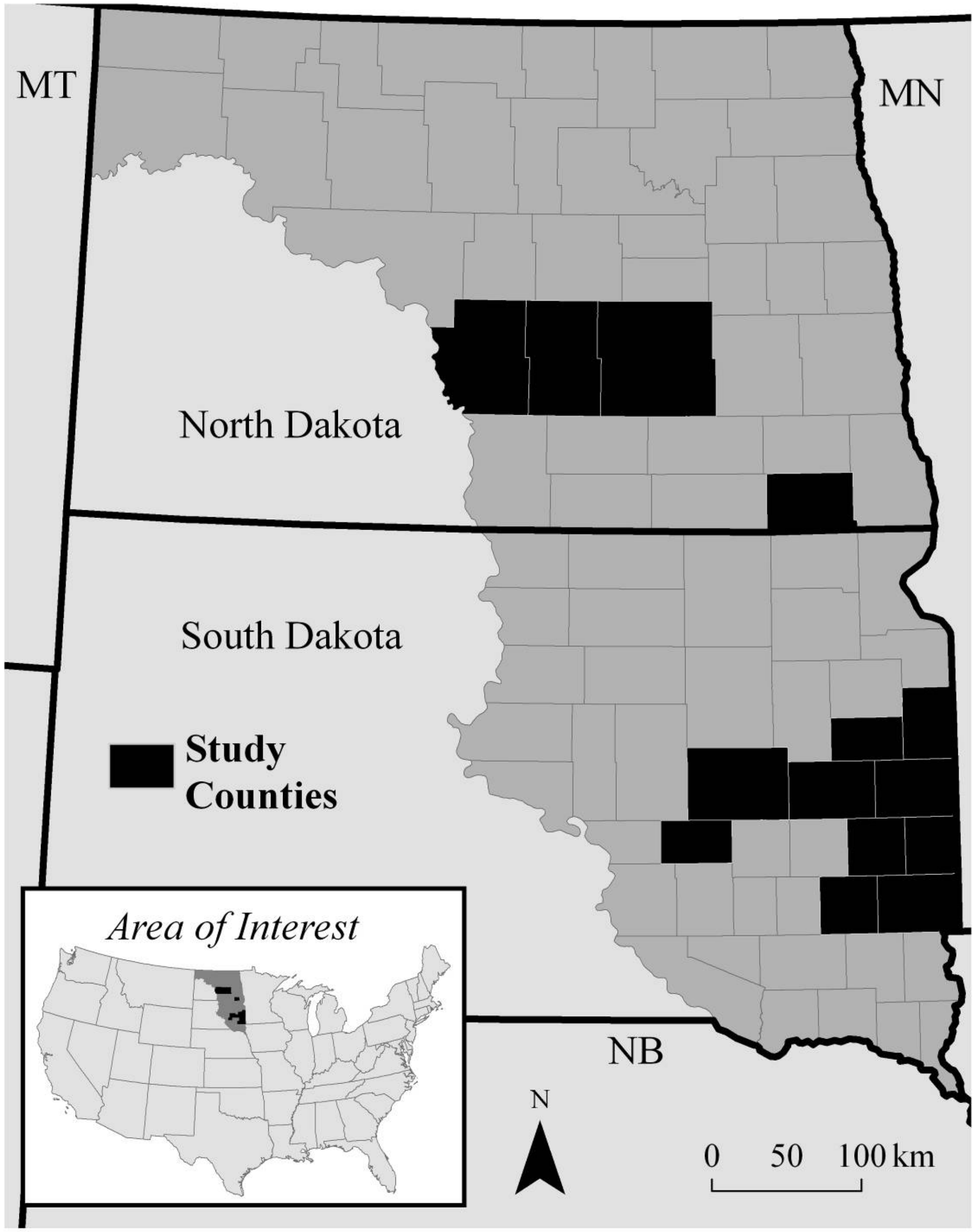

Figure 1. Fourteen study counties (black) in the Prairie Pothole Region (gray) of North and South Dakota.

USFWS. Buildings were removed after purchase, but treebelts were often left standing.

Survey Design

I surveyed grassland birds at 32 sites with treebelts, and at 16 treeless grasslands that served as control sites and were located >800m from any trees. These were chosen from available public land within the study counties. I removed trees on 15 of 32 sites after the first year of survey. In 2004-05, I surveyed 12 sites (4 tree control, 4 tree treatment and 4 treeless grassland control sites). In 2005-06, I included additional replicates and surveyed birds at 13 tree control, 11 tree treatment and 12 grassland control sites.

Vegetation Sampling

Idled grasslands were not grazed, mowed or burned during the duration of the study. I surveyed grasslands with similar composition and structure of vegetation to minimize effects on diversity and abundance of avian species (Millenbah et al. 1996). I estimated structural components of grassland habitats including visual obstruction readings (Robel et al. 1970, Higgins and Barker 1982), effective leaf height, and litter depth. Measurements were taken at 10-m intervals along fixed-width belt transects during the middle of breeding season. I assessed visual obstruction by obtaining a reading in a random direction 4 m from the pole at a height of 1 m horizontal to the Robel pole (Robel et al. 1970, Higgins and Barker 1982). I estimated effective leaf height at the average height of the tallest grass leaves within 4 m of the pole. I measured litter depth to the nearest millimeter with a ruler inserted into the detritus until it made contact with the soil. I pooled observations within a grassland site to avoid pseudoreplication (Hurlbert 1984).

Bird Surveys

I used fixed-width belt transects to survey birds from sunrise to 1000 hrs CST from 18 May through 10 July 2004 - 2006. I surveyed each of 5, 100-m long, 40-m fixed width transects (Wakeley 1987) paralleling each treebelt. Transects were placed at 50-m intervals from the edge of the treebelt (Figure 2) and >240 m from any other treebelts. One 100-m transect in each control site without trees was placed in a grassland >800 m from any treebelt. I counted all birds seen or heard within 20 m on either side of each transect, and noted bird movements to avoid double counting. I walked transects slowly (approximately 1km/hr; Mikol 1980, Wakeley 1987), stopping frequently to identify birds. I surveyed transects within each site in a different, random order upon each visit. Surveys were conducted only on mornings when weather conditions did not impede detection of birds (no rain, fog, or wind >20 km/h; Ralph et al. 1995). Five surveys of each transect were averaged into one bird density to avoid pseudoreplication (Hurlbert 1984). Only detections of males were used in analyses.

Tree Removal

I conducted bird surveys for one year before tree removal, and then removed all trees from 15 sites with chainsaws, tractors, and a skid-loader fitted with a tree shear attachment. Trees were either removed off-site, or burned and buried on-site before the

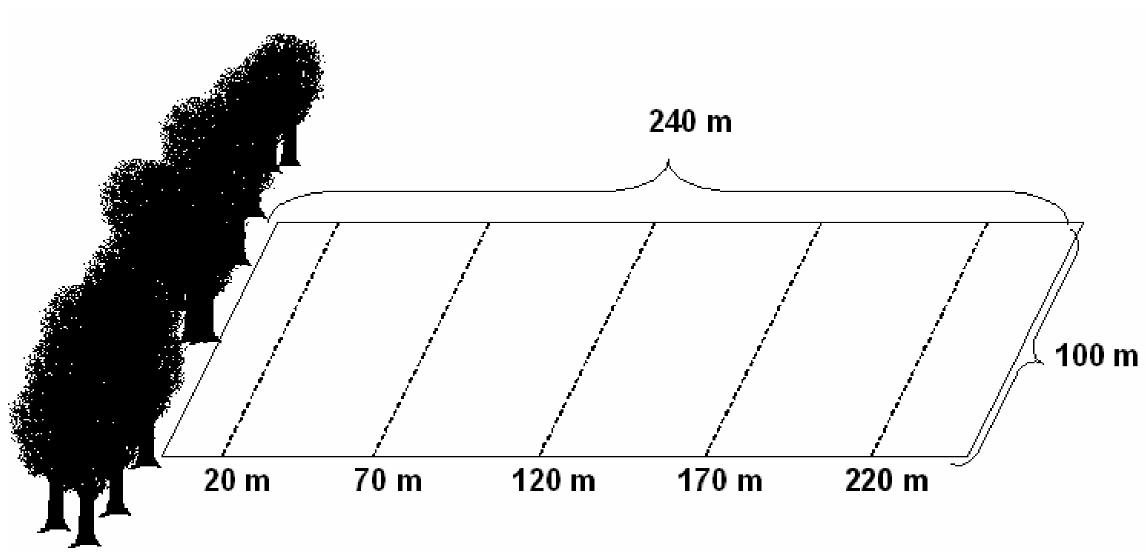

Figure 2. Layout of study design for transects along treebelts. Area surveyed is 2.40 ha (5.93 acres).

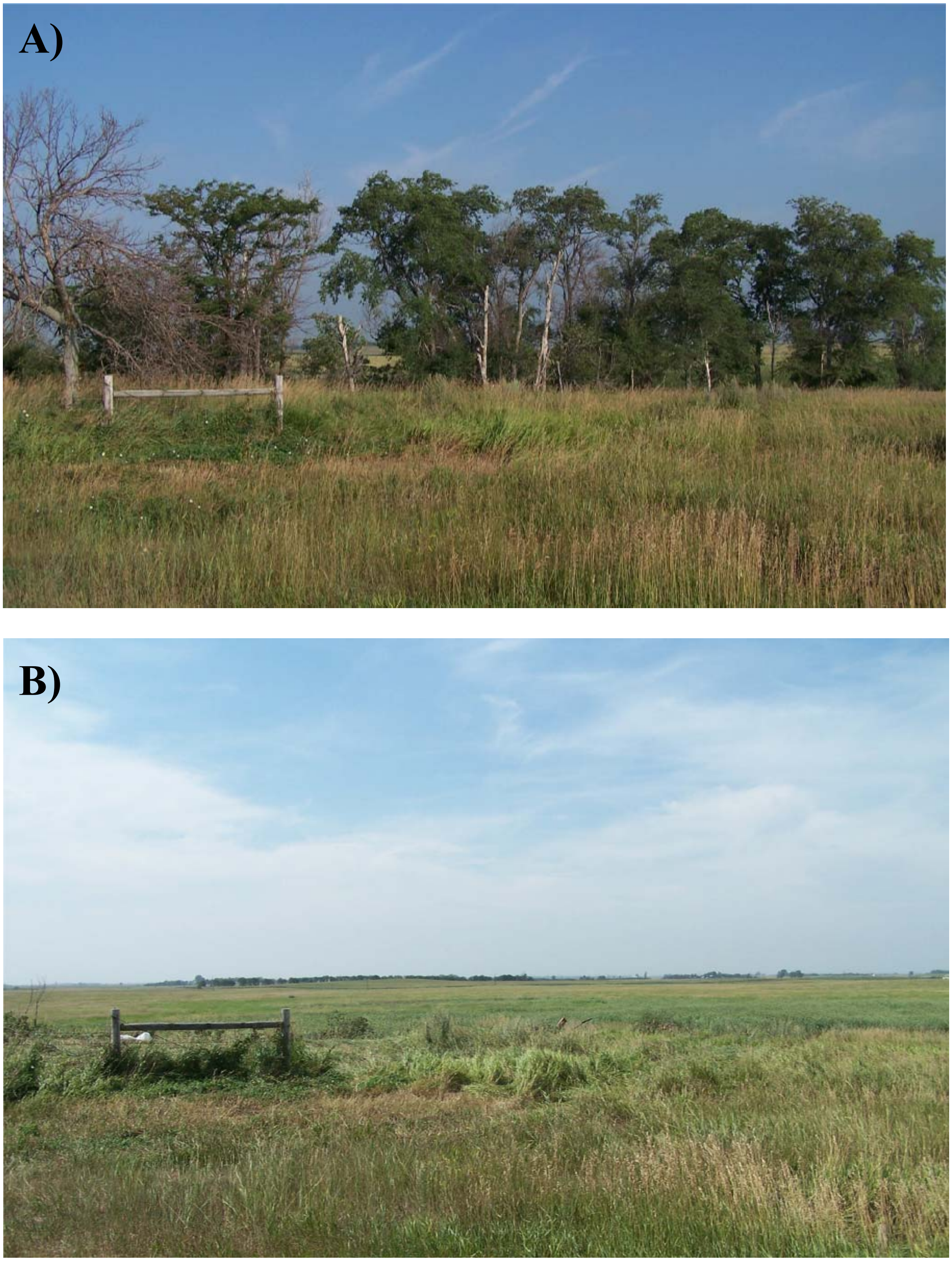

Figure 3. Photographs of a study site in SD before (A) and after (B) tree removal.

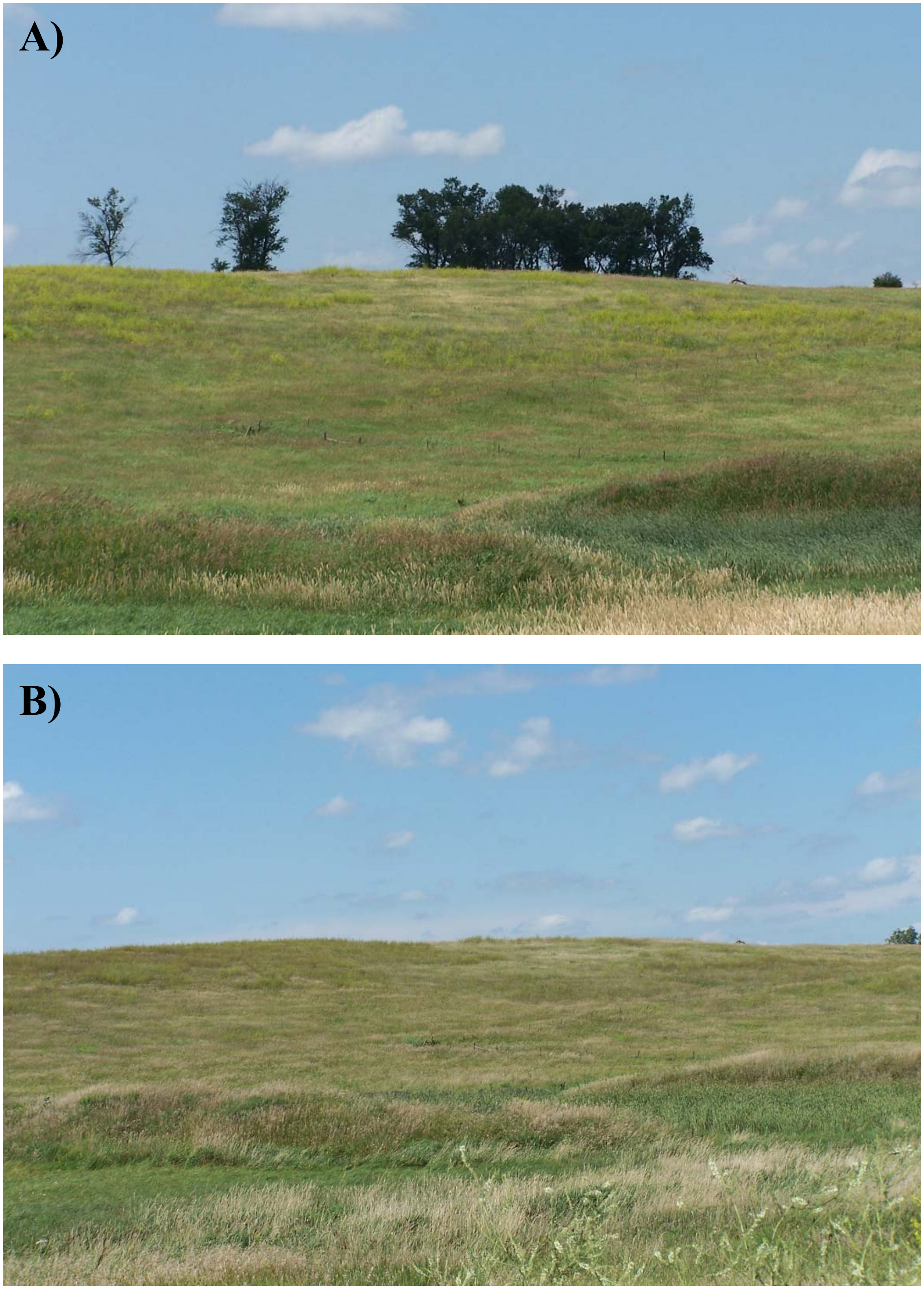

Figure 4. Photographs of a study site in SD before (A) and after (B) tree removal.

onset of the next breeding season (Figures 3 and 4). Disturbed areas were reseeded with native grass mixtures by the U.S. Fish and Wildlife Service.

Data Analysis

I compared visual obstruction, effective leaf height and litter depth at sites with and without treebelts using t-tests and ANOVA. My intention was to minimize vegetation structure as a source of variation between treatment and control groups. I included in analyses bird species with > 120 detections (Table 1). I used one-way ANOVA with linear contrasts to determine if bird abundance increased with increasing distance from treebelts. I also compared trends in bird abundance across transects for sites with trees and those where trees had been removed. Lastly, I compared trends in bird abundance in sites with trees and where trees had been removed to those in treeless grasslands.

Results

Measures of visual obstruction, effective leaf height and litter depth were similar for grasslands with and without treebelts ($P > 0.29$; Table 2). These same measures of grassland structure also were similar within transects that were near versus far from trees (visual obstruction $P = 0.87$, effective leaf height $P = 0.96$, litter depth $P = 0.37$). I detected 12 species of grassland passerines during surveys (Table 1). Sedge wren (n = 878), bobolink (n = 655), savannah sparrow (n = 397), clay-colored sparrow (n = 218), dickcissel (n = 187) and brown-headed cowbird (n = 130) were detected frequently enough to include in detailed analyses (Table 1). Abundances of bobolink, savannah sparrow and sedge wren were all lower in grasslands with trees than in treeless grasslands in all transects except those located farthest from woody edges (Table 3a and b; Figures 5, 6, and 7).

Positive trends ($p < 0.016$) in abundance with distance from trees show that bobolink, savannah sparrow, sedge wren (both years) and dickcissel (year 1 only) each avoid woody edges (Table 3A and B; Figures 5 and 6). Trends were no longer apparent the year after tree removal for bobolink, savannah sparrow and dickcissel ($p > 0.19$ each species; Figure 5 and 6). Overall abundance of sedge wren increased after trees were removed (Table 3A and B; Figure 6). Although birds used otherwise suitable habitats following tree removal, abundance of bobolink, savannah sparrow and sedge wren remained at or below levels observed in treeless grasslands (Table 3A and B; Figures 5 and 6). Dickcissel redistributed following tree removal and increased in abundance to levels that equal or exceed those observed in treeless grasslands (Table 3; Figure 6). Abundances of brown-headed cowbird and clay-colored sparrow were unrelated to distance from treebelts or presence of trees (Figure 7). Abundance of clay-colored sparrow before (year 1 only) and after tree removal remained at or above levels observed in treeless grasslands (Figure 7).

Table 1. Number of detections and frequency of occurrence (%) of birds in sites with and without trees and in sites where treebelts were experimentally removed in North and South Dakota, 2004-2006.

	Treeless Grassland (n = 160)		After tree removal (n = 375)		Sites with trees (n = 1225)		Total (n = 1760)	
Species	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**
sedge wren (*Cistothorus platensis*)	122	76%	185	49%	571	47%	878	50%
bobolink (*Dolichonyx oryzivorus*)	108	68%	142	38%	405	33%	655	37%
savannah sparrow (*Passerculus sandwichensis*)	94	59%	80	21%	223	13%	397	23%
clay-colored sparrow (*Spizella pallida*)	10	6%	45	12%	163	13%	218	12%
dickcissel (*Spiza americana*)	24	15%	65	17%	98	8%	187	11%
brown-headed cowbird (*Molothrus ater*)	11	7%	23	6%	96	5%	130	7%
grasshopper sparrow (*Ammodramus savannarum*)	20	13%	25	7%	67	3%	112	6%
western meadowlark (*Sturnella neglecta*)	3	2%	11	3%	21	2%	35	2%
vesper sparrow (*Pooecetes gramineus*)	1	1%	0	0%	12	0%	13	1%
Nelson’s sharp-tailed sparrow (*Ammodramus nelsoni*)	0	0%	0	0%	5	<1%	5	<1%
LeConte’s sparrow (*Ammodramus leconteii*)	1	<1%	0	0%	2	<1%	3	<1%
Baird’s sparrow (*Ammodramus bairdii*)	0	0%	1	<1%	1	<1%	2	<1%

Table 2. Comparison of grassland vegetation in sites with treebelts (< 240 m) and in treeless grasslands (> 800 m from treebelts) in eastern North and South Dakota.

	Treebelts (n = 64)	Open grasslands (n = 32)	
Attribute	Mean ± SE	Mean ± SE	P-value
Visual Obstruction (dm)	3.45 ± 0.13	3.20 ± 0.20	0.29
Effective Leaf Height (cm)	53.18 ± 1.32	51.81 ± 2.39	0.61
Litter Depth (mm)	54.59 ± 2.16	50.6 ± 4.72	0.43

Table 3a. Abundance (birds / 4000 m^2) of grassland birds along transects at increasing distances from treebelts and in treeless grasslands in North and South Dakota (2004-2005).

YEAR 1				***SPECIES***[a]			
Treatment	**Trans**	**BOBO**	**SAVS**	**SEWR**	**DICK**	**CCSP**	**BHCB**
Tree Control	**20**	0.08±0.03	0.04±0.03	0.18±0.06	0.00±0.00	0.15±0.07	0.15±0.07
	70	0.31±0.11	0.08±0.05	0.53±0.13	0.01±0.01	0.12±0.06	0.12±0.06
	120	0.36±0.12	0.11±0.05	0.52±0.13	0.02±0.02	0.08±0.04	0.08±0.04
	170	0.39±0.13	0.21±0.07	0.71±0.16	0.05±0.03	0.12±0.06	0.12±0.06
	220	0.52±0.15	0.45±0.17	0.79±0.18	0.07±0.06	0.08±0.05	0.08±0.05
Cut(Before)	**20**	0.04±0.03	0.03±0.03	0.32±0.11	0.03±0.03	0.05±0.05	0.05±0.05
	70	0.11±0.04	0.07±0.03	0.24±0.07	0.07±0.07	0.16±0.07	0.16±0.07
	120	0.24±0.10	0.17±0.07	0.24±0.10	0.07±0.07	0.17±0.08	0.17±0.08
	170	0.29±0.10	0.29±0.08	0.37±0.14	0.08±0.07	0.17±0.12	0.17±0.12
	220	0.47±0.13	0.37±0.15	0.39±0.12	0.15±0.13	0.19±0.11	0.19±0.11
Grass Site	**n/a**	0.81±0.18	0.64±0.03	0.68±0.20	0.05±0.04	0.05±0.03	0.05±0.03

[a] BOBO = bobolink, SAVS = savannah sparrow, SEWR = sedge wren, DICK = dickcissel, CCSP = clay-colored sparrow, BHCB = brown-headed cowbird.

Table 3b. Abundance (birds / 4000 m^2) of grassland birds along transects at increasing distances from treebelts and in treeless grasslands in North and South Dakota (2005-2006).

YEAR 2		***SPECIES***[a]					
Treatment	**Trans**	**BOBO**	**SAVS**	**SEWR**	**DICK**	**CCSP**	**BHCB**
Tree Control	**20**	0.09±0.03	0.06±0.03	0.12±0.03	0.07±0.05	0.18±0.08	0.18±0.08
	70	0.25±0.09	0.16±0.06	0.49±0.12	0.15±0.06	0.08±0.04	0.08±0.04
	120	0.55±0.16	0.18±0.05	0.61±0.17	0.08±0.04	0.13±0.09	0.13±0.09
	170	0.52±0.15	0.27±0.08	0.71±0.19	0.20±0.08	0.15±0.09	0.15±0.09
	220	0.68±0.16	0.25±0.09	0.69±0.17	0.15±0.07	0.16±0.10	0.16±0.10
Cut(After)	**20**	0.31±0.08	0.19±0.06	0.40±0.15	0.19±0.07	0.11±0.07	0.11±0.07
	70	0.33±0.10	0.15±0.06	0.44±0.16	0.11±0.04	0.11±0.07	0.11±0.07
	120	0.35±0.11	0.17±0.04	0.59±0.23	0.12±0.06	0.16±0.08	0.16±0.08
	170	0.43±0.12	0.32±0.08	0.49±0.14	0.15±0.06	0.11±0.06	0.11±0.06
	220	0.48±0.14	0.24±0.07	0.55±0.19	0.31±0.10	0.12±0.06	0.12±0.06
Grass Site	**n/a**	0.54±0.12	0.54±0.12	0.85±0.19	0.25±0.09	0.08±0.04	0.08±0.04

[a] BOBO = bobolink, SAVS = savannah sparrow, SEWR = sedge wren, DICK = dickcissel, CCSP = clay-colored sparrow, BHCB = brown-headed cowbird.

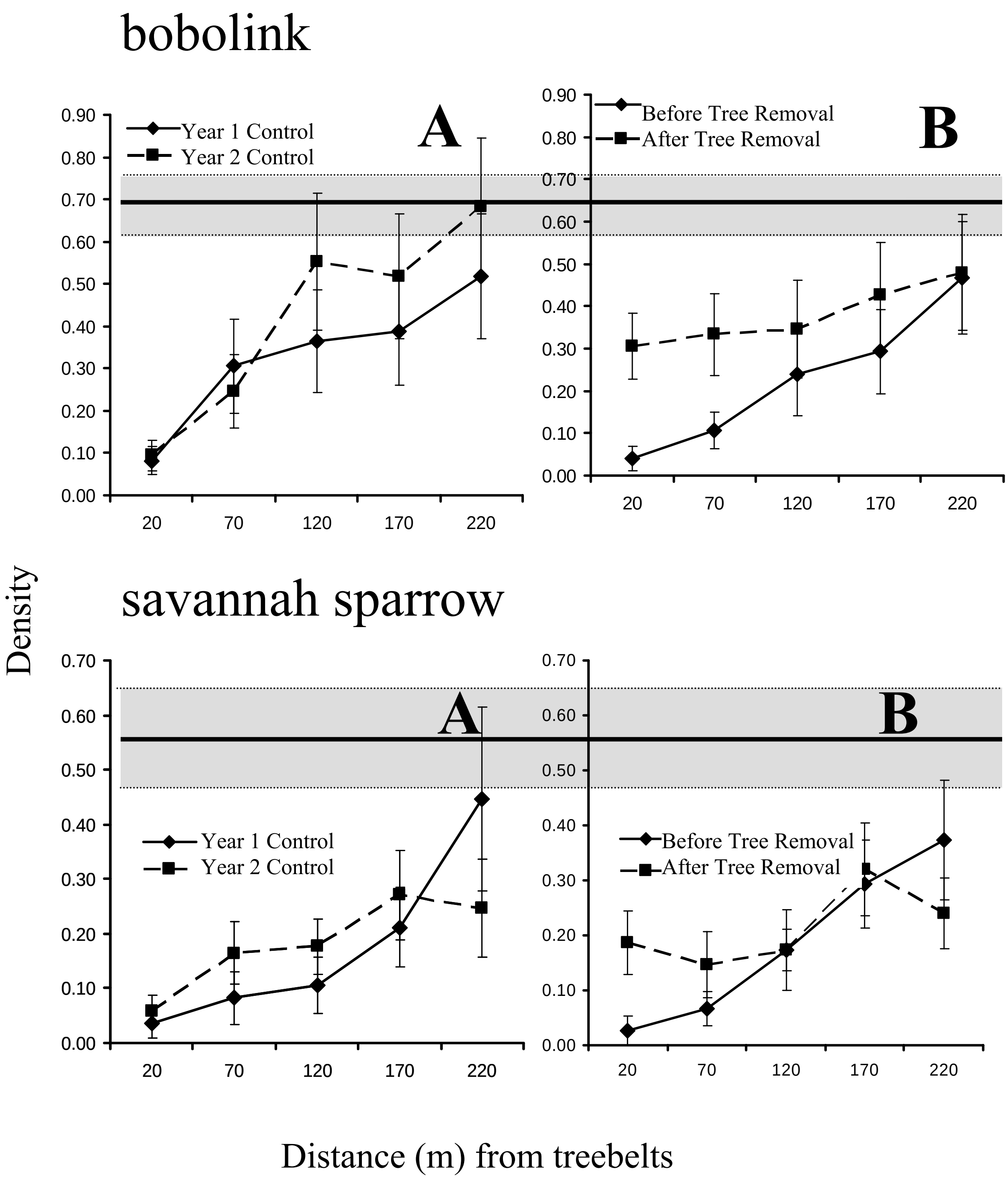

Figure 5. Densities (birds / 0.4 ha [~1 ac]) of bobolink and savannah sparrow in grasslands with trees (A) and the responses from tree removal (B). Shaded area shows bobolink and savannah sparrow densities (0.65 ± 0.11; 0.57 ± 0.09) in treeless grassland control sites (>800 m from trees).

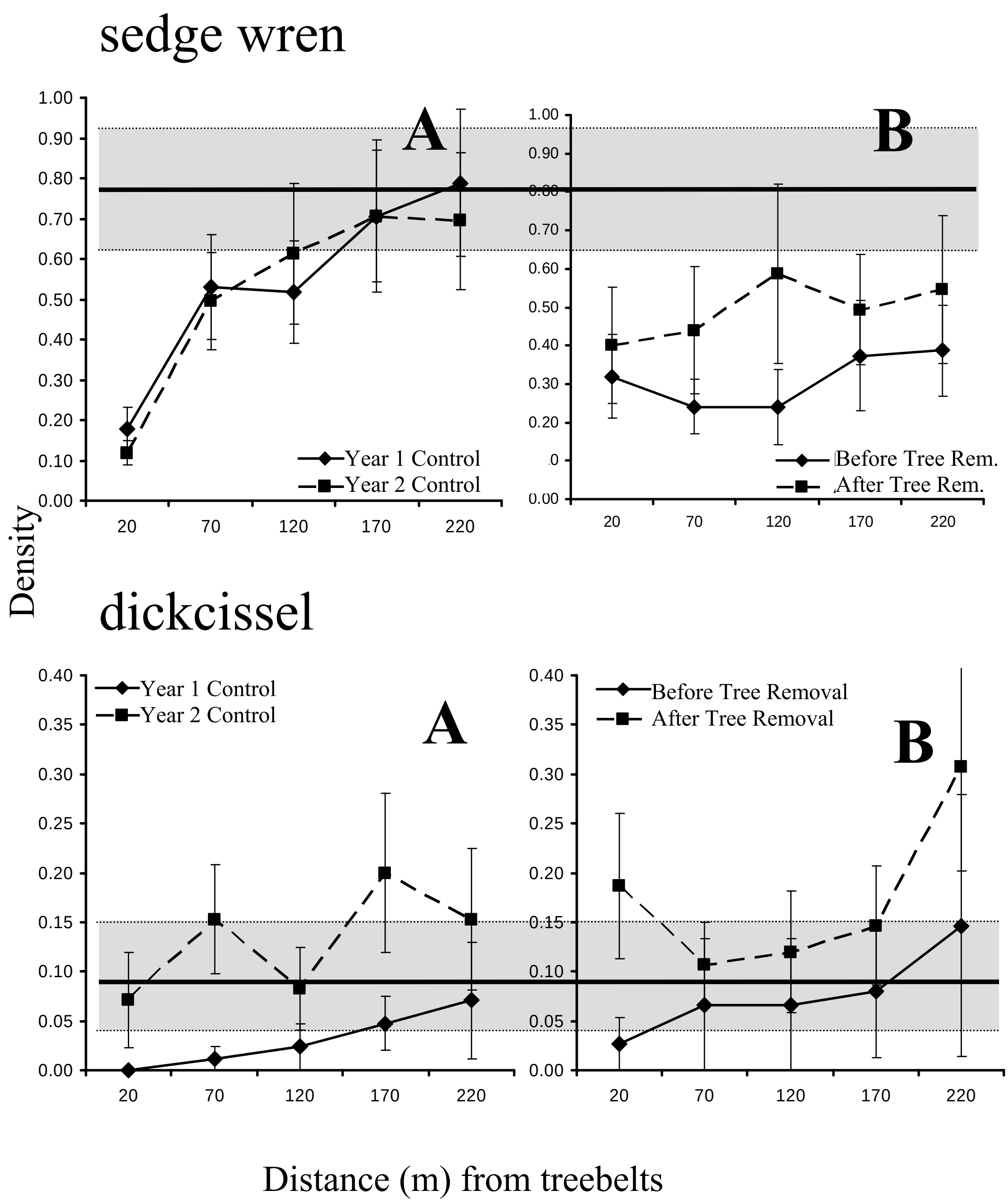

Figure 6. Densities (birds / 0.4 ha [~1 ac]) of sedge wrens and dickcissels in grasslands with trees (A) and the responses from tree removal (B). Shaded area shows sedge wren and dickcissel densities (0.79 ± 0.14; 0.11 ± 0.02) in treeless grassland control sites (>800 m from trees).

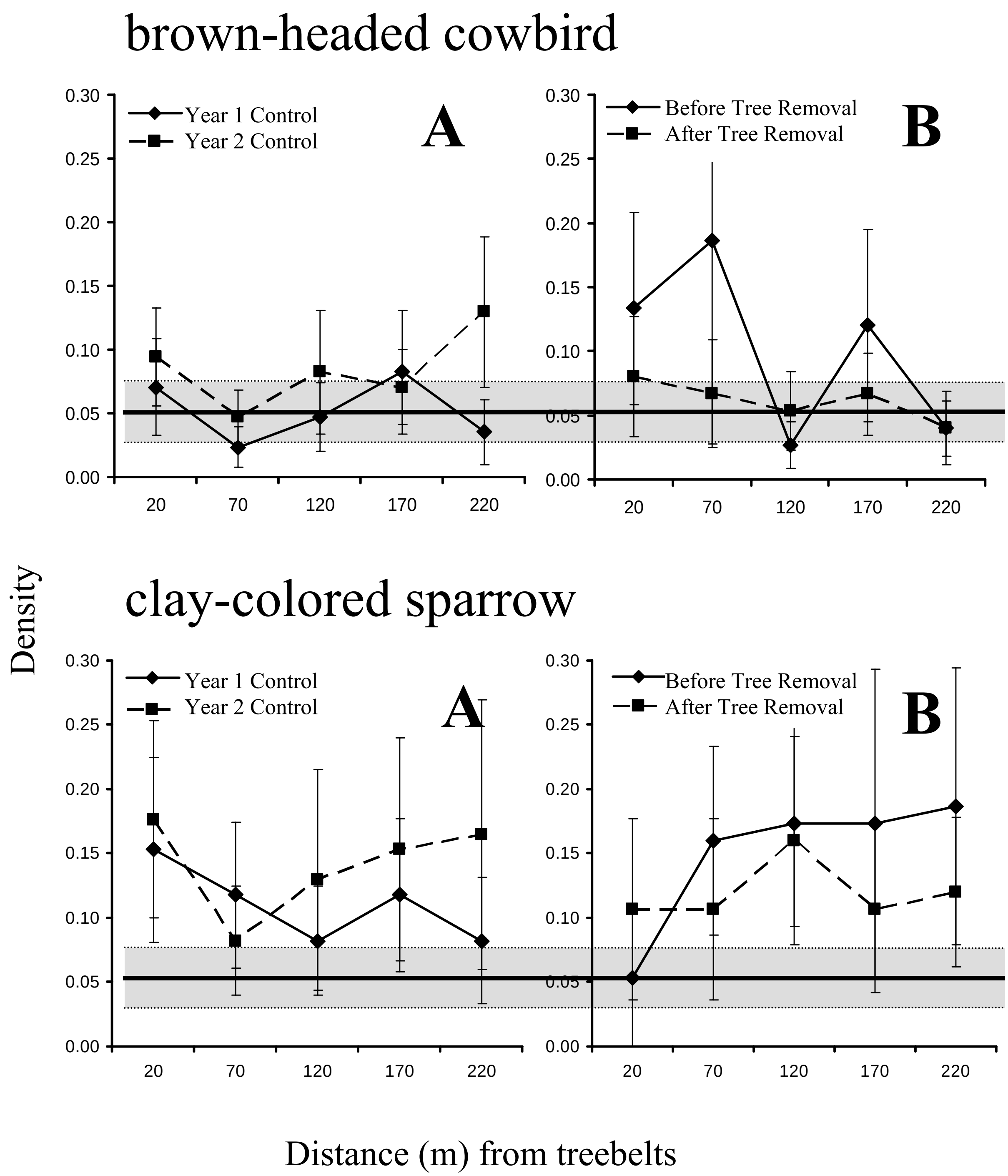

Figure 7. Densities (birds / 0.4 ha [~1 ac]) of brown-headed cowbird and clay-colored sparrow in grasslands with trees (A) and the responses from tree removal (B). Shaded area shows brown-headed cowbird and clay-colored sparrow densities (0.07 ± 0.02; 0.07 ± 0.02) in treeless grassland control sites (>800 m from trees).

Discussion

This study is the first to experimentally show that native passerines avoid woody edges in otherwise suitable grassland habitats. Avoidance of trees by the four most common grassland songbirds was apparent as far out as 240 m, the farthest away from woody edges that surveys were conducted. The following spring, bobolink, savannah sparrow, sedge wren and dickcissel distributed themselves ubiquitously in grasslands where trees had been experimentally removed. Although birds re-colonized grasslands following tree removal, their abundance generally remained below that observed in treeless grasslands. This finding suggests that effects of woody edges may extend beyond our transects such that trees within 240 – 800 m may need to be removed before grasslands attract the abundance of birds observed in treeless grasslands. Alternately, positive effects may not be fully realized one year after tree removal if site fidelity is high or if birds use their own reproductive success or that of others when choosing whether to return to a breeding location (Bollinger and Gavin 1989, 2004). Abundance of brown-headed cowbird, a common parasite of nests of grassland songbirds, was completely unrelated to the presence or removal of woody edges. Clay-colored sparrow, a brush land species, was unrelated to location of woody edges and was more abundant in grasslands with than without trees, findings that are consistent with almost all research involving this species (Grant et al. 2004).

Direct habitat loss is the greatest threat to populations, but management activities that degrade remaining habitats further heighten concern for conservation of populations of native grassland songbirds (Brennan and Kuvelsky et al. 2005). Research overwhelmingly shows that trees have negative impacts on the occurrence (Madden et al. 2000, Bakker et al. 2002, Grant et al. 2004), abundance (O'Leary and Nyberg 2000, Fletcher and Koford 2003, Davis 2004, 2005) and productivity (e.g., Johnson and Temple 1990, Winter et al. 2000, 2006, Scheiman et al. 2003, Bollinger and Gavin 2004, Patten et al. 2006) of native grassland songbirds. Furthermore, the ecological cost to grassland birds in planting trees in prairie landscapes outweighs potential benefits to forest birds of management concern. Kelsey et al. (2006) found that planted treebelts fail to provide habitat for these forest bird species.

Despite the ecological costs of planting treebelts, the exact mechanisms that determine avoidance are poorly understood. Many grassland songbirds avoid tall structures including treebelts (Fletcher and Koford 2002, Cunningham and Johnson 2006) and wind turbines (Leddy et al. 1999), but mechanisms have not been widely investigated. Though I did not explicitly quantify nest success or predation risk, Johnson and Temple (1990) report lower predation rates in grasslands located far from wooded edges. An undocumented yet plausible explanation is that nest predation risk increases near woody edges (Chalfoun et al. 2002, Kuehl and Clark 2002) that serve as important den sites and travel corridors for a host of potential predators that were historically uncommon in these areas (Sargent 1972, Sargent et al. 1987, Pedlar et al. 1997, Kuehl and Clark 2002).

Regardless of the mechanism, I recommend that land managers remove treebelts from grasslands where conservation of native grassland passerines is a primary management goal. Remnant treebelts on public grasslands no longer serve their intended purpose of reducing soil erosion and protecting homes and livestock from wind.

Extrapolations indicate that if the average area of a federally-owned tract of land in North Dakota is 87 ha (Susan Kvas, U.S. Fish and Wildlife Service, personal communication), and bird abundance is lower within 220 m of a woody edge, then just one treebelt centrally located on each tract could negate habitat benefits on 25% of public lands. This effect is exacerbated if additional treebelts are juxtaposed on private lands adjacent to public areas.

I further recommend that public land managers use these findings to strike a balance between the habitat needs of native grassland birds and those of popular game species such as white-tailed deer (*Odocoileus virginianus*) and ring-necked pheasants. Many government agencies recommend planting trees to private landowners as a way to increase native and exotic game species on their lands. The Conservation Reserve Program (CRP) administered by the Natural Resources Conservation Service provides monetary incentives to farmers to replace marginal cropland with undisturbed grassland habitat with an intended benefit to wildlife populations. Often included in this program are incentives to plant trees. If managers wish to promote native grassland bird habitat on private land, discouraging treebelts under the CRP program is advised.

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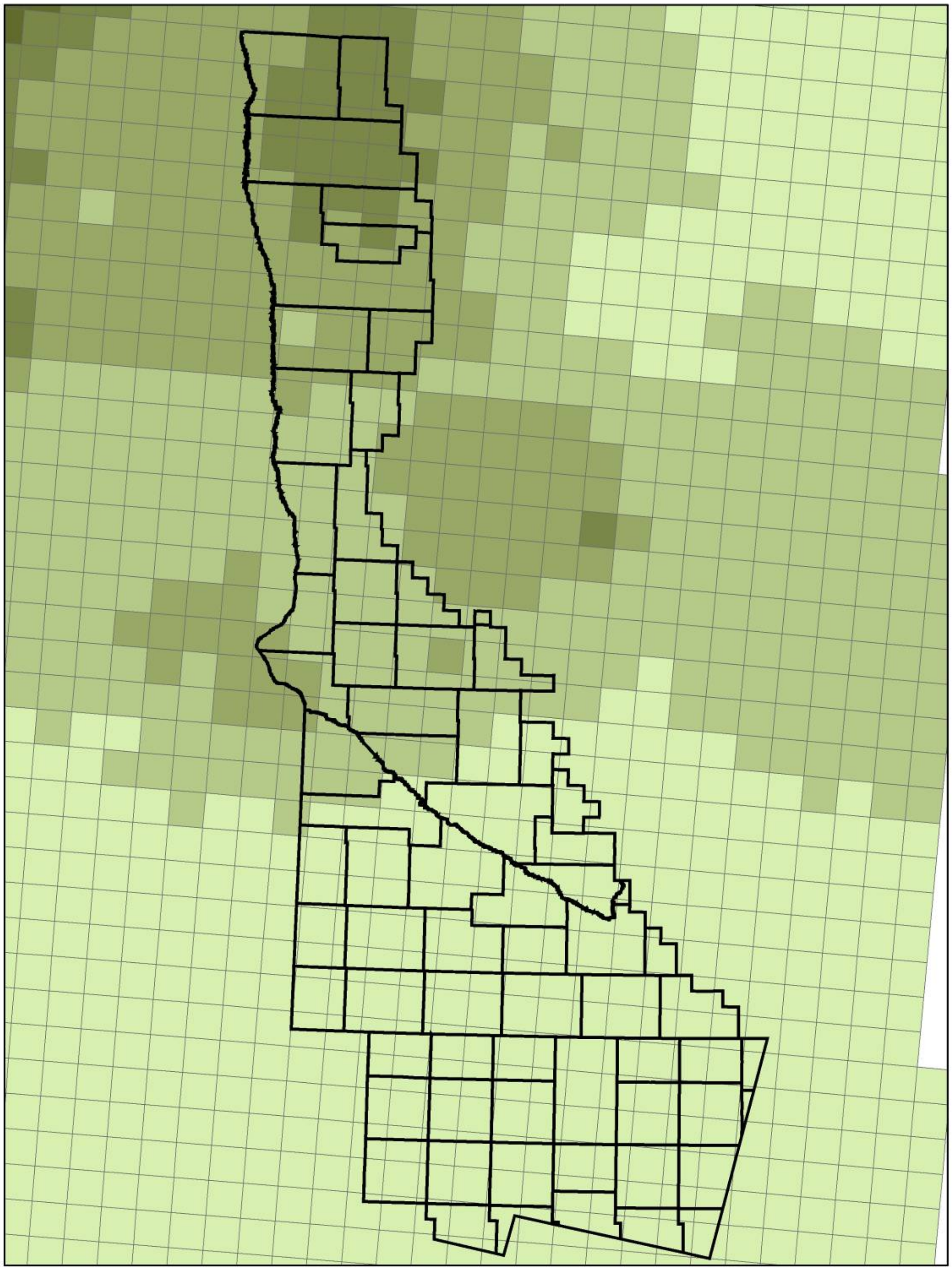
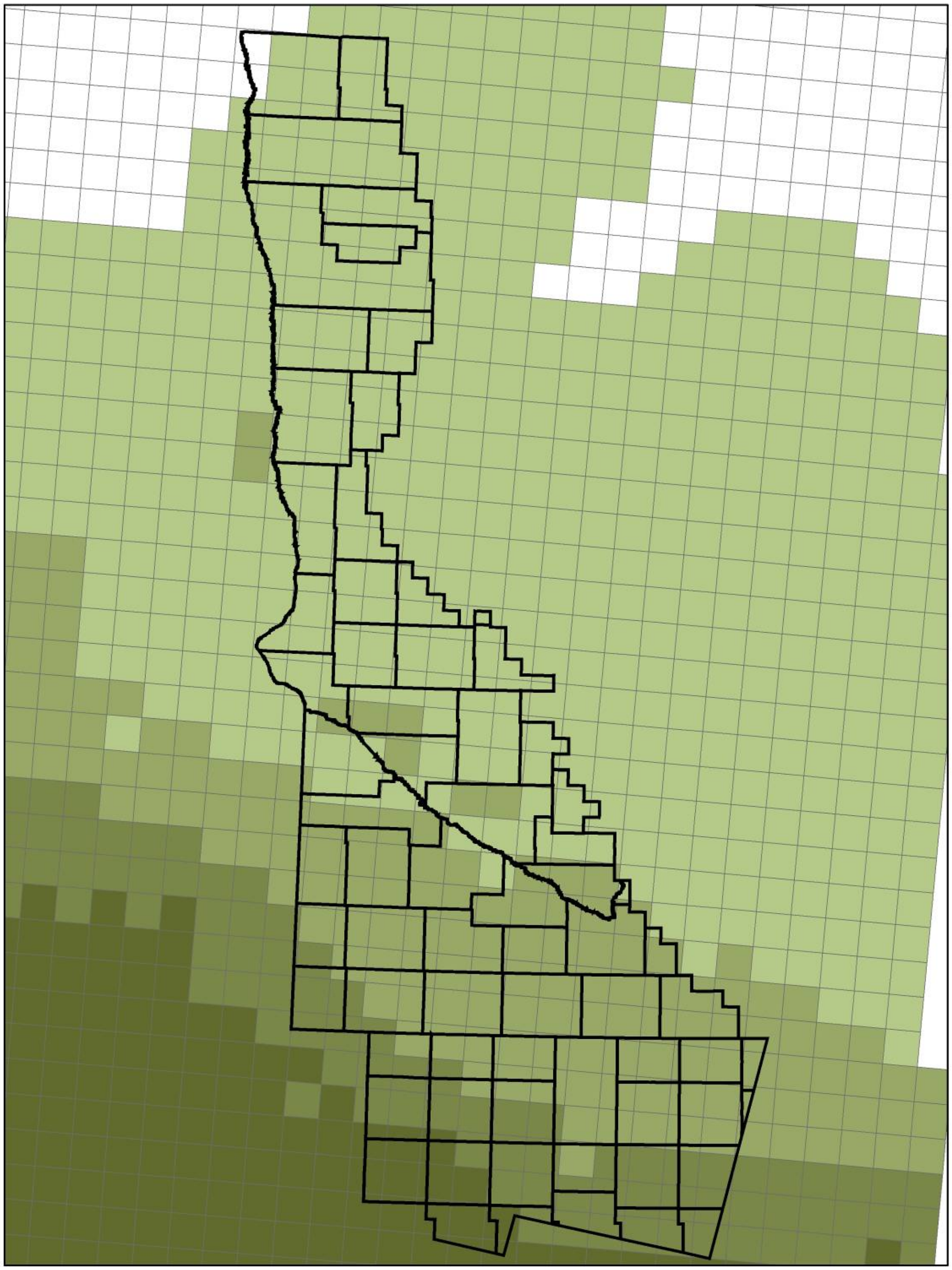
Appendix A. Breeding Bird Survey (BBS) data used as an autologistic term in habitat models in Chapter 2. Darker cells indicate higher predicted density. [pwrc.usgs.gov]

Bobolink

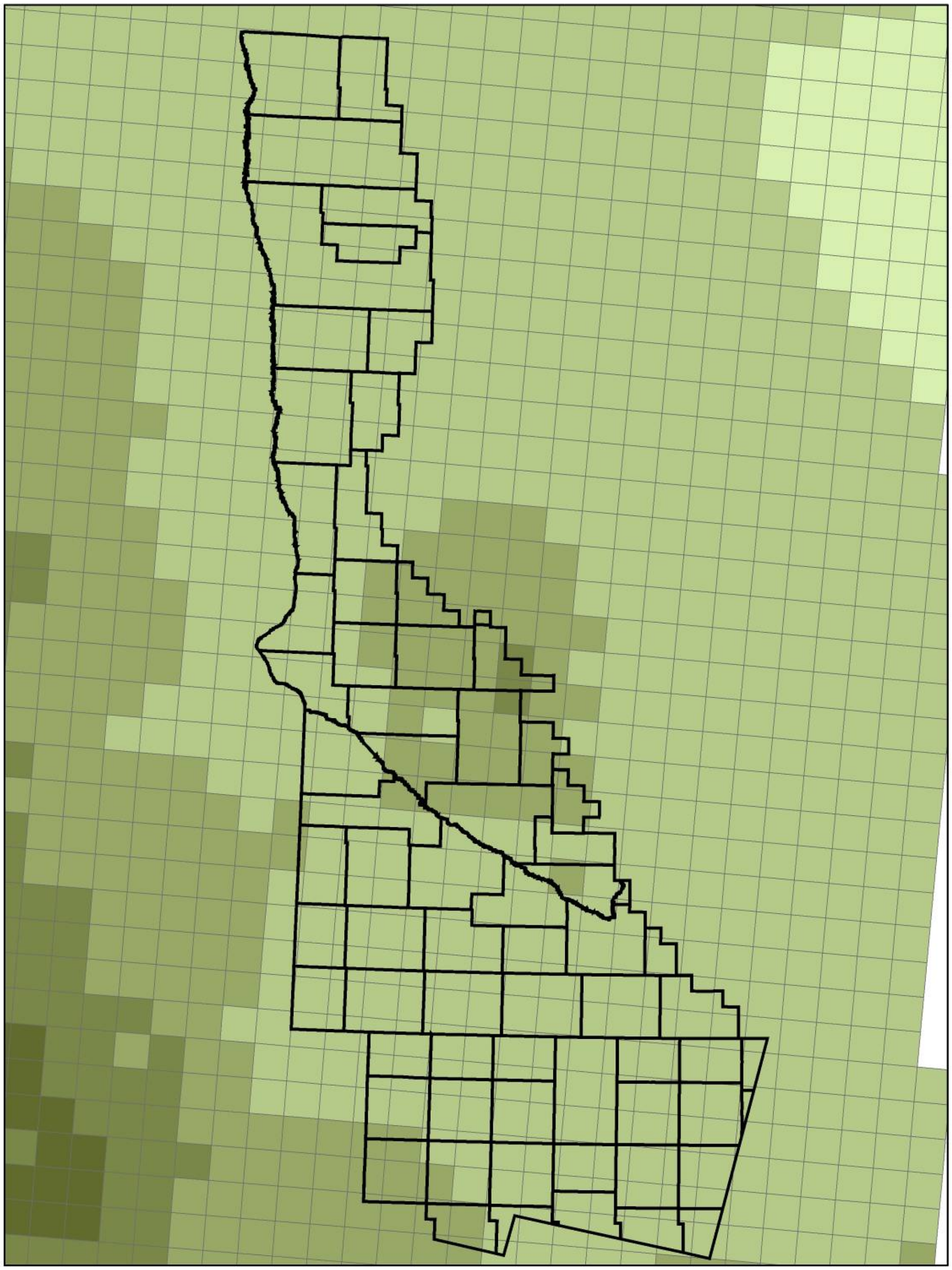
Clay-colored sparrow



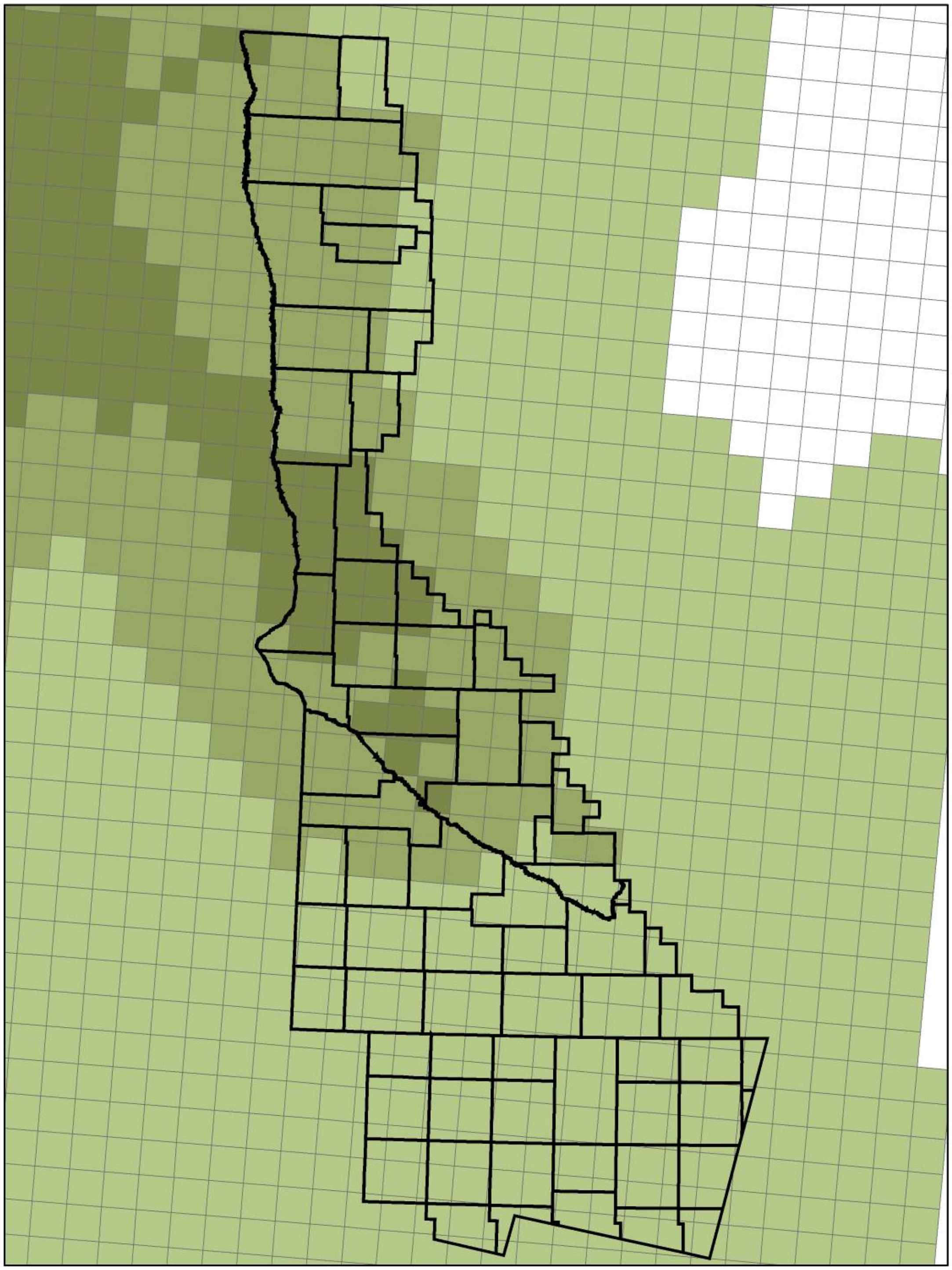
Dickcissel



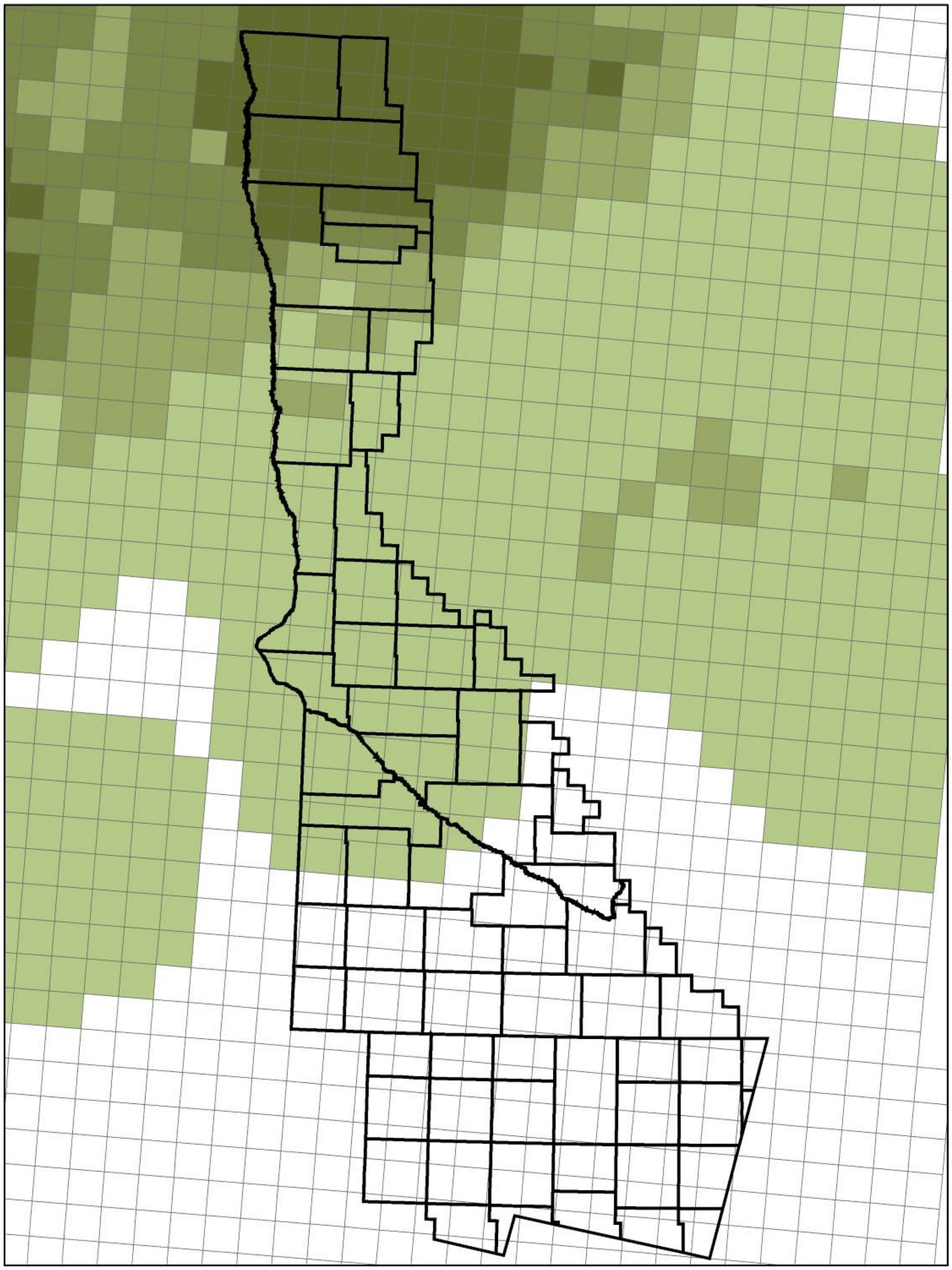
Grasshopper sparrow



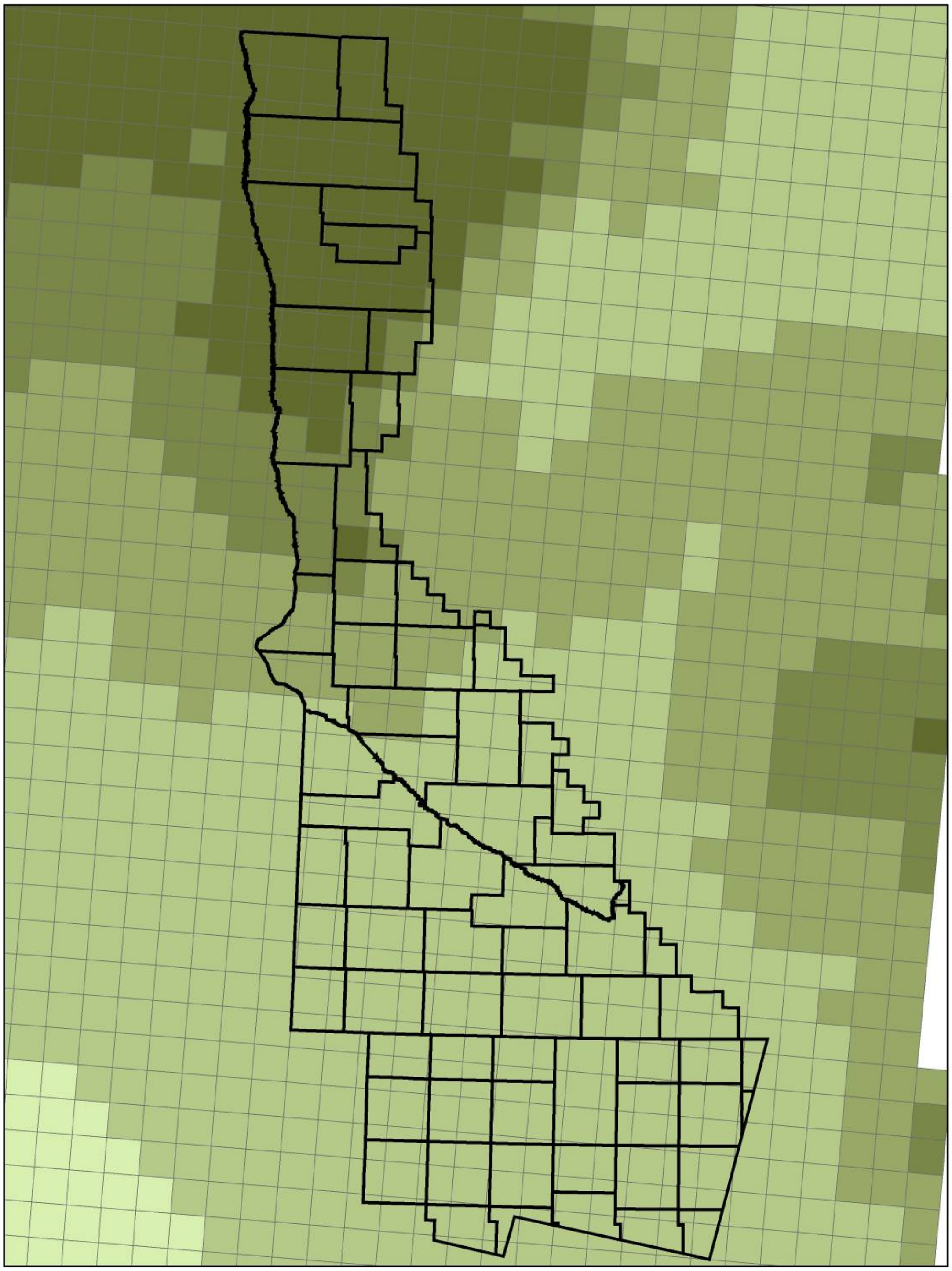
Horned lark



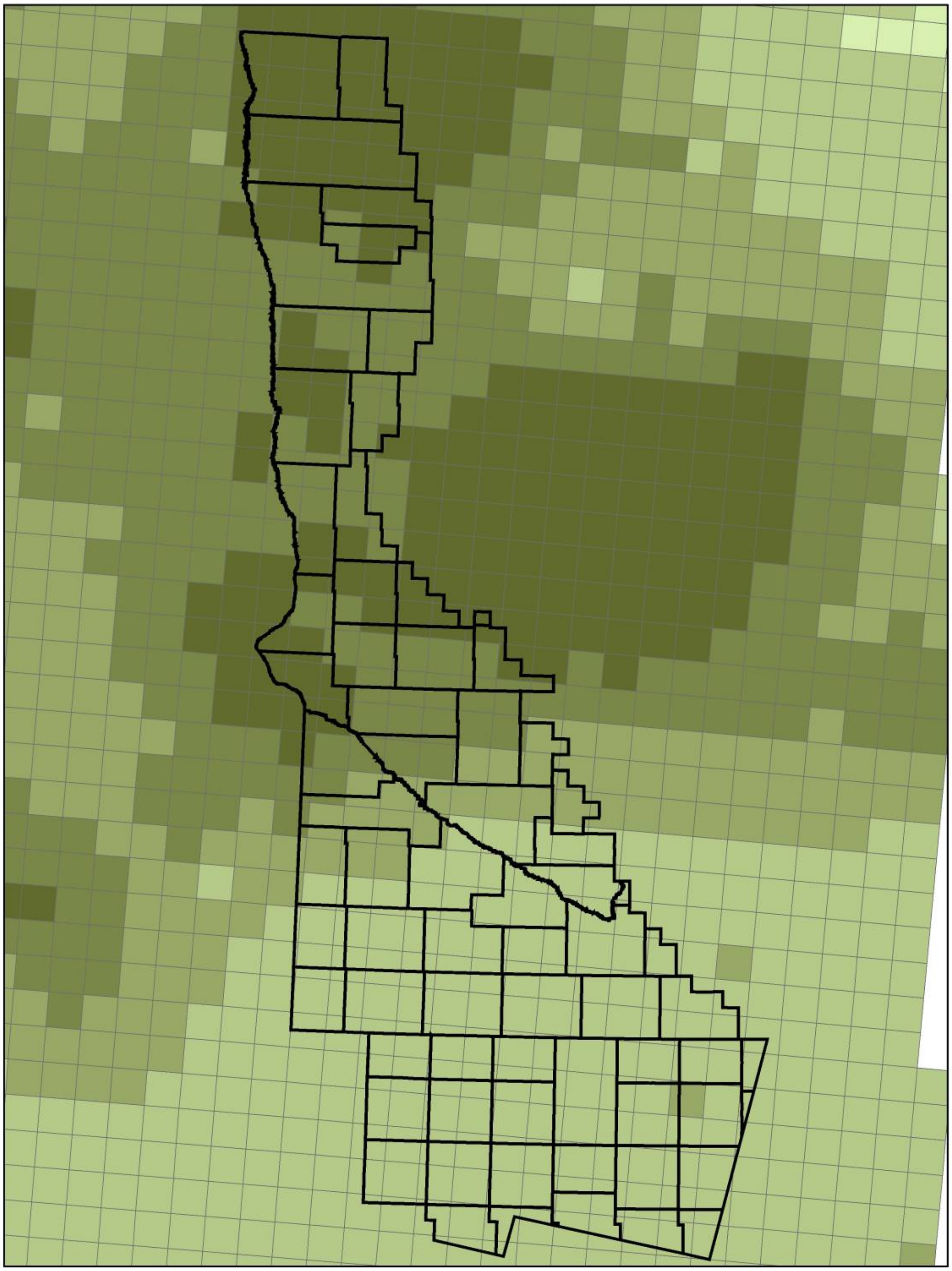
LeConte's sparrow



Savannah sparrow

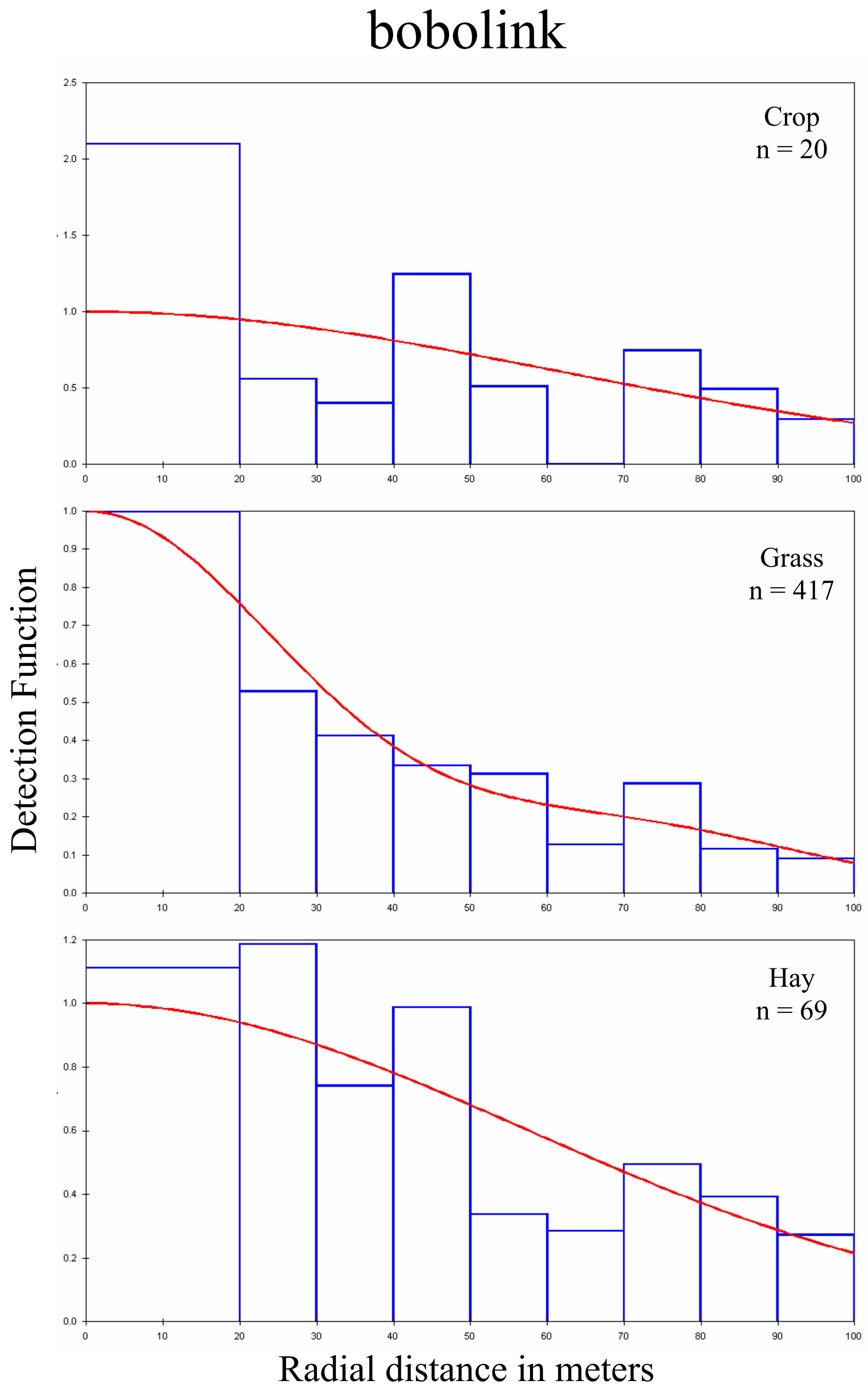


Sedge wren

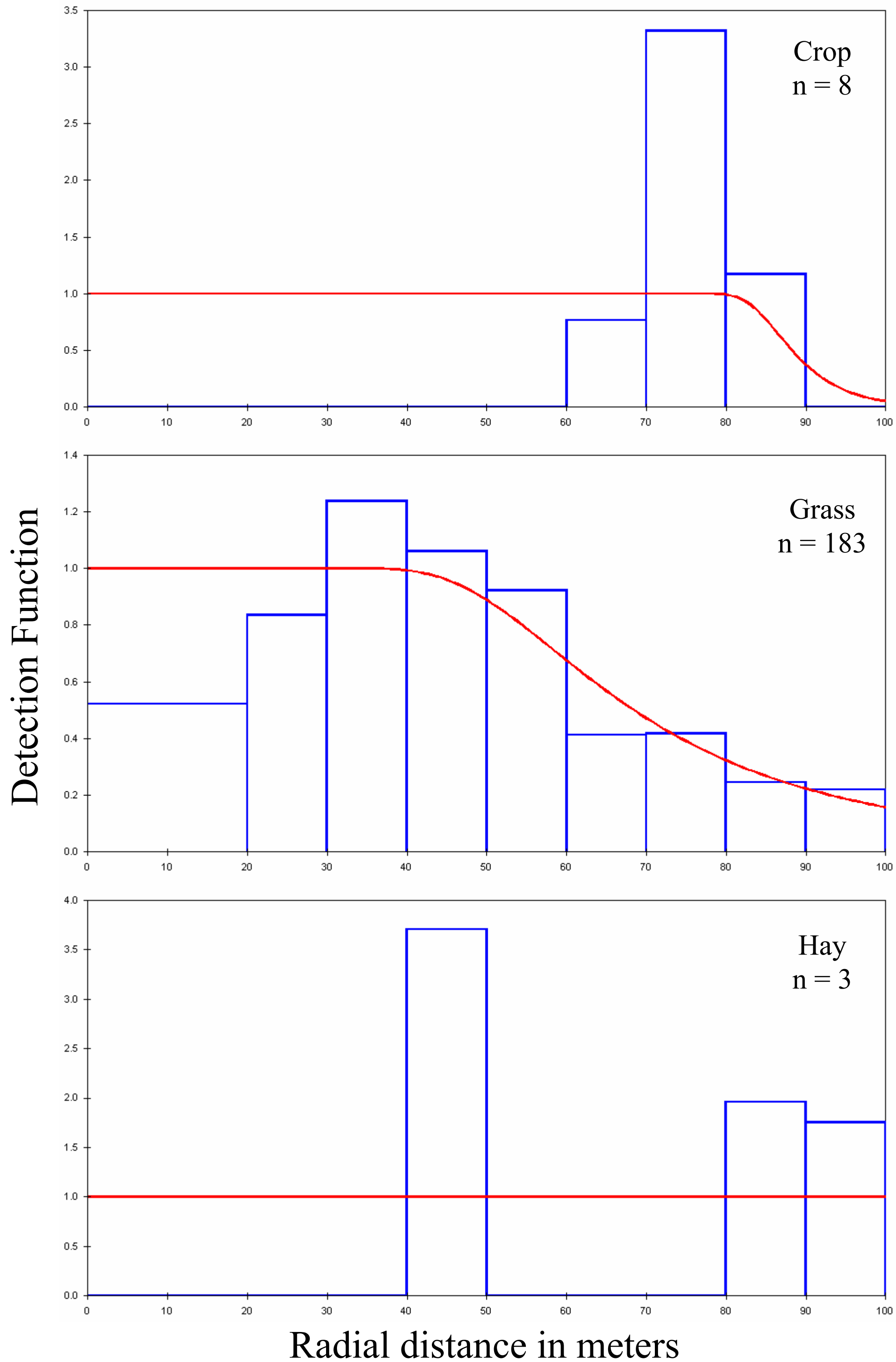


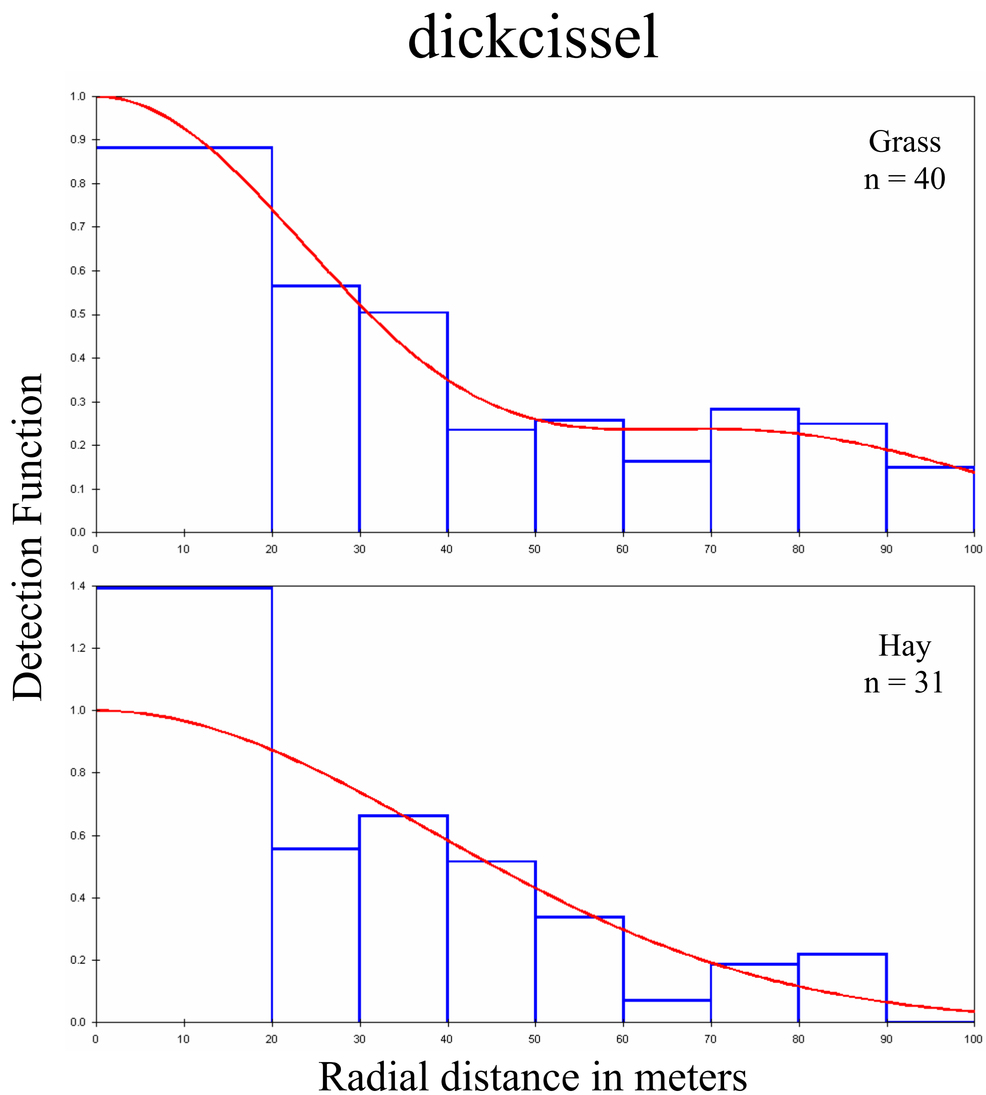
Western meadowlark

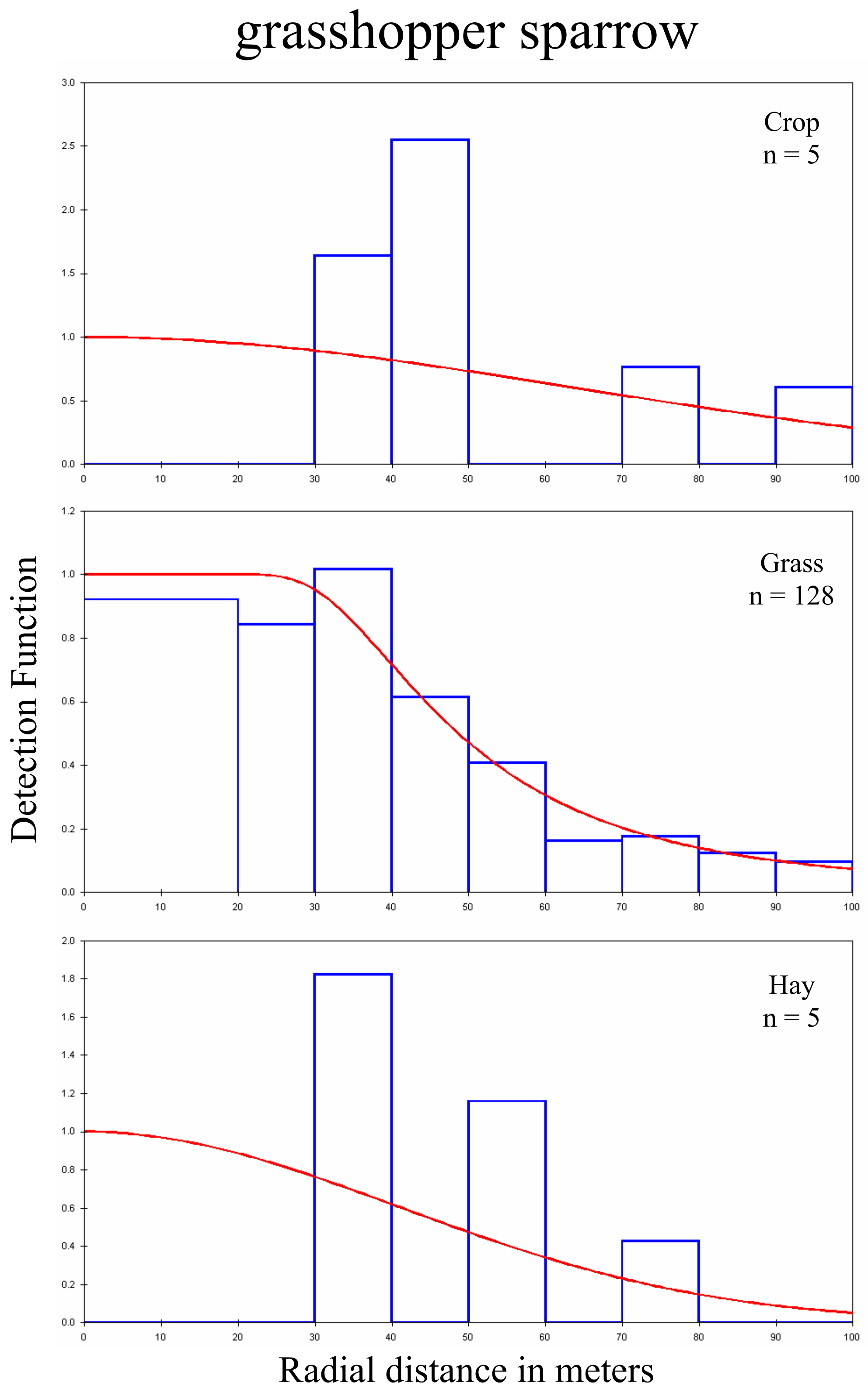
Appendix B. Output from Program DISTANCE output graphs for each species for which habitat models are constructed in Chapter 2.



clay-colored sparrow




dickcissel
Grass
n = 40
Hay
n = 31
Detection Function
Radial distance in meters
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1.2
1.4
0
10
20
30
40
50
60
70
80
90
100


grasshopper sparrow
Crop
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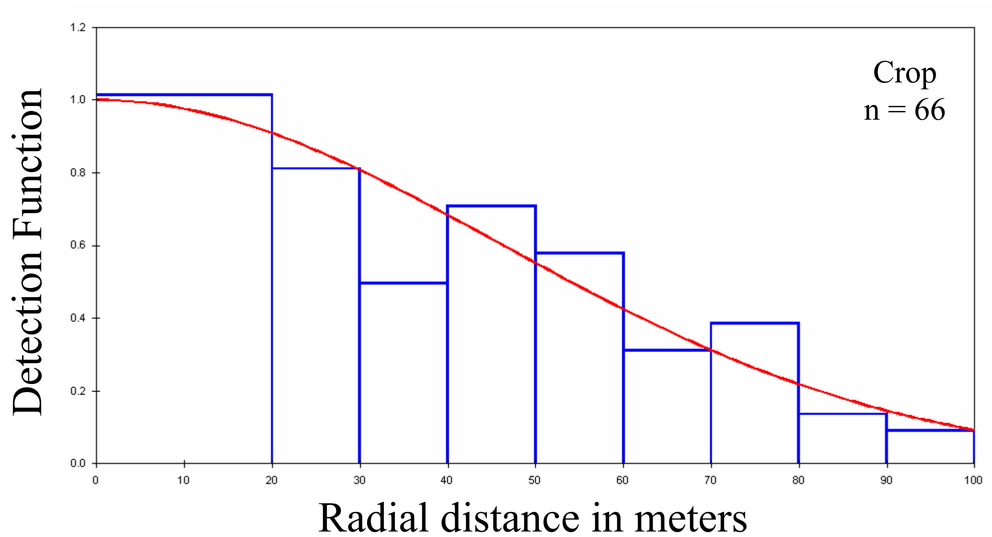
Grass
n = 128
Hay
n = 5
Detection Function
Radial distance in meters

horned lark


Crop
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Detection Function
Radial distance in meters
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1.0
0.8
0.6
0.4
0.2
0.0
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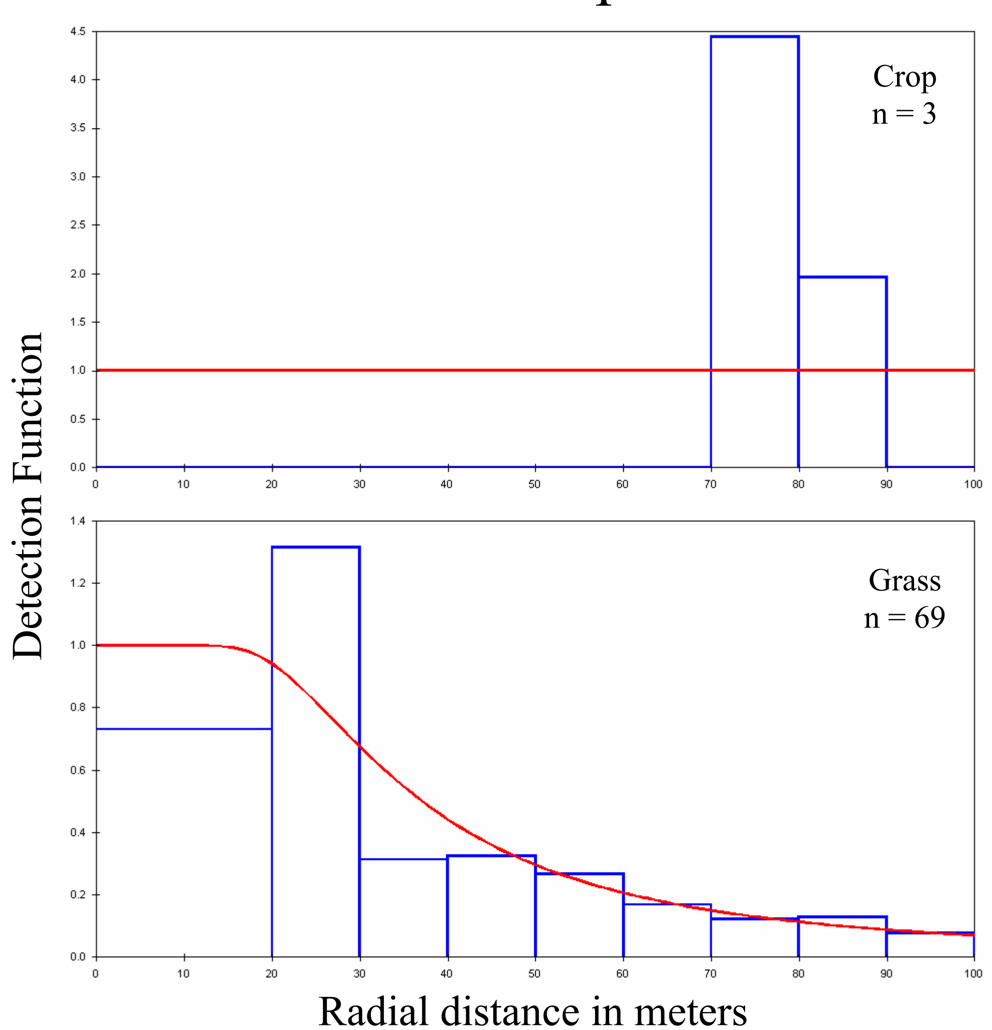
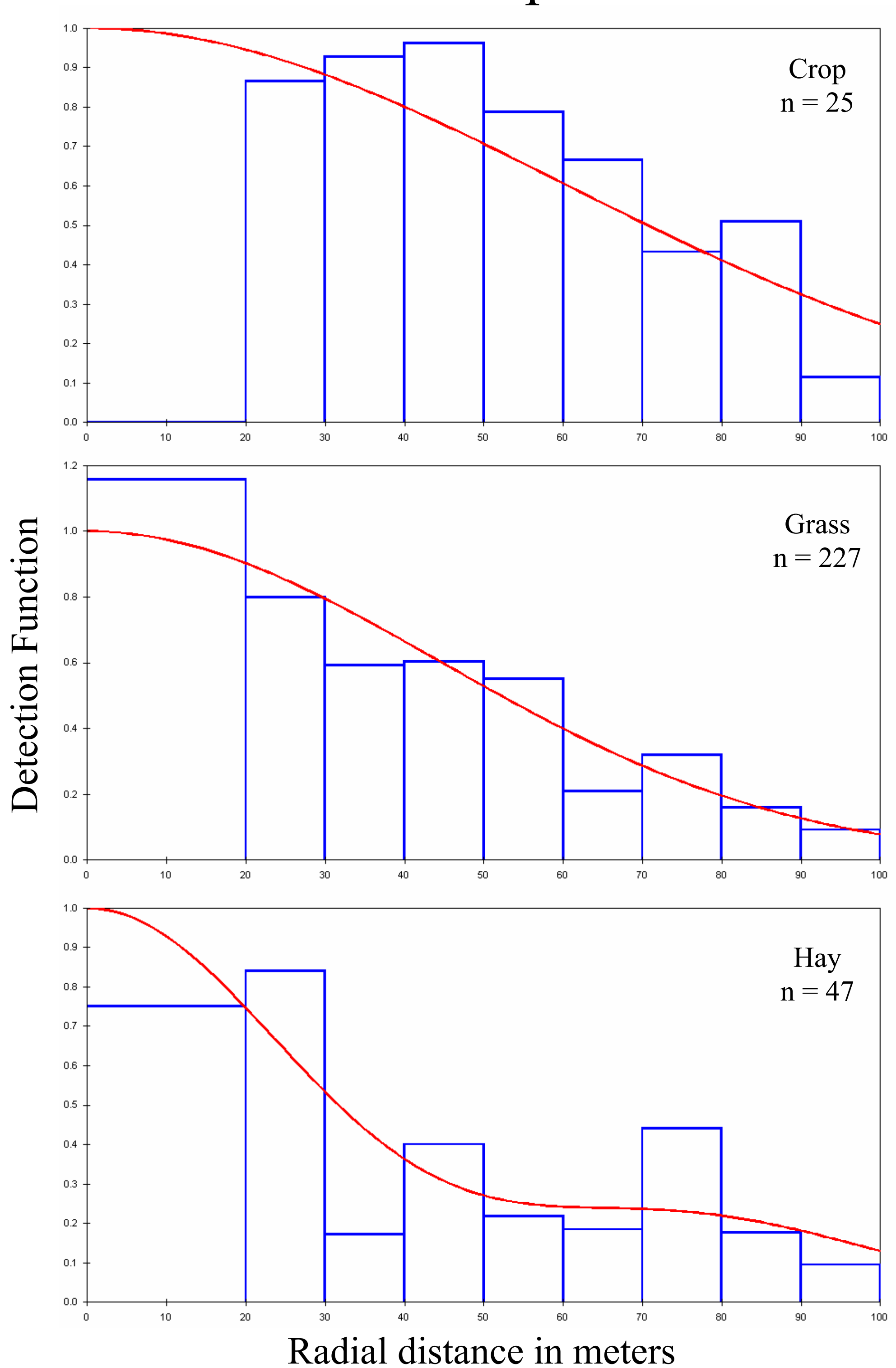
20
30
40
50
60
70
80
90
100

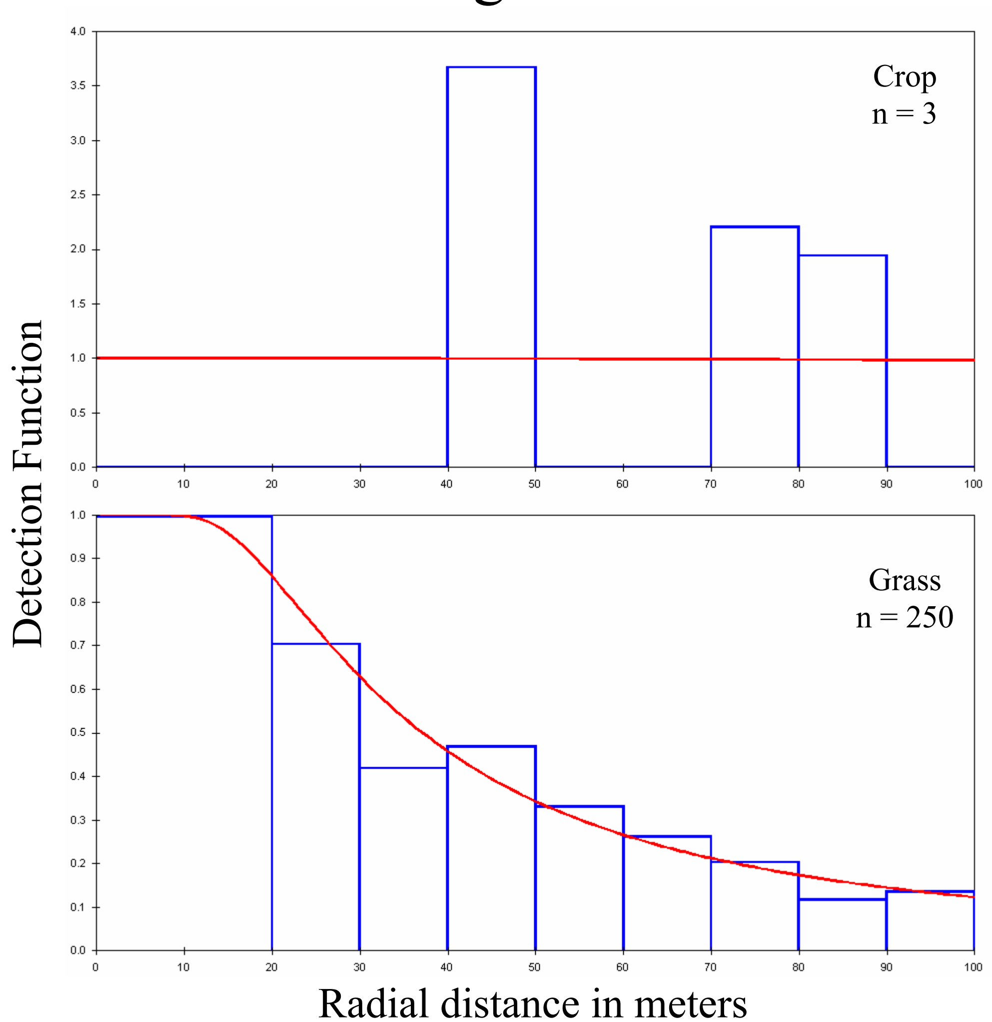
LeConte's sparrow



savannah sparrow



sedge wren


Detection Function
Crop
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Grass
n = 250
Radial distance in meters
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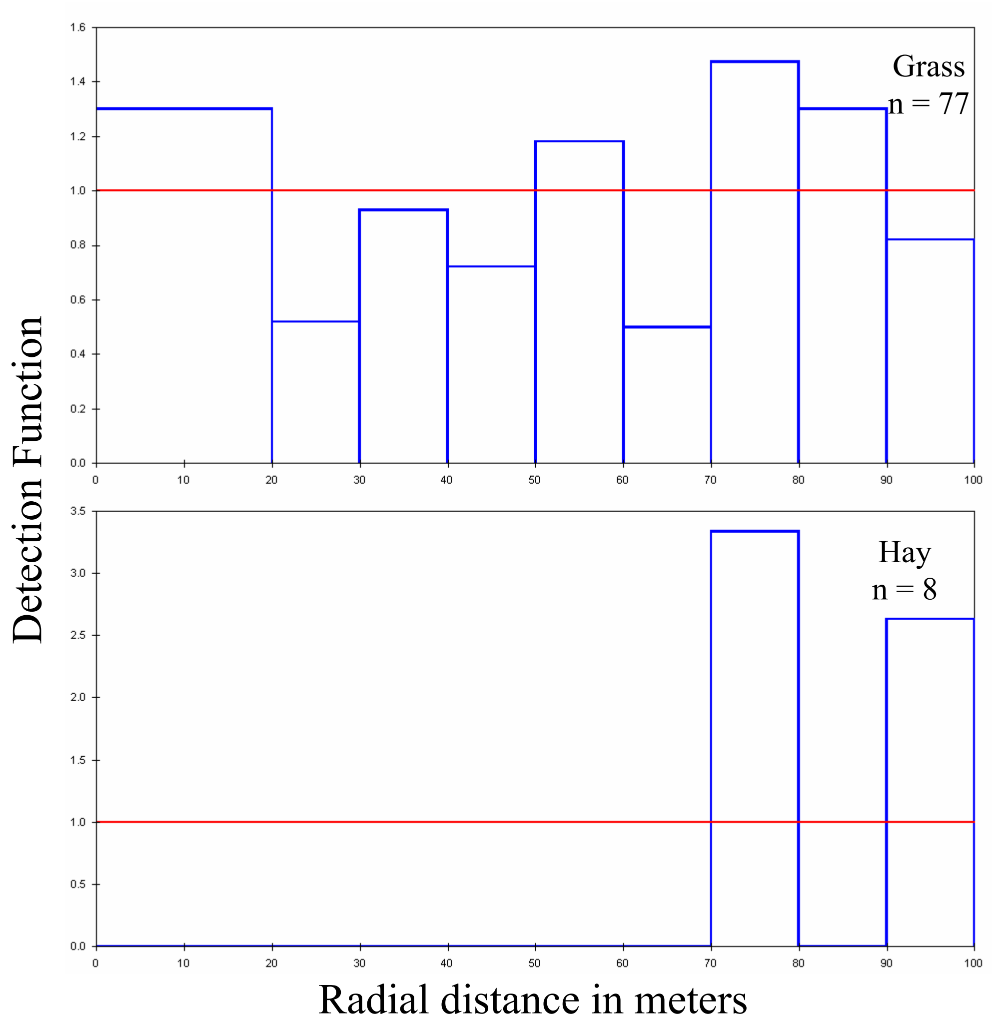
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0.9
0.8
0.7
0.6
0.4
0.3
0.2
0.1
0
10
20
30
40
50
60
70
80
90
100

western meadowlark



Appendix C. Complete NBREG, LOGIT, and ZINB models for each of 9 species for which habitat models were constructed in Chapter 2.

bobolink

NBREG	LL	K	AIC	BIC	ΔBIC	w
Grass400+Forbs+Grasses+Litter+Leaf-Treecover	-1086.994	8	2189.989	2228.857	0.000	1.000
Grass400+Grasses+Forbs-Treecover	-1102.135	6	2216.271	2245.422	-16.565	0.000
Grass400-Trees400+Grasses+Frobs+Leaf+Litter	-1098.574	8	2213.148	2252.016	-23.159	0.000
Leaf+Litter-Treecover+Grass400	-1105.896	6	2223.791	2252.943	-24.086	0.000
Forbs+Grasses+Leaf+Litter-Treecover	-1108.534	7	2231.068	2265.077	-36.220	0.000
Grass400-Trees400+Forbs+Grasses	-1113.799	6	2239.598	2268.750	-39.893	0.000
Grass400-Trees400+Litter+Leaf	-1118.638	6	2249.276	2278.428	-49.571	0.000
Grasses-Treecover	-1131.551	4	2271.102	2290.536	-61.679	0.000
Grasses+Forbs+Leaf+Litter	-1126.981	6	2265.962	2295.113	-66.256	0.000
Grass400-Trees400-Treecover	-1130.817	5	2271.635	2295.928	-67.071	0.000
Leaf+Litter+Treecover	-1133.685	5	2277.370	2301.663	-72.806	0.000
Land	-1143.244	4	2294.487	2313.921	-85.064	0.000
Grasses+Forbs	-1146.705	4	2301.410	2320.845	-91.988	0.000
Litter+Leaf	-1152.259	4	2312.518	2331.952	-103.095	0.000
(-)Treecover	-1170.904	3	2347.807	2362.383	-133.526	0.000
LOGIT	**LL**	**K**	**AIC**	**BIC**	**ΔBIC**	**w**
Grass400+Leaf+Litter+Grasses-Treecover	-566.917	6	1145.834	1174.986	0.000	0.767
Grass400+Leaf+Litter-Treecover	-571.580	5	1153.160	1177.453	-2.467	0.223
Grass400+Grasses+Leaf+Litter	-574.827	5	1159.653	1183.946	-8.960	0.009
Grass400+Leaf+Litter	-580.008	4	1168.016	1187.450	-12.464	0.002
Grasses+Leaf+Litter-Treecover	-581.021	5	1172.042	1196.335	-21.349	0.000
Grass400+Grasses-Treecover	-585.891	4	1179.781	1199.215	-24.229	0.000
Grass400+Grasses	-591.984	3	1189.967	1204.543	-29.557	0.000
Grasses+Leaf+Litter	-589.424	4	1186.848	1206.282	-31.296	0.000
Leaf+Litter-Treecover	-590.219	4	1188.437	1207.871	-32.885	0.000
Leaf+Litter	-599.071	3	1204.141	1218.717	-43.731	0.000
Grass400-Treecover	-601.955	3	1209.910	1224.486	-49.500	0.000
Grass400	-607.742	2	1219.484	1229.201	-54.215	0.000
Grasses+Wetcover-Treecover	-602.156	4	1212.312	1231.746	-56.760	0.000
Grasses	-610.917	2	1225.834	1235.551	-60.565	0.000
BBS+Grasses	-608.424	3	1222.848	1237.424	-62.438	0.000
BBS+Grasses+Wetcover	-606.953	4	1221.906	1241.341	-66.355	0.000
Wetcover-Treecover	-632.617	3	1271.234	1285.810	-110.824	0.000
BBS+Wetcover-Treecover	-629.750	4	1267.499	1286.934	-111.948	0.000
BBS	-638.707	2	1281.413	1291.130	-116.144	0.000
ZINB	**LL**	**K**	**AIC**	**BIC**	**ΔBIC**	**w**
Grass400+Grasses-Treecover; Leaf+Litter	-1059.984	8	2135.969	2174.837	0.000	1.000
Grass400-Trees400; Grass400	-1137.591	6	2287.182	2316.333	-141.496	0.000

clay-colored sparrow

NBREG	LL	K	AIC	BIC	ΔBIC	w_i
BBS+Grass400+Grasses+Shrubs	-369.355	5	748.709	773.002	0.000	0.691
BBS+Grass400+Grasses+Shrubs+Litter	-366.753	6	745.506	774.657	-1.655	0.302
BBS+Grass400+Litter	-377.631	4	763.263	782.697	-9.695	0.005
BBS+Grass400	-382.476	3	770.951	785.527	-12.525	0.001
BBS+Grasses+Shrubs	-383.862	4	775.724	795.159	-22.157	0.000
Grasses+Shrubs+BBS+Litter	-380.723	5	771.447	795.740	-22.738	0.000
BBS+Litter	-396.290	3	798.580	813.155	-40.153	0.000
BBS	-404.977	2	813.954	823.671	-50.669	0.000
Grass400+Grasses+Shrubs+Litter	-400.417	5	810.833	835.126	-62.124	0.000
Grass400_Grasses+Shrub	-405.688	4	819.377	838.811	-65.809	0.000
Grass400+Leaf+Litter	-408.819	4	825.638	845.072	-72.070	0.000
Trees3200+Grass400	-418.201	3	842.403	856.978	-83.976	0.000
Grasses+Shrubs+Litter	-417.633	4	843.267	862.701	-89.699	0.000
Grasses+Shrubs	-424.561	3	855.123	869.699	-96.697	0.000
Leaf+Litter	-432.574	3	871.148	885.724	-112.722	0.000
LOGIT	**LL**	**K**	**AIC**	**BIC**	**ΔBIC**	w_i
BBS+Grass400+Grasses+Shrubs+Litter	-340.476	6	692.952	722.103	0.000	0.982
BBS+Grass400+Grasses+Shrubs	-348.087	5	706.174	730.467	-8.364	0.015
BBS+Grass400+Litter	-353.635	4	715.270	734.704	-12.601	0.002
BBS+Grass400+Litter+Treecover	-351.061	5	712.122	736.415	-14.312	0.001
BBS+Grasses+Shrubs+Litter	-353.760	5	717.519	741.812	-19.709	0.000
BBS+Grasses+Shrubs	-363.136	4	734.273	753.707	-31.604	0.000
BBS+Grass400	-368.765	3	743.529	758.105	-36.002	0.000
BBS+Grass400+Treecover	-365.945	4	739.890	759.324	-37.221	0.000
BBS+Litter	-373.377	3	752.754	767.330	-45.227	0.000
BBS+Litter+Treecover	-371.499	4	750.997	770.431	-48.328	0.000
BBS	-395.826	2	795.652	805.369	-83.266	0.000
BBS+Treecover	-393.780	3	793.561	808.137	-86.034	0.000
Grass400+Trees3200+Grasses+Shrubs+Litter	-398.060	6	808.120	837.271	-115.168	0.000
Grass400+Trees3200+Shrub+Grasses	-410.332	5	830.663	854.956	-132.853	0.000
Grass400+Trees3200+Leaf+Litter	-412.055	5	834.110	858.403	-136.300	0.000
Leaf+Litter+Treecover+Grass400+Trees3200	-408.752	6	829.504	858.655	-136.552	0.000
Grasses+Shrubs+Litter	-420.627	4	849.253	868.688	-146.585	0.000
Grass400+Trees3200+Treecover	-431.083	4	870.166	889.600	-167.497	0.000
Trees3200+Grass400	-435.288	3	876.575	891.151	-169.048	0.000
Shrubs+Grasses	-436.338	3	878.676	893.251	-171.148	0.000
Leaf+Litter+Treecover	-437.389	4	882.778	902.213	-180.110	0.000
Leaf+Litter	-442.656	3	891.312	905.888	-183.785	0.000
Treescover+Wetcover	-469.472	3	944.945	959.520	-237.417	0.000
ZINB	**LL**	**K**	**AIC**	**BIC**	**ΔBIC**	w_i
Grass400+Grasses+Shrub; BBS+Grass400	-338.571	8	693.141	732.010	0.000	1.000

dickcissel

NBREG	LL	df	AIC	BIC	ΔBIC	w_i
BBS+Forbs+Leaf-Wetcover	-319.300	6	650.599	679.751	0.000	0.764
BBS+Leaf+Forbs	-324.147	5	658.293	682.586	-2.835	0.185
BBS+Hay400-Trees400+Forb+Leaf	-319.117	7	652.233	686.243	-6.492	0.030
BBS+Hay400-Trees400+Leaf-Wetcover	-320.062	7	654.123	688.133	-8.382	0.012
BBS+Leaf-Wetcover	-327.514	5	665.029	689.322	-9.571	0.006
BBS+Forbs	-332.225	4	672.449	691.883	-12.132	0.002
BBS+Hay400-Trees400+Leaf	-325.802	6	663.604	692.755	-13.004	0.001
BBS+Leaf-Litter	-331.234	5	672.468	696.761	-17.010	0.000
BBS+Hay400-Wetcover	-334.874	5	679.749	704.042	-24.291	0.000
BBS-Wetcover	-338.914	4	685.827	705.262	-25.511	0.000
BBS+Hay400	-339.026	4	686.051	705.486	-25.735	0.000
BBS	-343.767	3	693.534	708.109	-28.358	0.000
Forbs+Leaf-Wetcover	-355.060	5	720.121	744.413	-64.662	0.000
(-)Trees400+Leaf-Litter-Wetcover	-352.298	6	716.595	745.747	-65.996	0.000
(-)Trees400+Forbs-Wetcover	-356.573	5	723.146	747.438	-67.687	0.000
(-)Trees400+Forbs+Leaf-Litter	-353.398	6	718.796	747.948	-68.197	0.000
Forbs+Wetcover	-360.354	4	728.709	748.143	-68.392	0.000
Leaf-Litter-Wetcover	-357.968	5	725.935	750.228	-70.477	0.000
Trees400+Forbs	-361.656	4	731.311	750.745	-70.994	0.000
Trees400-Litter+Leaf	-358.384	5	726.768	751.061	-71.310	0.000
Forbs+Leaf-Litter	-358.946	5	727.892	752.185	-72.434	0.000
Forbs	-365.918	3	737.837	752.413	-72.662	0.000
Leaf-Litter	-364.793	4	737.587	757.021	-77.270	0.000
(-)Wetcover	-370.940	3	747.879	762.455	-82.704	0.000
Hay400+Grass400-Wetcover	-364.896	5	739.793	764.086	-84.335	0.000
Hay400-Trees400	-369.718	4	747.437	766.871	-87.120	0.000
LOGIT	**LL**	**df**	**AIC**	**BIC**	**ΔBIC**	w_i
BBS+Forbs+VOR	-231.542	4	471.085	490.519	0.000	0.794
BBS+Hay400+Forbs+VOR	-229.503	5	469.006	493.299	-2.780	0.198
BBS+Forbs	-239.782	3	485.565	500.140	-9.621	0.006
BBS+Hay400+Forbs	-237.643	4	483.285	502.720	-12.201	0.002
BBS+Hay400+VOR	-240.156	4	488.313	507.747	-17.228	0.000
BBS+VOR-Litter	-242.518	4	493.036	512.470	-21.951	0.000
BBS+Hay400	-249.514	3	505.028	519.604	-29.085	0.000
BBS	-255.125	2	514.250	523.967	-33.448	0.000
BBS-Wetcover	-252.784	3	511.568	526.143	-35.624	0.000
(-)Trees400+Forbs+VOR	-264.258	4	536.515	555.950	-65.431	0.000
Forbs+VOR	-270.126	3	546.252	560.828	-70.309	0.000
Hay400-Trees400+Forbs	-267.963	4	543.925	563.360	-72.841	0.000
Forbs	-275.447	2	554.894	564.611	-74.092	0.000
Hay400-Trees400+VOR-Litter	-267.682	5	545.364	569.657	-79.138	0.000
VOR-Litter-Wetcover	-272.858	4	553.716	573.150	-82.631	0.000
VOR-Litter	-276.437	3	558.874	573.449	-82.930	0.000
Hay400-Trees400-Wetcover	-274.657	4	557.315	576.749	-86.230	0.000
Hay400-Trees400	-278.454	3	562.908	577.483	-86.964	0.000
(-)Wetcover	-283.498	2	570.996	580.713	-90.194	0.000
ZINB	**LL**	**df**	**AIC**	**BIC**	**ΔBIC**	**wi**
BBS+Leaf-Wetcover+Forbs; BBS	-300.030	8	616.060	654.929	0.000	0.828
BBS+Hay400+Forbs+Leaf; BBS	-301.604	8	619.208	658.077	-3.148	0.172

grasshopper sparrow

NBREG	LL	K	AIC	BIC	ΔBIC	w_i
Grass400-Trees400+Grasses-Treecover-Wetcover	-418.028	7	850.055	884.065	0.000	0.999
Grass400-Trees400+Grasses	-431.432	5	872.865	897.157	-13.092	0.001
Grass400-Trees400-Treecover-Wetcover	-435.377	6	882.753	911.905	-27.840	0.000
Grasses-Treecover-Wetcover	-442.048	5	894.095	918.388	-34.323	0.000
Grass400-Trees400	-449.320	4	906.641	926.075	-42.010	0.000
Grasses	-458.530	3	923.060	937.635	-53.570	0.000
(-)Treecover-Wetcover	-472.560	4	953.120	972.554	-88.489	0.000
LOGIT	**LL**	**K**	**AIC**	**BIC**	**ΔBIC**	**w_i**
Grass400+Grasses-Wetcover	-338.131	4	684.261	703.695	0.000	0.934
Grass400-Trees400+Grasses	-340.813	4	689.626	709.061	-5.366	0.064
Grass400-Wetcover	-347.489	3	700.979	715.554	-11.859	0.002
Grass400-Trees400	-350.829	3	707.657	722.233	-18.538	0.000
Grasses-Treecover-Wetcover	-354.745	4	717.490	736.924	-33.229	0.000
Grasses	-363.849	2	731.697	741.414	-37.719	0.000
(-)Treecover-Wetcover	-375.643	3	757.287	771.862	-68.167	0.000
ZINB	**LL**	**K**	**AIC**	**BIC**	**ΔBIC**	**w_i**
(-)Trees400+Grasses-Treecover-Wetcover; Grass400	-423.910	8	863.819	902.688	0.000	0.999
(-)Trees400-Treecover+Grasses; Grass400-Wetcover	-430.948	8	877.896	916.764	-14.076	0.001
Grass400-Trees400-Treecover; Grasses-Wetcover	-434.367	8	884.734	923.602	-20.914	0.000
(-)Trees400-Treecover-Wetcover; Grass400+Grasses	-435.623	8	887.246	926.114	-23.426	0.000

horned lark

NBREG	LL	K	AIC	BIC	ΔBIC	w_i
(-)Grass400-Forbs-Grasses	-144.807	5	299.613	323.906	0.000	0.879
(-)Forbs-Grasses	-150.217	4	308.433	327.867	-3.961	0.121
(-)Grass400-Leaf-Litter	-153.068	5	316.136	340.429	-16.523	0.000
(-)Leaf-Litter	-158.599	4	325.197	344.632	-20.726	0.000
(-)Grass400-Treecover	-198.384	4	404.768	424.202	-100.296	0.000
(-)Grass400	-203.497	3	412.994	427.570	-103.664	0.000
(-)Treecover	-227.337	3	460.674	475.250	-151.344	0.000
LOGIT	**LL**	**K**	**AIC**	**BIC**	**ΔBIC**	w_i
(-)Grass400-Grasses-Leaf	-150.337	4	308.675	328.109	0.000	0.963
(-)Grasses-Leaf	-157.396	3	320.792	335.368	-7.259	0.026
(-)Grass400-Leaf	-158.156	3	322.311	336.887	-8.778	0.012
(-)Grass400-Grasses	-165.965	3	337.930	352.506	-24.397	0.000
(-)Leaf-Litter	-168.024	3	342.048	356.623	-28.514	0.000
(-)Grasses	-177.133	2	358.266	367.984	-39.875	0.000
(-)Grass400-Treecover	-192.373	3	390.746	405.322	-77.213	0.000
(-)Grass400	-196.314	2	396.627	406.345	-78.236	0.000
(-)Treecover-Wetcover	-220.478	3	446.957	461.533	-133.424	0.000
ZINB	**LL**	**K**	**AIC**	**BIC**	**ΔBIC**	w_i
(-)Grass400-Forbs; (-)Grasses-Leaf	-162.215	7	338.430	372.440	0.000	1.000

LeConte’s sparrow

NBREG	LL	K	AIC	BIC	ΔBIC	wi
BBS+Grass3200+Leaf+Litter	-279.474	6	570.947	600.098	0.000	0.572
BBS+Grass3200	-286.623	4	581.247	600.681	-0.583	0.428
BBS+Leaf+Litter	-300.212	5	610.423	634.716	-34.618	0.000
BBS	-311.855	3	629.710	644.286	-44.188	0.000
BBS+Shrubs	-309.300	4	626.600	646.035	-45.937	0.000
Grass3200+Trees3200+Leaf	-311.513	5	633.027	657.319	-57.221	0.000
Grass3200+Trees3200	-319.990	4	647.979	667.413	-67.315	0.000
Leaf+Litter	-335.773	4	679.547	698.981	-98.883	0.000
Shrubs	-343.814	3	693.627	708.203	-108.105	0.000
Wetcover	-345.223	3	696.446	711.022	-110.924	0.000

LOGIT	LL	K	AIC	BIC	ΔBIC	wi
BBS+Grass3200	-179.630	3	365.260	379.835	0.000	1.000
BBS+Litter	-189.717	3	385.434	400.010	-20.175	0.000
BBS	-193.687	2	391.374	401.091	-21.256	0.000
Grass3200+Trees3200+Hay3200+Leaf+Treecover +Wetcov.	-206.251	7	426.501	460.511	-80.676	0.000
Grass3200+Trees3200+Hay3200+Treecover +Wetcover	-211.076	6	434.151	463.303	-83.468	0.000
Grass3200+Trees3200+Hay3200+Leaf+Litter	-211.267	6	434.533	463.685	-83.850	0.000
Grass3200+Trees3200+Hay3200+Shrubs+Leaf +Litter	-208.499	7	430.997	465.007	-85.172	0.000
Grass3200+Hay3200+Trees3200+Shrubs	-216.046	5	442.092	466.385	-86.550	0.000
Grass3200+Hay3200+Trees3200	-220.116	4	448.231	467.665	-87.830	0.000
Leaf+Treecover	-240.314	3	486.629	501.204	-121.369	0.000
Shrubs+Leaf+Litter	-237.156	4	482.312	501.746	-121.911	0.000
Shrubs+Leaf+Litter+Treecover	-234.537	5	479.075	503.368	-123.533	0.000
Leaf+Litter	-243.220	3	492.439	507.015	-127.180	0.000
Shrubs	-246.875	2	497.751	507.468	-127.633	0.000
Treecover+Wetcover	-244.572	3	495.143	509.719	-129.884	0.000

ZINB	LL	K	AIC	BIC	ΔBIC	wi
Grass3200; BBS	-242.594	5	495.189	519.482	0.000	0.444
Grass3200+Litter; BBS	-239.329	6	490.657	519.809	-0.327	0.377
Grass3200+Leaf; BBS	-240.076	6	492.153	521.304	-1.822	0.179
BBS; Grass3200	-297.061	5	604.121	628.414	-108.932	0.000

savannah sparrow

NBREG	LL	K	AIC	BIC	ΔBIC	wi
BBS+Grass3200-Forbs-Treecover	-762.027	6	1536.055	1565.206	0.000	0.921
BBS+Forbs-Treecover	-767.907	5	1545.815	1570.108	-4.902	0.079
BBS+Grass3200+Hay3200-Treecover	-773.460	6	1558.919	1588.071	-22.865	0.000
BBS-Treecover	-781.277	4	1570.554	1589.988	-24.782	0.000
BBS+Forbs	-789.738	4	1587.476	1606.911	-41.705	0.000
BBS+Grass3200+Hay3200	-795.046	5	1600.092	1624.385	-59.179	0.000
BBS	-804.483	3	1614.966	1629.542	-64.336	0.000
Grass3200+Hay3200+Forbs-Treecover	-808.258	6	1628.515	1657.667	-92.461	0.000
Grass3200+Hay3200+Forbs+Leaf-Treecover	-805.250	7	1624.501	1658.511	-93.305	0.000
Grass3200+Hay3200-Treecover	-817.548	5	1645.095	1669.388	-104.182	0.000
Grass3200+Hay3200-Treecover+Leaf	-814.776	6	1641.551	1670.703	-105.497	0.000
Grass3200+Hay3200+Forbs	-819.717	5	1649.435	1673.728	-108.522	0.000
Grass3200+Hay3200+Forbs	-819.717	5	1649.435	1673.728	-108.522	0.000
Grass3200+Hay3200+Forbs+Leaf	-817.360	6	1646.719	1675.871	-110.665	0.000
Grass3200+Hay3200	-830.084	4	1668.167	1687.602	-122.396	0.000
Grass3200+Hay3200+Leaf	-827.974	5	1665.947	1690.240	-125.034	0.000
Forbs+Leaf-Treecover	-835.011	5	1680.022	1704.315	-139.109	0.000
Forbs-Treecover	-840.053	4	1688.106	1707.540	-142.334	0.000
Leaf-Treecover	-844.298	4	1696.595	1716.029	-150.823	0.000
(-)Treecover	-848.935	3	1703.871	1718.446	-153.240	0.000
Forbs+Leaf	-846.936	4	1701.873	1721.307	-156.101	0.000
Forbs	-851.132	3	1708.263	1722.839	-157.633	0.000
Leaf	-857.397	3	1720.795	1735.370	-170.164	0.000
LOGIT	**LL**	**K**	**AIC**	**BIC**	**ΔBIC**	**wi**
BBS+Grasses+Forbs-Treecover	-496.720	5	1003.440	1027.733	0.000	1.000
BBS+Grasses+Forbs	-509.231	4	1026.463	1045.897	-18.164	0.000
BBS-Treecover	-529.009	3	1064.017	1078.593	-50.860	0.000
BBS+Hay3200-Treecover	-526.873	4	1061.745	1081.179	-53.446	0.000
BBS	-541.785	2	1087.571	1097.288	-69.555	0.000
BBS+Grass3200+Hay3200	-538.940	3	1083.879	1098.455	-70.722	0.000
Grass3200+Hay3200+Grasses+Forbs-Treecover	-558.597	6	1129.194	1158.345	-130.612	0.000
Grass3200+Hay3200+Grasses+Forbs	-562.418	5	1134.835	1159.128	-131.395	0.000
Grasses+Forbs-Treecover	-574.232	4	1156.464	1175.898	-148.165	0.000
Forbs	-578.357	3	1162.714	1177.290	-149.557	0.000
Grass3200+Hay3200-Treecover	-575.987	4	1159.974	1179.408	-151.675	0.000
Grass3200+Hay3200+Leaf-Treecover	-572.727	5	1155.453	1179.746	-152.013	0.000
Grass3200+Hay3200	-580.190	3	1166.380	1180.955	-153.222	0.000
Grass3200+Hay3200+Leaf	-577.420	4	1162.840	1182.275	-154.542	0.000
Leaf-Treecover	-592.979	3	1191.957	1206.533	-178.800	0.000
Leaf	-597.831	2	1199.661	1209.379	-181.646	0.000
(-)Treecover	-597.934	2	1199.867	1209.584	-181.851	0.000
ZINB	**LL**	**K**	**AIC**	**BIC**	**ΔBIC**	**wi**
Grass3200+Forbs-Treecover; BBS	-799.675	7	1613.349	1647.359	0.000	1.000

sedge wren

NBREG	LL	K	AIC	BIC	ΔBIC	wi
Grass400+Grasses+Leaf+Litter	-852.979	6	1717.959	1747.110	0.000	0.359
Grass400+Grasses+Leaf+Litter-Treecover	-849.659	7	1713.317	1747.327	-0.217	0.322
Grass400+Leaf+Litter-Treecover	-853.640	6	1719.280	1748.432	-1.322	0.185
Grass400+Leaf+Litter	-857.398	5	1724.797	1749.090	-1.980	0.133
Grasses+Leaf+Litter-Treecover	-873.915	6	1759.830	1788.982	-41.872	0.000
Grasses+Leaf+Litter	-878.818	5	1767.636	1791.929	-44.819	0.000
Leaf+Litter-Treecover	-881.246	5	1772.492	1796.785	-49.675	0.000
Leaf+Litter	-886.757	4	1781.515	1800.949	-53.839	0.000
BBS+Grass400+Grasses	-905.730	5	1821.460	1845.753	-98.643	0.000
BBS+Grass400+Grasses+Wetcover-Treecover	-900.964	7	1815.928	1849.938	-102.828	0.000
Grass400+Grasses+Wetcover	-909.204	5	1828.407	1852.700	-105.590	0.000
Grass400+Grasses	-913.236	4	1834.472	1853.906	-106.796	0.000
BBS+Grass400	-922.366	4	1852.732	1872.167	-125.057	0.000
Grass400	-927.828	3	1861.655	1876.231	-129.121	0.000
Grass300+Wetcover	-924.785	4	1857.571	1877.005	-129.895	0.000
BBS+Grass400+Wetcover-Treecover	-918.235	6	1848.470	1877.622	-130.512	0.000
BBS+Grasses+Wetcover-Treecover	-929.247	6	1870.493	1899.644	-152.534	0.000
Grasses+Wetcover-Treecover	-937.378	5	1884.755	1909.048	-161.938	0.000
Grasses	-945.895	3	1897.790	1912.366	-165.256	0.000
BBS	-963.673	3	1933.346	1947.922	-200.812	0.000
BBS+Wetcover-Treecover	-957.203	5	1924.406	1948.698	-201.588	0.000
Wetcover-Treecover	-962.595	4	1933.190	1952.624	-205.514	0.000
LOGIT	**LL**	**K**	**AIC**	**BIC**	**ΔBIC**	**wi**
Grass400+Leaf+Litter+Wetcover	-447.571	5	905.142	929.435	0.000	0.918
Grass400+Leaf+Litter	-454.045	4	916.089	935.523	-6.088	0.044
Grass400+Grasses_Shrub+Leaf+Litter+Wetcover	-443.900	7	901.800	935.810	-6.375	0.038
Grasses+Shrubs+Leaf+Litter+Wetcover	-459.506	6	931.011	960.162	-30.727	0.000
Leaf+Litter+Wetcover	-467.371	4	942.742	962.176	-32.741	0.000
Grasses+Shrubs+Leaf+Litter	-466.556	5	943.112	967.405	-37.970	0.000
Leaf+Litter	-474.062	3	954.124	968.700	-39.265	0.000
Grass400+Grasses+Shrubs+Wetcover	-492.671	5	995.343	1019.636	-90.201	0.000
Grass400+Wetcover	-512.811	3	1031.621	1046.197	-116.762	0.000
Grass400+Grasses+Shrubs	-511.187	4	1030.374	1049.808	-120.373	0.000
Grasses+Shrubs+Wetcover	-512.160	4	1032.320	1051.755	-122.320	0.000
BBS+Grass400+Grasses+Shrubs	-509.143	5	1028.285	1052.578	-123.143	0.000
Grass400	-532.037	2	1068.073	1077.790	-148.355	0.000
BBS+Grass400	-529.160	3	1064.320	1078.896	-149.461	0.000
BBS+Grasses+Shrub	-529.018	4	1066.036	1085.470	-156.035	0.000
Grasses+Shrubs	-532.470	3	1070.940	1085.515	-156.080	0.000
Wetcover	-549.019	2	1102.037	1111.755	-182.320	0.000
BBS+Wetcover	-545.877	3	1097.754	1112.330	-182.895	0.000
BBS	-566.071	2	1136.142	1145.859	-216.424	0.000
ZINB	**LL**	**K**	**AIC**	**BIC**	**ΔBIC**	**wi**
Grass400+Leaf; Grass400+Leaf+Litter						

western meadowlark

LOGIT	LL	K	AIC	BIC	ΔBIC	w_i
BBS+Grass800+Hay800-Trees400+Grasses-VOR	-346.232	7	706.465	740.474	0.000	0.722
BBS+Grass800+Hay800-Trees400+Grasses-VOR - Treecover	-343.765	8	703.530	742.399	-1.925	0.270
BBS+Grass800+Hay800-Trees400+Grasses	-353.283	6	718.567	747.718	-7.244	0.019
BBS+Grasses-VOR-Treecover	-358.949	5	727.897	752.190	-11.716	0.002
BBS+Grass800+Hay800-Trees400-VOR	-356.140	6	724.280	753.432	-12.958	0.001
BBS+Grass800+Hay800-Trees400	-360.020	5	730.040	754.333	-13.859	0.001
BBS+Grasses-VOR	-364.633	4	737.266	756.701	-16.227	0.000
Grass800+Hay800-Treecover+Grasses-VOR - Treecover	-355.427	7	724.853	758.863	-18.389	0.000
Grass800+Hay800-Trees400+Grasses-VOR	-358.899	6	729.799	758.950	-18.476	0.000
BBS+Grasses-Treecover	-366.023	4	740.047	759.481	-19.007	0.000
BBS+Grasses	-370.891	3	747.782	762.358	-21.883	0.000
Grass800+Hay800-Trees400+Grasses	-367.028	5	744.056	768.349	-27.875	0.000
Grass800+Hay800-Trees400+Grasses-Treecover	-364.466	6	740.932	770.083	-29.609	0.000
BBS-Treecover	-376.189	3	758.378	772.954	-32.480	0.000
BBS-VOR-Treecover	-373.481	4	754.962	774.397	-33.923	0.000
Grass800+Hay800-Trees400+VOR	-370.256	5	750.513	774.806	-34.332	0.000
BBS	-380.715	2	765.431	775.148	-34.674	0.000
Grass800+Hay800-Trees400-VOR-Treecover	-367.171	6	746.342	775.493	-35.019	0.000
Grass800+Hay800-Trees400	-374.575	4	757.150	776.585	-36.111	0.000
BBS-VOR	-378.167	3	762.335	776.911	-36.436	0.000
Grass800+Hay800-Trees400-Treecover	-371.932	5	753.865	778.158	-37.684	0.000
Grasses-VOR-Treecover	-375.808	4	759.616	779.050	-38.576	0.000
Grasses-VOR	-383.652	3	773.304	787.880	-47.406	0.000
Grasses-Treecover	-384.259	3	774.518	789.094	-48.620	0.000
Grasses	-390.837	2	785.675	795.392	-54.918	0.000
(-)Treecover	-396.782	2	797.564	807.282	-66.808	0.000
(-)VOR-Treecover	-394.023	3	794.047	808.623	-68.148	0.000
(-)VOR	-400.298	2	804.595	814.312	-73.838	0.000