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Multi-Scale Response of Upland Birds to Targeted Agricultural Conservation

Kristine Oswald Evans

MULTI-SCALE RESPONSE OF UPLAND BIRDS TO TARGETED AGRICULTURAL CONSERVATION

By

Kristine Oswald Evans

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By

Kristine Oswald Evans

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By

Kristine Oswald Evans

Approved:

Loren W. Burger, Jr.
Professor of Wildlife Ecology and Management
Associate Director Forest and Wildlife Research Center and Mississippi Agricultural and Forestry Experiment Station
(Director of Dissertation)

Samuel K. Riffell
Associate Professor of Wildlife Ecology and Management
(Co-director of Dissertation)

Mark D. Smith
Assistant Professor/Extension Specialist
(Committee Member)

Guiming Wang
Assistant Professor of Wildlife Ecology and Management
(Committee Member)

Eric D. Dibble
Professor of Aquatic Sciences
(Graduate Coordinator)

Bruce D. Leopold
Professor and Department Head of Wildlife, Fisheries and Aquaculture

George M. Hopper
Dean of the College of Forest Resources

Name: Kristine Oswald Evans

Date of Degree: May 11, 2012

Institution: Mississippi State University

Major Field: Forest Resources (Wildlife Ecology)

Major Professor: Loren W. Burger, Jr.

Title of Study: MULTI-SCALE RESPONSE OF UPLAND BIRDS TO TARGETED
AGRICULTURAL CONSERVATION

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Candidate for Degree of Doctorate of Philosophy

As human populations rise exponentially, agricultural production systems must be adapted to sustain ecosystem function. Government administered agricultural conservation programs may actualize greater gains in ecosystem services, including wildlife population gains, if conservation practices designed to target specific environmental outcomes are implemented strategically in agricultural landscapes. I evaluated multi-scale, multi-species, and multi-season avian population responses to a targeted native herbaceous buffer practice (CP33: Habitat Buffers for Upland Birds) under the continuous sign-up Conservation Reserve Program administered by the U.S. Department of Agriculture. CP33 is the first conservation practice targeted directly to support habitat and population recovery objectives of a national wildlife conservation initiative (Northern Bobwhite Conservation Initiative). I coordinated breeding season, fall, and winter point transect surveys for northern bobwhite (*Colinus virginianus*), priority early-succession, and overwintering birds on ≈1,150 buffered and non-buffered fields in 14 states (10 ecoregions) from 2006-2009. I also assessed northern bobwhite-landscape associations within each ecoregion to determine effects of landscape structure on observed northern bobwhite abundances. Breeding season and autumn northern bobwhite densities were 60-74% and 52% greater, respectively, over all survey points in the near term (1-4 years post-establishment). However, breeding season and autumn response and associations between northern bobwhite abundance and landscape structure exhibited substantial regional variation, suggesting northern bobwhite conservation and management should be implemented on a regional basis. Breeding season densities of dickcissel (*Spiza americana*) and field sparrow (*Spizella pusilla*) were up to 190% greater on buffered fields, whereas overwintering densities of several Emberizid sparrow species were up to 2,707% greater on buffered fields. Species sensitive to patch area or those requiring vegetation structure different from that provided by buffers exhibited limited, but regionally and annually variable responses to buffered habitats. Increased bird densities of several species in several seasons suggest wildlife-friendly farming practices delivered strategically and requiring minimal change in primary land use can benefit species across broad landscapes when conservation practices are targeted toward specific recovery objectives. Targeted conservation systems combining multiple conservation practices to provide an array of ecosystem services may be a mechanism for meeting multifarious conservation objectives and enhancing biodiversity in agricultural landscapes.

Key words: agricultural conservation, *Colinus virginianus*, conservation buffers, grassland birds, northern bobwhite, targeted conservation

DEDICATION

I dedicate this dissertation to my amazingly patient husband, Brian Keith Evans and to my 2 beautiful daughters, Summer Marie and Brianna Kristine. You are my heart and soul.

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CHAPTER I

INTRODUCTION

Increasing production demands and an intensified agricultural matrix necessitate innovative conservation to enhance working landscapes such that a broad suite of ecological services are provided (Tilman et al. 2002, Benton 2007). Wildlife conservationists, in particular, face a difficult task in that the intrinsic value of wildlife is often secondary compared to financial profits from agricultural production (Burger 2006). However, agricultural producers and other private entities hold the single greatest potential for persistence and restoration of many wildlife populations in the United States (Burger 2006). Conversion of native grasslands to cropland and modern intensive cropping practices are key factors contributing to grassland bird species declines in North America (O'Conner et al. 1999, Murphy 2003) and Europe (Fuller et al. 1995, Siriwardena et al. 1998, Chamberlain et al. 2000, Gates and Donald 2000, Donald et al. 2006), producing an acute global threat to grassland bird populations (Green et al. 2005, Robertson and Swinton 2005).

In the mid-1900's, advances in mechanization and technology coupled with public policy promoting commodity production, produced large-scale changes in the agricultural matrix (Ormerod and Watkinson 2000). In the latter half of the 20th century, broad-scale population declines of grassland and other early-succession bird species in response to net habitat losses became evident (Samson and Knopf 1994, Warner 1994, Chamberlain et al. 2000, Gates and Donald 2000, Brennan and Kuvlesky 2005). The

North American Breeding Bird Survey [BBS] provided the first indication that grassland obligate and early-succession species in the United States were experiencing severe declines (Peterjohn 2003). Since 1966, 43% of grassland and 36% of scrub-successional bird species have declined significantly in the U.S. (Sauer et al. 2011). Among these, some of the most severe rates of annual declines are in populations of northern bobwhite (*Colinus virginianus*) (3.8%), eastern meadowlark (*Sturnella magna*) (3.1%), grasshopper sparrow (*Ammodramus savannarum*) (2.7%) and field sparrow (*Spizella pusilla*) (2.3%; Sauer et al. 2011).

Decline of northern bobwhite (hereafter, bobwhite), a socioeconomically valuable game bird species, is of particular concern (Burger et al. 2006*a*). Bobwhite populations have been impacted negatively by agricultural intensification, reforestation and industrial silviculture, urbanization, replacement of native communities with exotic forage grasses, and fire exclusion (Klimstra 1982, Brennan 1991, Burger et al. 1999, Murphy 2003). Ironically, management to maintain the species' persistence has been well documented for 50-80 years (e.g., Stoddard 1931, Rosene 1969), but bobwhite populations continue to decline sharply (Brennan 1991, Sauer et al. 2011).

The National Bobwhite Conservation Initiative [NBCI] is a habitat-based recovery plan to restore bobwhite populations to sustainable densities (Dimmick et al. 2002, National Bobwhite Technical Committee 2011). Achieving the original NBCI's population recovery goals would require addition of 2,770,922 coveys on 33 million ha (~10%) of the bobwhite's 318 million ha range (Dimmick et al. 2002). Dimmick et al. (2002) suggested most (~80%) of population recovery could be achieved on agricultural lands through alteration of crop and grazing lands management. Similarly, the NBCI revision suggests appropriate management in prioritized landscapes has potential to add

2.4 million bobwhite coveys to the current population (National Bobwhite Technical Committee 2011). These recovery goals and measures necessary to achieve them could be accomplished partially by realizing potential wildlife benefits of USDA Farm Bill conservation programs and practices (Burger et al. 2006*a*).

U. S. Agricultural Policy and Wildlife Conservation

The role of agricultural policy is paramount in modern economies of the U.S. (Burger et al. 2006*a*) and Europe (Donald et al. 2006), and ultimately directs effects that agriculture has on the natural environment. In the U.S., commodity programs created under Farm Bill legislation and administered by the United States' Department of Agriculture [USDA] have been the primary source of federal subsidies for commodity production since 1933 (Gray 2009). However, Farm Bill legislation has diversified in recent decades and now includes measures to enhance soil and water quality and provide wildlife habitat. The Conservation Reserve Program [CRP] was included in the first Farm Bill conservation title (Food Securities Act of 1985) with intent of offsetting excess commodity production while concomitantly reducing soil erosion (Burger 2005). CRP is an incentives-driven program that provides annual payments and cost share to private landowners for retirement and management of "highly erodible" and other sensitive lands. Although wildlife habitat was only included recently in statutory objectives of CRP (U. S. Department of Agriculture 2004*a*), since its inception, CRP has contributed to enhancement of wildlife habitat on private lands throughout the U.S. (Carmichael 1997, Classen et al. 2001).

Cropland diversion programs like CRP, replace cropped land with non-cropped herbaceous or forest communities, which may provide suitable habitat for many at-risk species (Koford 1999, O'Conner et al. 1999, Clawson and Rotella 2005, Gill et al. 2006) and may help slow or reverse declines of several grassland bird species (Igl and Johnson 1999, Koford 1999, Haufler 2005, Herkert 2006, Veech 2006). CRP has increased abundance and reproductive rates of grassland birds compared to croplands (King and Savidge 1995, Best et al. 1997, Farrand and Ryan 2005, Johnson 2005). CRP fields may also provide year-round habitat for grassland and early-succession species that would not otherwise be available in intensive agricultural landscapes (Johnson and Schwartz 1993, Johnson and Igl 1995, Best et al. 1998, Ryan et al. 1998, Johnson 2000). However, grassland bird response to CRP varies not only by species, but also by stand age, climate, vegetation structure (Johnson 2005, Farrand and Ryan 2005, Riffell et al. 2008), practice type, and management regime (Delisle and Savidge 1997; Burger 2000, 2005; Burger et al. 2006*a*).

Conservation Buffers

Uncultivated field margins and fallow areas have been a component of agricultural landscapes throughout history and their value as wildlife habitat has long been recognized (Stoddard 1931, Potts 1986). However, intentional use of linear strips of vegetation to address specific resource concerns (e.g., to trap soil and chemical runoff) as a feature of designed landscapes has become increasingly widespread (Lovell and Sullivan 2006). Commonly called conservation buffers, these vegetative strips also have potential to enhance biodiversity (Lovell and Sullivan 2006) and provide remnant patches of natural habitat within the agricultural matrix (Burger 2005). Conservation buffers were first incentivized broadly in the 1996 Farm Bill following establishment of the Continuous Conservation Reserve Program [CCRP]. CCRP was designed to encourage establishment of conservation cover on select environmentally-sensitive lands, and compared to the general signup CRP program, provides additional incentives and automatic acceptance of offered eligible lands. Vegetative conservation buffers (e.g., filter strips, riparian forest buffers, grassed waterways) are among the primary practices implemented under CCRP (Clark and Reeder 2005). Linear habitats, like those implemented through CCRP, increase breeding, fall, and winter bobwhite and songbird abundances compared to standard row-crop agriculture (Marcus et al. 2000; Puckett et al. 2000; Palmer et al. 2005; Smith et al. 2005*a*, *b*; Riddle et al. 2008). However, concerns about inadequate width (Major et al. 1999; Conover et al. 2007, 2009, 2011), decreased reproductive output (Ryan et al. 1998, Best 2000, Clark and Reeder 2005, Henningsen and Best 2005) and sensitivity to patch size (see review in Ribic et al. 2009) are raised frequently. Effects these factors have on wildlife response depends largely on design and management of strip-cover habitats, composition of surrounding landscape, and species-specific response to vegetation structure (Best 2000).

CP33 – Habitat Buffers for Upland Birds

Continuous CRP Conservation Practice 33 [CP33], Habitat Buffers for Upland Birds was initiated in 2004 by the USDA Farm Service Agency [FSA] as part of the Bush administration's "Presidential Bobwhite Habitat Initiative" (U. S. Department of Agriculture 2004*b*). CP33 offers landowner incentives to establish a non-crop herbaceous community along crop field edges to provide habitat for bobwhite and other upland birds (U. S. Department of Agriculture 2004*b*). CP33 exemplifies progressive conservation in working landscapes because it allows landowners to remove lessproductive field margins from production while economically enhancing net whole-field returns (Barbour et al. 2007, Stamps et al. 2008, McConnell 2011).

FSA originally allocated 101,172 CP33 ha to 35 states within the bobwhite range to establish 9-37 m upland habitat buffers for 10-year contracts (U. S. Department of Agriculture 2004*b*). Acreage allocation was increased to 141,640 CP33 ha in 2010 (U.S. Department of Agriculture 2010). Eligibility requirements include cropland with potential to establish bobwhite populations, as well as meeting CRP cropping history and eligibility criteria. CP33 buffer establishment requires initial site preparation followed by either re-establishment through natural succession or planting to native warm-season grass, legume, and forb mixtures with a limited shrub/tree component (U. S. Department of Agriculture 2004*b*). CP33 also requires annual disturbance (disking, burning, or herbicide application) beginning contract year 4 on 1/3 of buffer acreage to set back succession and maintain early-succession habitat (U. S. Department of Agriculture 2004*b*). Incentives offered for eligible participants include $247/ha Signup Incentive Payment, 50% cost-share and 40% Practice Incentive Payment for CP33 establishment, annual rental payments based on county-specific soil rental rates, Maintenance Incentive Payment of up to $12.35/ha, and up to 50% cost-share reimbursement to perform mid-contract management (U. S. Department of Agriculture 2004*b*). Sign-up for CP33 initiated October 1, 2004, and buffer establishment commenced during the 2005 growing season with continuous sign-up based on state-level acreage caps. There are currently over 96,552 ha enrolled in CP33 (U. S. Department of Agriculture 2011; Fig. 1.1).

There are several components inimitable to design and implementation of the CP33 practice. Because wildlife habitat and not water quality is the goal of CP33, entire field boundaries, and not simply down-slope or drainage field edges, may be enrolled.

CP33 is also the first federal conservation practice designed specifically to achieve habitat goals of a large-scale wildlife conservation initiative, the NBCI. Finally, because species-specific targeting is novel among federal conservation practices, FSA mandated that states allocated CP33 acreage monitor bobwhite and priority upland bird species response to CP33 (U. S. Department of Agriculture 2004*b*). Monitoring results would be used to evaluate practice effectiveness and be ultimately the deciding factor in continuation or expansion of the CP33 practice.

National CP33 Monitoring Program

Monitoring is critical to evaluate successes or failures of conservation provisions, make informed management plans, and provide public accountability for government funded initiatives (Ellingson and Lukacs 2003, Bart et al. 2004, Lyons et al. 2008, Sauer and Knutson 2008). Most proponents of monitoring stress the need to coordinate large-scale, long-term monitoring programs and collate smaller monitoring efforts to draw inference across a species' range (Peterjohn 2003, Ruth et al. 2003, Bart et al. 2004, Winter et al. 2005, Evans et al. 2011). When the CP33 practice was initiated, FSA called for development and implementation of state-level monitoring plans in states allocated the most acreage to "demonstrate that CP33 practices have a positive effect for upland birds" (U. S. Department of Agriculture 2004*b, c*). FSA required that all 35 states allocated CP33 acreage conduct monitoring of bobwhite and other upland songbird response to practice establishment (U. S. Department of Agriculture 2004*b*). FSA charged the Research Committee of the Southeast Quail Study Group [SEQSG] with development of a standard protocol to coordinate monitoring efforts among 35 states (Burger et al. 2006*b*). However, in realizing potential limitations of a practice-wide monitoring program, SEQSG recommended intensive sampling in 20 states containing 95% of CP33 acreage allocation with extrapolation or some lesser degree of sampling in the remaining 15 peripheral states (U. S. Department of Agriculture 2004*c*; Table 1.1). A national CP33 monitoring protocol was developed subsequently by SEQSG and Southeast Partners in Flight [PIF] in 2006, and administered by Mississippi State University (Burger et al. 2006*b*). The coordinated national monitoring effort included ultimately 14 of 20 states required to conduct CP33 monitoring, representing 80% of actual enrolled acreage (U.S. Department of Agriculture 2011; Table 1.1). The remaining 6 states implemented an alternative monitoring protocol, did not have enough CP33 enrollment acreage to warrant monitoring, or were incapable logistically of implementing monitoring.

Study area and sampling design

Using a multi-stage sampling approach, FSA personnel selected randomly 50 CP33 contracts from the pool of all CP33 contracts available in each of 14 participating states as of 31 December 2005 (Burger et al. 2006*b*). A subset of 40 contracts per state was then selected from the initial pool of contracts (Smith et al. 2009). Within that subset of contracts, 1-3 CP33 buffered fields were selected randomly per contract for sampling (Burger et al. 2006*b*). Multiple fields within a single contract were selected only if fields were >500 m apart to avoid detecting the same birds on multiple points. Survey points were then established along the exterior edge and linear midpoint of selected buffers (Burger et al. 2006*b*). Assessment of buffered fields prior to buffer establishment was impracticable; therefore, in lieu of a pre- and post-treatment approach, a comparative approach was taken. Under the comparative approach, non-buffered reference row-crop fields exhibiting similar cropping systems were selected 1-3 km from each respective buffered field (Burger et al. 2006*b*). Under this sampling design, a minimum of 80 fields (40 CP33 buffered, 40 non-buffered) were sampled in each state annually (Fig. 1.2).

As evaluation and conservation of bird communities beyond local scales is a key goal of bird conservation initiatives (Dimmick et al. 2002, N. A. Waterfowl Management Plan 2004, N. A. Bird Conservation Initiative 2007), one of my primary objectives was to understand variation in effects of targeted upland habitat buffers on bird densities among distinct ecological regions. Bird Conservation Regions [BCR] are defined ecological regions with similar habitat structure and land use that support similar bird communities (N. A. Bird Conservation Initiative 2000). Selected survey points were located in 10 BCRs, with most located in one of 5 BCRs (Central Mixed-grass Prairie [BCR 19], Eastern Tallgrass Prairie [BCR 22], Central Hardwoods [BCR 24], Mississippi Alluvial Valley [BCR 26], Southeastern Coastal Plain [BCR 27]; Fig. 1.2).

Research Objectives

Native herbaceous cover may be a limiting factor for early-succession wildlife in U.S. agricultural landscapes. If limiting, then restoration of native herbaceous habitats in agricultural landscapes may elicit a disproportionate ecological response by early-succession species, whereby small changes (5-7%) in habitat amount may engender large population effects. However, ecological effects of linear patches of native herbaceous cover and interrelationships among wildlife abundance, linear habitat patches and landscape structure are understood poorly in these landscapes, particularly at large spatial scales and over long temporal periods. From a broader conservation design perspective, biodiversity value of conservation in working agricultural landscapes (e.g., wildlife-friendly farming) is currently under scrutiny (Green et al. 2005, Godfrey 2011, Phalan et al. 2011). The long-term and large-scale data set provided by the national CP33 monitoring program affords opportunity to evaluate many aspects of bobwhite and upland songbird response to implementation of linear patches of native herbaceous cover provided by the CP33 practice. Given these opportunities, my research objectives included assessment of:

1) densities of male breeding northern bobwhite and priority upland songbirds on CP33 buffered vs. non-buffered row-crop fields at multiple spatial scales;

2) multi-scale associations of regional breeding bobwhite abundances with characteristics of landscape composition and configuration in agricultural landscapes;

3) densities of fall northern bobwhite coveys on CP33 buffered vs. non-buffered row-crop fields at multiple spatial scales; and

4) densities, species richness, diversity, and Total Avian Conservation Value of overwintering songbirds on CP33 buffered vs. non-buffered row-crop fields.

Table 1.1 Distribution of breeding season, fall, and winter bird surveys on CP33 buffered vs. non-buffered fields across 14 states, 2006-2009.

	CP33 monitoring (SEQSG protocol)	CP33 monitoring (other protocol)
2006 breeding season	GA, IA, IL, IN, KY, MO, MS, OH, SC, TN, TX	
2006-2008 fall covey counts	AR, GA, IA, IL, IN, KY, MO, MS, NC, OH, SC, TN, TX	KS, OK
2007-2009 breeding season	AR, GA, IA, IL, IN, KY, MO, MS, NC, NE, OH, SC, TN, TX	
2007 winter transects	AR, KY, MS	
2008 winter transects	KY, MS	

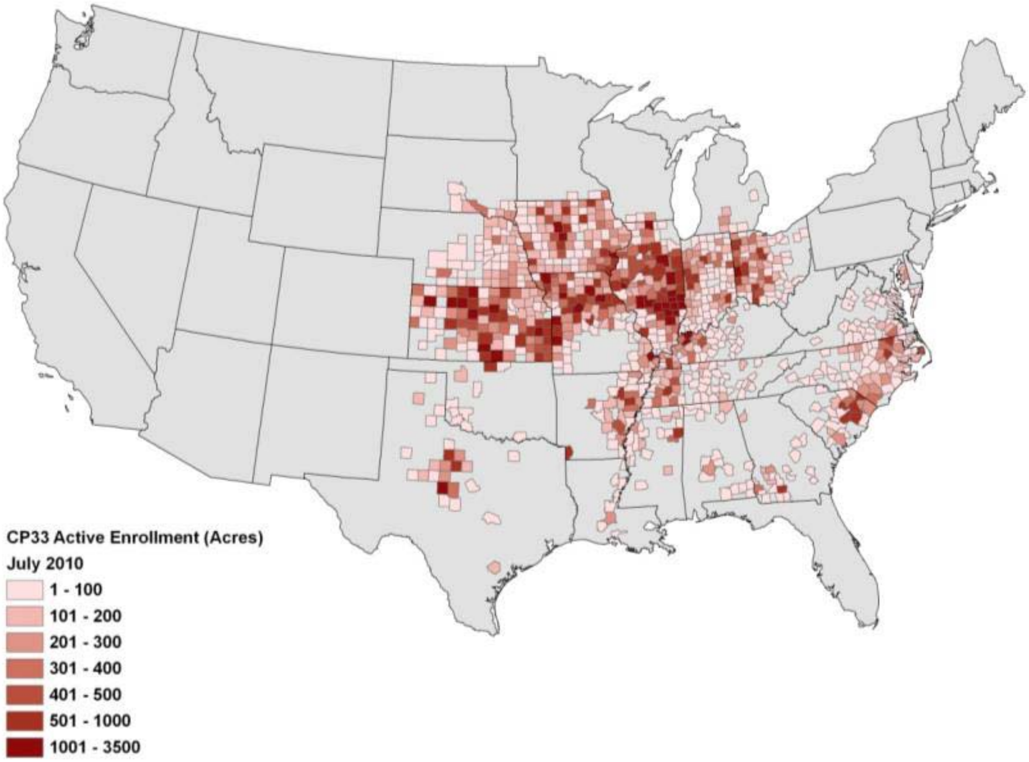

Figure 1.1 National distribution of Continuous Conservation Reserve Program conservation practice CP33, Habitat Buffers for Upland Birds acreage, July 2010.

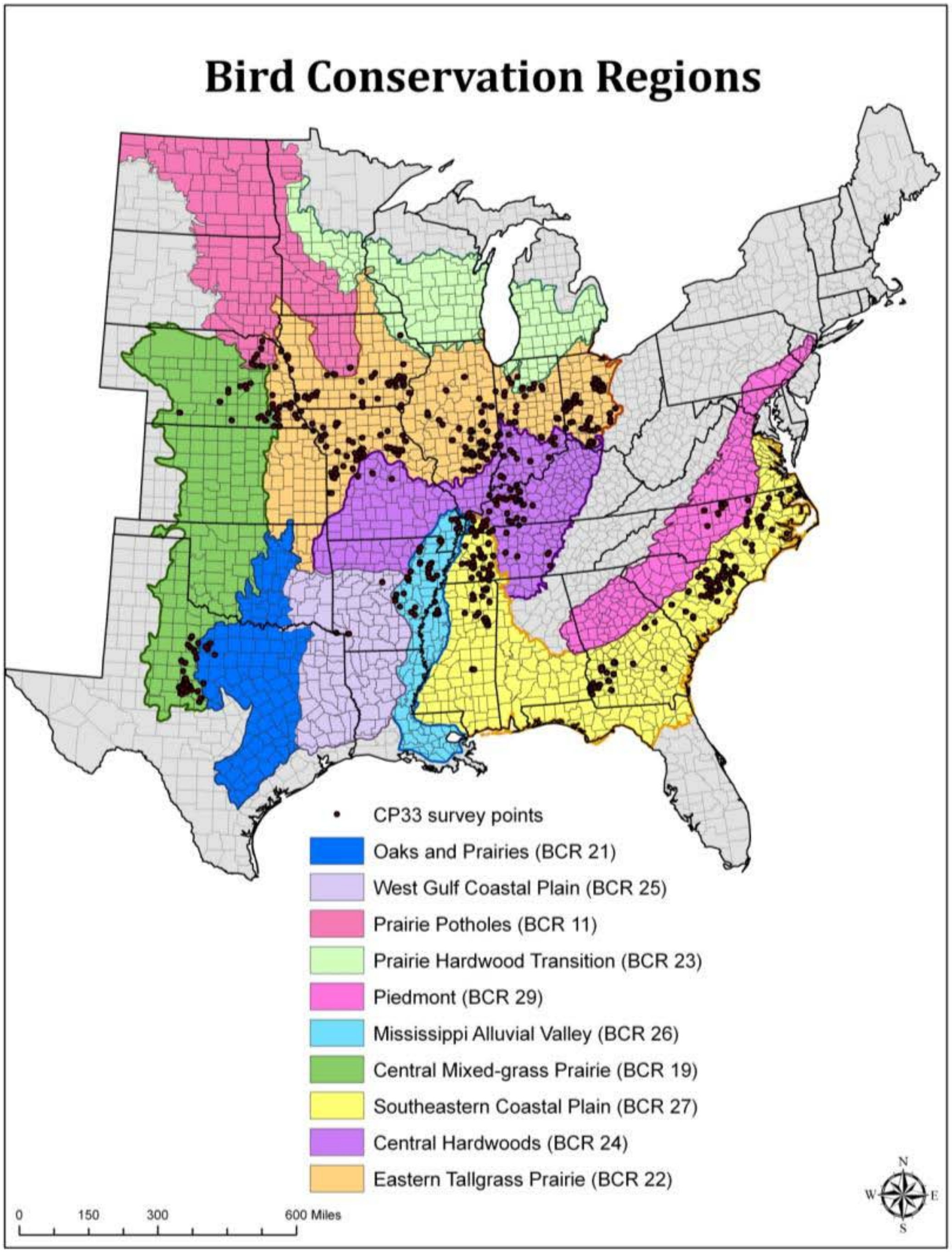

Figure 1.2 Distribution of points for breeding season and fall northern bobwhite and upland songbird surveys in the National CP33 Monitoring Program in 14 states, 10 Bird Conservation Regions [BCR], 2006-2009.

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CHAPTER II

BREEDING SEASON UPLAND BIRD RESPONSE TO TARGETED CP33 UPLAND HABITAT BUFFERS

Global trade agreements and impetus to sustain ecosystem services have created greater reliance on economic incentives to encourage environmental stewardship in agricultural landscapes (Tilman et al. 2002, Benton 2007). In the United States and Europe, government-subsidized conservation programs (or agri-environmental schemes) provide financial incentives for producers to alter production systems voluntarily in ways that foster multiple environmental services while offsetting excess commodity production (Sullivan et al. 2004, Lovell and Sullivan 2006). Several of these conservation programs were designed to ameliorate market failures generated by surplus production of commodities and have produced broad environmental benefits including reduced soil erosion, improved water quality, restoration of wetlands, and providing wildlife habitat (Sullivan et al. 2004, Schonhart et al. 2011). However, increased global food demands and diversion of grain supplies to renewable fuel production have increased demands to reduce enrollment in broad scale set-aside programs such as the Conservation Reserve Program [CRP], necessitating greater reliance on targeted practices that impact production minimally.

As defined by United States Congress, the U. S. Department of Agriculture [USDA] administers and delivers conservation programs via periodic reauthorizations of agricultural legislation referred to commonly as Farm Bills. Wildlife conservation has been historically an anticipated byproduct rather than an explicit programmatic objective of Farm Bill conservation programs, with wildlife habitat objectives achieved typically through creative exploitation of select practices within existing programs (e.g., CRP) and not through targeting habitat and population recovery goals of national conservation initiatives (Burger et al. 2006*a*). Recent Farm Bills brought wildlife habitat into equity with other resource objectives and established new practices targeting goals of national conservation initiatives (Burger et al. 2006*a*). This novel approach to conservation policy implies a shift from spatially diffuse conservation actions with nebulous broad-scale objectives to targeted practices to achieve specific environmental outcomes linked to regional and national conservation priorities (Burger et al.2006*a*).

Recent Farm Bills have also placed greater emphasis on working-lands payment programs [WLPP] to enhance programmatic impacts on lands in production (Cattaneo et al. 2005). If designed carefully and implemented strategically, targeted "wildlife-friendly" conservation practices (Green et al. 2005) established by WLPPs may provide a realistic option to harmonize conservation objectives with economic needs of agricultural producers. These practices integrate readily into agricultural production systems with federal incentives offsetting opportunity costs via neutral or net-positive effects on whole-farm profitability (Barbour et al. 2007, Stamps et al. 2008, McConnell 2011). However, evaluating programmatic outcomes (i.e., population increases) of targeted wildlife-friendly practices is necessary to determine practice efficacy, justify government expenditures, and inform future policy (Whitfield 2006). A myriad of site-specific studies have evaluated wildlife response to conservation practices (Haufler 2005), but few programmatic evaluations of wildlife response to targeted or non-targeted conservation practices exist currently, particularly at large spatial scales following probabilistic sampling designs (Kleijn and Sutherland 2003, Green et al. 2005, Whitfield 2006).

Continuous sign-up CRP Conservation Practice CP33: Habitat Buffers for Upland Birds targets population recovery goals for northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) and a suite of North American grassland bird species (U.S. Department of Agriculture 2004). The practice was designed to meet habitat goals of a national conservation partnership titled the National Bobwhite Conservation Initiative ([NBCI]; Dimmick et al. 2002, National Bobwhite Technical Committee 2011). In the U.S., bobwhite populations have declined 75% in the past 40 years (Sauer et al. 2011) and are subject to similar population pressures common to many declining grassland bird species in North America (Brennan and Kuvlesky 2005) and globally (Green et al. 2005). Moreover, the bobwhite is a flagship species for grassland bird conservation and holds great social and economic value (Burger et al 1999, Burger et al. 2006*a*).

Development of a spatially extensive targeted conservation practice like CP33 brought an unprecedented opportunity to mandate a comprehensive evaluation of avian response to buffer implementation from programmatic inception. Working with a consortium of 24 state and federal agencies, non-governmental organizations, and universities in 14 states comprising the core bobwhite range, I developed and implemented a regional monitoring program to measure comparative densities of targeted avian species (bobwhite and select grassland songbirds) on a random sample of row-crop fields where upland habitat buffers were established compared to those without this practice. I demonstrate that upland habitat buffers targeted strategically for recovery of declining bird species elicit a regionally variable, measurable and disproportionate population response by priority breeding bird species in agricultural landscapes with minimal (5-10%) change in primary land use.

Study Area

The study area for breeding season monitoring included 11 states in 2006 and 14 states for the remainder of the monitoring program (Table 1.1). A complete description of the study area and multi-stage sampling design is available in Chapter I (Fig. 2.1). Surveys were conducted on 904 fields (buffered=458; non-buffered=446) in 11 states in 2006, 1,151 fields (buffered=581; non-buffered=570), 1,124 fields (buffered=564; non-buffered=560), and 1,146 fields (buffered=572; non-buffered=574) in 14 states in 2007, 2008, and 2009, respectively. Interest in the coordinated CP33 monitoring program resulted in an additional 3 states, increasing state participation in breeding season surveys from 11 to 14 in 2007 (Table 1.1). Variation in sample size across years from 2007-2009 resulted from changes in field accessibility at some sites, caused primarily by weather events (e.g., flooding). The unbalanced design (among-year differences in number of buffered and non-buffered fields) occurred because of combined effects of lack of availability of non-buffered fields in some landscapes, enrollment of non-buffered fields into the buffer practice after 2006, and field accessibility issues.

Methods

Survey methods

Breeding season point transect bird surveys were conducted 1-4 times annually by state collaborators at each survey point (May-July) from 2006-2009. Paired buffered and non-buffered fields were surveyed simultaneously to ensure similar weather conditions. Singing/whistling and observed male bobwhite and selected priority grassland birds

(Table 2.1) were recorded between sunrise and 3 hours following sunrise during a 10-min period with detections recorded into one of 3 time intervals (0-3, 4-5, 6-10 min) and 6 pre-determined distance intervals (0-25, 26-50, 51-100, 101-250, 251-500, >500 m). Potential covariates of date, time, observer, and weather characteristics (% cloud cover, wind speed, fog) were collected following each survey (Marques et al. 2007, Rexstad 2007). Priority facultative and obligate grassland birds were selected for each BCR within each state by Southeast Partners in Flight by identifying species: 1) most likely to be impacted by Farm Bill conservation programs, particularly the CP33 practice, 2) with declining relative abundances (as determined by the North American Breeding Bird Survey [Sauer et al. 2011]) and distributions overlapping that of the CP33 practice, and 3) abundant enough to be measurable statistically, or those of specific regional interest (Burger et al. 2006b). In addition to bobwhite, priority species with adequate sample size for analysis included eastern kingbird (*Tyrranus tyrannus*), eastern meadowlark (*Sturnella magna*), dickcissel (*Spiza americana*), field sparrow (*Spizella pusilla*) and grasshopper sparrow (*Ammodramus savannarum*).

Statistical analysis

I analyzed regional and overall bird observation data using conventional [CDS] and multiple covariate [MCDS] distance sampling for each species in program DISTANCE 6.0 Release 2 (Thomas et al. 2010). I right-truncated data where detection probability g(w) < 0.1. Within CDS analysis, I evaluated fit of 3 key function models (uniform, half-normal, and hazard rate) followed by 3 series expansion adjustments (cosine, simple polynomial, hermite polynomial; Buckland 1992). Within MCDS, I evaluated half-normal and hazard rate key functions with cosine and hermite polynomial adjustments. I evaluated potential differences in detection probabilities on buffered vs. non-buffered fields and by comparing stratified detection functions (by habitat type over all years, and by habitat type-within year) to a pooled detection function (assuming equal detectability across buffered and non-buffered strata for all years) using Akaike's Information Criteria ([AIC]; Akaike 1973), goodness of fit tests, and probability density function plots generated for each model (Buckland et al. 2001, Marques and Buckland 2003, Pacifica et al. 2008). I calculated stratum-specific density (males/ha) by incorporating species-specific estimates of detection probability at regional and overall scales (Buckland et al. 2001). I calculated simple effect sizes by subtracting non-buffered from buffered density estimates, and relative effect sizes by dividing simple effect size by non-buffered density. I then calculated 95% confidence intervals on effect size [ES] of buffered and non-buffered point estimates as

$$ES \pm 1.96 * \sqrt{var_{buffered} + var_{non-buffered}} \qquad \text{(Equation 2.1)}$$

with those including zero deemed non-significant (Gardner and Altman 1989, Sim and Reid 1999).

Results

Breeding bobwhite densities varied regionally and annually but were collectively 60-74% (0.069 [0.038-0.100 95% CI] to 0.087 [0.050-0.124 95% CI] males/ha) greater on buffered vs. non-buffered row-crop fields across the 14 state range 1-4 years post establishment (2006-2009; Table 2.2, Fig. 2.2). Dickcissel densities were 80-129% (0.183 [0.070-0.296 95% CI] to 0.763 [0.503-1.024 95% CI] males/ha) greater on buffered vs. non-buffered fields (Table 2.2, Fig. 2.2) whereas field sparrow densities were 94-190% (0.182 [0.114-0.251 95% CI] to 0.345 [0.236-0.455 95% CI] males/ha) greater on buffered vs. non-buffered fields (2006-2009; Table 2.2, Fig. 2.2). Eastern meadowlark response varied annually with densities 12-22% (0.010 [-0.020-0.000 95% CI] to 0.026 [-0.067-0.017 95% CI] males/ha) greater on non-buffered than buffered fields in 2006 and 2009, and 9-41% (0.010 [-0.033-0.053 95% CI] to 0.044 [-0.010-0.099 95% CI] males/ha) greater on buffered than non-buffered fields in 2007 and 2008 (Table 2.2, Fig. 2.2). Grasshopper sparrow densities were 3% (0.005 [-0.137-0.128 95% CI] male/ha) greater on non-buffered vs. buffered fields in 2006, and 6%-43% (0.005 [-0.013-0.024 95% CI] to 0.025 [0.000-0.050 95% CI] males/ha) greater on buffered vs. non-buffered fields from 2007-2009 (Table 2.2, Fig. 2.2). Eastern kingbird densities were 42% (0.053 [-0.131-0.026 95% CI] males/ha) greater on non-buffered than buffered fields in 2006, but 1-29% (0.002 [-0.101-0.105 95% CI] to 0.041 [-0.024-0.107 95% CI] males/ha) greater on buffered than non-buffered fields from 2007-2009 (Table 2.2, Fig. 2.2).

Regional bobwhite densities were greatest in the semi-arid Central Mixed-grass Prairie (BCR 19), representing the westernmost survey points in the monitoring program (Texas and Nebraska), and least in the intensively cropped Mississippi Alluvial Valley (BCR 26), representing survey points along the alluvial floodplain of the Mississippi River (including points in Arkansas, Kentucky, Mississippi, Missouri and Tennessee) (Fig. 3A). Effect sizes were greatest in the Eastern Tallgrass Prairie (BCR 22) region (including points in Illinois, Indiana, Iowa, Missouri, Nebraska and Ohio) in 2007 and 2008, with 211% and 255% greater bobwhite densities on buffered fields than non-buffered fields (Table 2.2, Fig. 2.3A).

Dickcissel densities varied by region and year and were greatest on buffered fields in the Mississippi Alluvial Valley, and least in the Southeastern Coastal Plain (BCR 27) region (including points in Georgia, Kentucky, Mississippi, North Carolina, South Carolina, and Tennessee; Table 2.2, Fig. 2.3B). Effect sizes were greatest in the Mississippi Alluvial Valley from 2007-2008 and Central Mixed-grass Prairie in 2007, with 165% and 294% greater densities on buffered than non-buffered fields in the Mississippi Alluvial Valley and Central Mixed-grass Prairie, respectively (Table 2.2).

Field sparrow densities on buffered fields were consistent across regions, except in the Southeastern Coastal Plain. However, densities on non-buffered fields were greater in the Central Hardwoods (BCR 24) region (including points in Indiana, Kentucky, Missouri and Tennessee), and in the Southeastern Coastal Plain in 2006 compared to other regions (Table 2.2, Fig. 2.3C). Effect sizes were greatest in the Eastern Tallgrass Prairie in 2007 and 2008, with 232% and 311% greater densities on buffered than non-buffered fields (Table 2.2).

Similar to bobwhite, eastern meadowlark densities were greatest on buffered and non-buffered fields in the Central Mixed-grass Prairie, but exhibited negative or minimal effect sizes in that region (Table 2.2, Fig. 2.3D). Effect sizes were greatest in the Central Hardwoods in 2007, with 118% greater meadowlark densities on buffered than non-buffered fields (Table 2.2). However, Central Hardwoods and Mississippi Alluvial Valley were the only regions with consistently greater densities on buffered fields across all 4 years (Table 2.2, Fig. 2.3D). Effect sizes relative to densities on non-buffered fields were greatest in the Mississippi Alluvial Valley in 2006, with the Central Hardwoods and Mississippi Alluvial Valley being the only regions exhibiting consistently greater densities on buffered fields across all 4 years (Table 2.2, Fig. 2.3D).

Grasshopper sparrows exhibited annual variability in response to buffers across all regions, with largest effect sizes (344% and 250%) observed in the Central Mixed-grass Prairie in 2008 and 2009, respectively (Table 2.2, Fig. 2.3E). Grasshopper sparrows exhibited consistently greater densities on non-buffered than buffered fields in the Eastern Tallgrass Prairie from 2006-2008, but then exhibited 47% greater density on buffered fields in 2009 in this region (Table 2.2, Fig. 2.3E). Grasshopper sparrows in the Southeastern Coastal Plain were 19% more abundant on buffered fields in 2006, but were 41-72% more abundant on non-buffered fields from 2007-2009 (Table 2.2, Fig. 2.3E).

Eastern kingbird also exhibited substantial annual and regional variability, with greatest density and largest effect size (177-265%) observed in the Central Mixed-grass Prairie region from 2007-2009 (Table 2.2, Fig. 2.3F). Effect sizes in the Eastern Tallgrass Prairie and Southeastern Coastal Plain were small, and densities were greater on buffered fields in some years and on non-buffered fields in other years (Table 2.2). Eastern kingbird density in the Central Hardwoods was 67% greater on buffered fields in 2006, but 2% greater on non-buffered fields in 2009 (Table 2.2, Fig. 2.3F).

Discussion

Targeted conservation using CP33 buffers had immediate and positive effects on density of some species though change in primary land use was minimal. On average, buffers composed only 10% and 5.3% of the landscape within 250 and 500 m radii from survey points, respectively, yet resulted in up to 190% greater densities of select grassland birds. Effect sizes suggest response by targeted species to habitat buffers is disproportionate to amount of habitat available in the immediate landscape and indicates near-term success of the practice (1-4 years post-establishment). Disproportionate response might be expected if presence of buffers increases total usable space (Guthery

1997) by altering functional use of adjacent croplands as suggested by Smith and Burger (2009).

Few other comprehensive evaluations of direct response by wildlife species to agricultural conservation practices at regional or national scales exist, particularly those using robust methods for analytical comparison (Kleijn and Sutherland 2003, Green et al. 2005, Whitfield 2006). Previous farm-scale studies suggest greater breeding and overwintering bird densities on field margins bordered by native herbaceous vegetation in Mississippi and North Carolina (Marcus et al. 2000; Smith et al. 2005a, b; Riddle et al. 2008; Conover et al. 2009). In the U.K., grey partridge (Perdix perdix) abundance was greater where conservation headlands and wild bird cover practices were implemented (Ewald et al. 2010), and yellowhammer (Emberiza citrinella) density was greater where Entry Level Stewardship margins were established (Davey et al. 2010a). Conservation practices (including field buffers) targeting restoration of threatened cirl bunting (Emberiza cirlus) populations also increased abundance 83% compared to non-managed areas (Peach et al. 2001). Further, conservation practices targeting restoration of corn buntings (Emberiza calandra) increased abundances 5.6% annually, compared to a 14.5% annual decrease on conventional farms (Perkins et al. 2011). At the programmatic level, studies of wildlife response to conservation in Europe have suggested overwhelmingly increased species richness and abundance where conservation programs were implemented, though increases were affected by landscape complexity (Batary et al. 2010) and differences among regions (Davey et al. 2010b).

Differences in climatic conditions, land use, landscape composition, and habitat structure among regions may influence habitat selection by birds at local and landscape scales (Bakker et al. 2002). Regional differences in bird densities and response to conservation are therefore an expected result and the impetus behind evaluating regional variability in large-scale monitoring programs. Failure to account for region-specific response to conservation will likely bias conclusions and may lead to inappropriate management recommendations for some species in some regions (Bakker et al. 2002). Bird responses to field margin and boundary management varied among regions in the U.K. and were attributed to differences in boundary incentives participation, management of boundary vegetation, and differences in vegetative establishment and growth among regions (Davey et al. 2010b). My results also suggest regional variability among each priority species in response to CP33 buffers.

Regional differences in bobwhite densities and effect size were apparent with greatest effect size observed in the region most dominated by agriculture (i.e., Eastern Tallgrass Prairie) and not in the region with greatest observed densities (i.e., Central Mixed-grass Prairie) where large patches of intact grasslands and quality shrubland habitat remain abundant (N. A. Bird Conservation Initiative 2000). As expected, bobwhite and some grassland bird species exhibited strong responses to establishment of habitat patches in an otherwise inhospitable matrix, but not when alternative quality habitats already exist in the landscape. This was also observed with practices targeted for restoration of corn buntings in Scotland (Perkins et al. 2011). In other regions of greater landscape heterogeneity (e.g., Central Hardwoods, Southeastern Coastal Plain), I observed intermediate and annually varying response to habitat buffer patches, possibly related to annually varying climatic conditions that may elicit increased or decreased use of buffer habitats. These differences were also observed in other priority species, including substantial variation in eastern meadowlark and grasshopper sparrow effect size across regions and years.

Bobwhites occupy typically a mosaic of early-succession habitats characterized by small patches of grassland, forest, and cropland (Brennan 1999). However, other grassland obligate and facultative bird species may exhibit different habitat area and configuration requirements. Some grassland bird species may be susceptible to patch size dependency when patches reflecting native (i.e., prairie) habitat are made available (Brennan and Kuvlesky 2005). For some grassland species requiring large contiguous patches of habitat, small fragments of native grasses will not be sufficient to sustain population viability (Johnson 2001). This “area-sensitivity” has been demonstrated in several North American grassland species including dickcissel, eastern meadowlark and grasshopper sparrow (see review in Ribic et al. 2009), but has been shown to be regionally variable by species (Johnson and Igl 2001, Bakker et al. 2002). Sensitivity to patch area (Ribic et al. 2009) in some years may explain lack of response to CP33 buffers by eastern meadowlark and grasshopper sparrow within some regions, but provides no explanation for changes between positive and negative response across years within a given region. It also provides no explanation for strong consistently positive responses by dickcissels across all regions and years, provided that previous evidence suggesting area sensitivity in dickcissels is valid. A more likely explanation is that CP33 buffers provided appropriate vegetation structure required by dickcissels, but did not meet vegetation structure requirements for eastern meadowlarks and grasshopper sparrows during breeding season in some years. Dickcissels prefer dense and moderate to tall herbaceous vegetation with moderate to deep litter during breeding season (Temple 2002), whereas eastern meadowlarks and grasshopper sparrows may prefer grasslands with decreased cover height (e.g., pastures, hayfields) over that of buffers (Lanyon 1995, Vickery 1996). Response by grasshopper sparrows to buffers increased substantially in 3 of 4 regions in 2009, following mid-contract management, reflecting greater use of buffer habitats after vegetation height and density was set back by disturbance.

Increased densities of some targeted species where conservation practices are applied strategically suggests WLPPs that promote wildlife-friendly farming practices (e.g., maintaining natural habitat patches in working agricultural landscapes [Green et al. 2005]) have potential to benefit some grassland bird species across broad landscapes provided increases in density represent actual population increases. Though targeted single-species conservation practices cannot address multiple resource requirements of all grassland bird species (Brennan and Kuvlesky 2005), I recommend conservation managers implement targeted conservation management systems that combine multiple conservation practices delivered strategically to provide an array of nesting and foraging habitats for multi-species recovery objectives and enhancement of biodiversity and ecosystem services (Grice et al. 2004, Batary et al. 2010). Targeted conservation practices applied strategically at the landscape level under a conservation management framework could increase landscape heterogeneity (Fahrig et al. 2011) and ameliorate wildlife population declines by providing necessary habitat to meet life history needs with minimal impact on agricultural production systems (Schonhart et al. 2011, Barbour et al. 2007). Extensive implementation of a low-intensity practice across broad landscapes will increase landscape heterogeneity, improve connectivity, and elevate background population levels of select species of conservation concern, potentially enhancing their ability to respond positively to more intensive management within geographically-disjunct designed reserves. Given that 360 million ha (46%) of U.S. land is currently in agricultural production (crop and grazing lands) (U.S. Department of Agriculture 2007), targeted wildlife-friendly farming practices via WLPPs may potentially address multiple environmental concerns across broad landscapes at lesser programmatic costs (Aillery 2006).

In the U.S. and Europe, mercurial economic climates render government-funded conservation programs increasingly vulnerable (Whitfield 2006). Proof of conservation benefits from conservation programs has become increasingly important, resulting in greater influence of policy on ecosystem services in agricultural landscapes (Burger et al. 2006a). To be effective, policy-driven agricultural conservation must be based on sound scientific research. The CP33 monitoring program demonstrates that multi-scale evaluation of wildlife response to a conservation practice is fully achievable and should be a critical "feedback" component to future conservation policy (Whittingham 2007, Perkins et al. 2011). Total federal costs for CP33 monitoring were on ~1-2% of total programmatic costs. I therefore suggest evaluation of future government-sponsored conservation provisions will be a cost-effective means to "self-correct" agricultural policy where knowledge of programmatic outcomes of conservation will allow for optimization of policy decisions (Grice et al. 2004, Robertson and Swinton 2005).

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Table 2.1 Species (by American Ornithologists' Union alpha-code) of interest selected for each Bird Conservation Region (BCR) for CP33 contract monitoring in 2006.

Bird Conservation Region	Species
Central Mixed-grass Prairie (BCR 19)	BEVI[a], DICK[b], EAKI[c], EAME[d], FISP[e], GRSP[f], INBU[g], NOBO[h], PABU[i], STFL[j], UPSA[k]
Eastern Tallgrass Prairie (BCR 22)	DICK, EAKI, EAME, FISP, GRSP, INBU, NOBO, VESP[l], UPSA
Prairie Hardwood Transition (BCR 23)	DICK, EAKI, EAME, FISP, INBU, NOBO, VESP
Central Hardwoods (BCR 24)	DICK, EAKI, EAME, FISP, INBU, NOBO
Western Gulf Coast Plain (BCR 25)	DICK, EAKI, EAME, INBU, NOBO, PABU
Mississippi Alluvial Valley (BCR 26)	DICK, EAKI, EAME, FISP, GRSP, INBU, NOBO, PABU
Southeast Coastal Plain (BCR 27)	DICK, EAKI, EAME, FISP, GRSP, INBU, NOBO, PABU
Piedmont (BCR 29)	EAKI, EAME, FISP, INBU, NOBO

[a] Bell's vireo(*Vireo bellii*)
[b] dickcissel (*Spiza americana*)
[c] eastern kingbird (*Tyrranus tyrannus*)
[d] eastern meadowlark (*Sturnella magna*)
[e] field sparrow (*Spizella pusilla*)
[f] grasshopper sparrow (*Ammodramus savannarum*)
[g] indigo bunting (*Passerina cyanea*)
[h] northern bobwhite (*Colinus virginianus*)
[i] painted bunting (*Passerina ciris*)
[j] scissor-tailed flycatcher (*Tyrannus forficatus*)
[k] upland sandpiper (*Bartramia longicauda*)
[l] vesper sparrow (*Pooecetes gramineus*)

Table 2.2 Regional and overall effect size (D_{buffered}-$D_{\text{non-buffered}}$) and relative effect size ([D_{buffered}-$D_{\text{non-buffered}}$]/$D_{\text{non-buffered}}$ × 100) for focal bird species on CP33 buffered vs. non-buffered row-crop fields across 14 U.S. states, 2006-2009.

Species	Bird Conservation Region	Year	Effect size (males/ha)	Relative effect size	95% CI effect size
Northern bobwhite	Central Mixed-grass Prairie (BCR 19)	2006	-0.168	-19.57%	-0.557-0.222
		2007	0.110	33.52%	-0.023-0.243
		2008	0.114	41.22%	0.015-0.212
		2009	0.017	3.88%	-0.075-0.110
	Eastern Tallgrass Prairie (BCR 22)	2006	0.098	122.11%	-0.142-0.339
		2007	0.145	255.87%	0.043-0.248
		2008	0.177	211.60%	0.038-0.316
		2009	0.221	171.63%	0.112-0.330
	Central Hardwoods (BCR 24)	2006	0.063	59.24%	-0.010-0.136
		2007	0.064	31.89%	-0.113-0.241
		2008	0.040	31.33%	-0.042-0.122
		2009	0.048	33.12%	-0.030-0.127
	Mississippi Alluvial Valley (BCR 26)	2006	0.022	23.53%	-0.088-0.132
		2007	0.042	177.03%	0.008-0.076
		2008	0.038	264.45%	0.012-0.063
		2009			
	Southeastern Coastal Plain (BCR 27)	2006	0.140	243.50%	0.078-0.201

Table 2.2 (Continued)

		2007	0.078	97.05%	-0.086-0.242
		2008	0.084	50.46%	-0.108-0.276
		2009	0.050	217.35%	0.033-0.067
	Overall	2006	0.087	74.40%	0.050-0.124
		2007	0.079	70.56%	0.042-0.116
		2008	0.085	72.61%	0.050-0.119
		2009	0.069	60.01%	0.038-0.100
Field sparrow	Eastern Tallgrass Prairie (BCR 22)	2006	0.342	190.79%	0.229-0.454
		2007	0.356	231.96%	0.247-0.465
		2008	0.385	311.27%	0.268-0.502
		2009	0.415	173.47%	0.248-0.582
	Central Hardwoods (BCR 24)	2006	0.203	88.13%	0.042-0.363
		2007	0.189	59.63%	0.005-0.373
		2008	0.153	53.14%	-0.013-0.319
		2009	0.130	61.59%	0.009-0.251
	Southeastern Coastal Plain (BCR 27)	2006	-0.017	-3.96%	-0.356-0.322
		2007	0.250	154.44%	0.052-0.449
		2008	0.102	69.38%	0.011-0.193
		2009	0.071	74.51%	0.027-0.115
	Piedmont (BCR 29)	2007	0.352	300.00%	0.097-0.607
		2008	0.223	211.11%	0.040-0.406

Table 2.2 (Continued)

		2009	0.018	100.00%	0.004-0.031
	Overall	2006	0.214	93.73%	0.111-0.318
		2007	0.345	189.82%	0.236-0.455
		2008	0.216	157.81%	0.138-0.294
		2009	0.182	121.29%	0.114-0.251
Eastern meadowlark	Central Mixed-grass Prairie (BCR 19)	2006	-0.066	-19.53%	-0.245-0.114
		2007	0.002	0.89%	-0.145-0.150
		2008	-0.011	-4.10%	-0.119-0.098
		2009	-0.010	-9.52%	-0.031-0.012
	Eastern Tallgrass Prairie (BCR 22)	2006	-0.085	-59.96%	-0.149--0.021
		2007	0.092	75.27%	-0.027-0.212
		2008	0.042	31.88%	-0.065-0.149
		2009	-0.031	-25.22%	-0.054--0.006
	Central Hardwoods (BCR 24)	2006	0.033	74.96%	-0.023-0.091
		2007	0.110	117.82%	-0.033-0.255
		2008	0.036	33.34%	-0.096-0.169
		2009	0.021	24.50%	-0.004-0.046
	Mississippi Alluvial Valley (BCR 26)	2006	0.050	510.12%	-0.011-0.110
		2007	0.031	48.90%	-0.038-0.101
		2008	0.038	33.18%	-0.062-0.139

Table 2.2 (Continued)

	2009	0.024	18.03%	-0.067-0.115
Southeastern Coastal Plain (BCR 27)	2006	-0.019	-25.37%	-0.068-0.030
	2007	-0.015	-17.51%	-0.062-0.032
	2008	-0.010	-11.59%	-0.067-0.049
	2009	-0.008	-34.74%	-0.014--0.001
Overall	2006	-0.026	-21.72%	-0.067-0.017
	2007	0.044	40.80%	-0.010-0.099
	2008	0.010	8.96%	-0.033-0.053
	2009	-0.010	-12.38%	-0.020-0.000

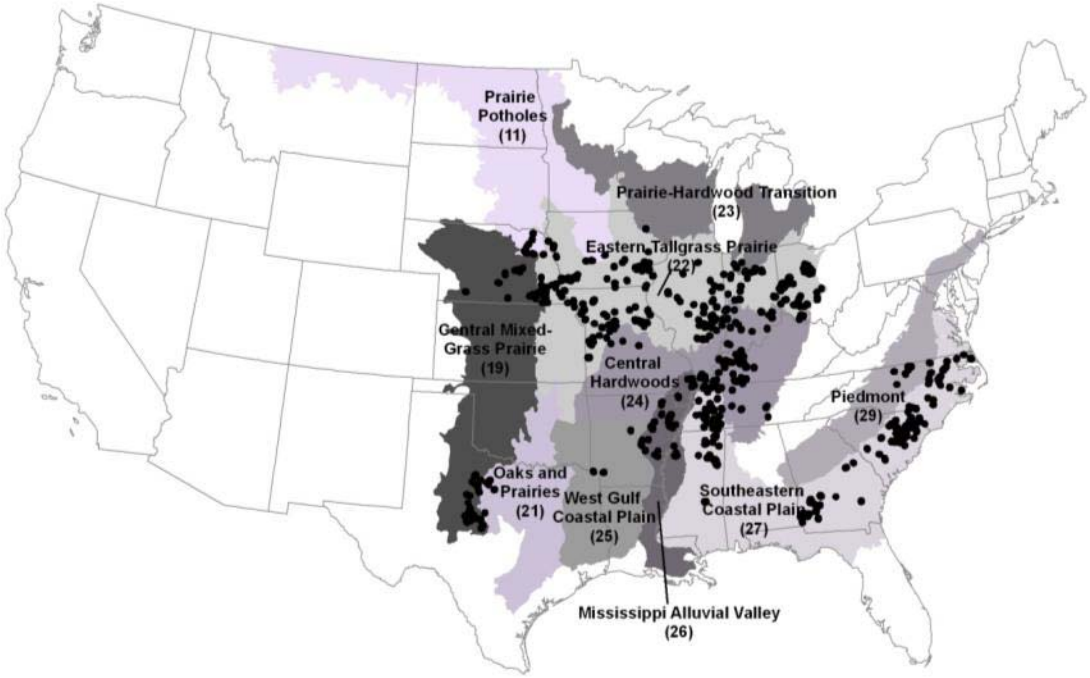

Figure 2.1 Geographic locations of bird survey points and Bird Conservation Regions [BCR] for 2006-2009 breeding season CP33 monitoring in 14 states. BCRs include Prairie Potholes (BCR 11), Central Mixed-grass Prairie (BCR 19), Oaks and Prairies (BCR 21), Eastern Tallgrass Prairie (BCR 22), Prairie Hardwood Transition (BCR 23), Central Hardwoods (BCR 24), Western Gulf Coast Plain (BCR 25), Mississippi Alluvial Valley (BCR 26), Southeastern Coastal Plain (BCR 27), and Piedmont (BCR 29).

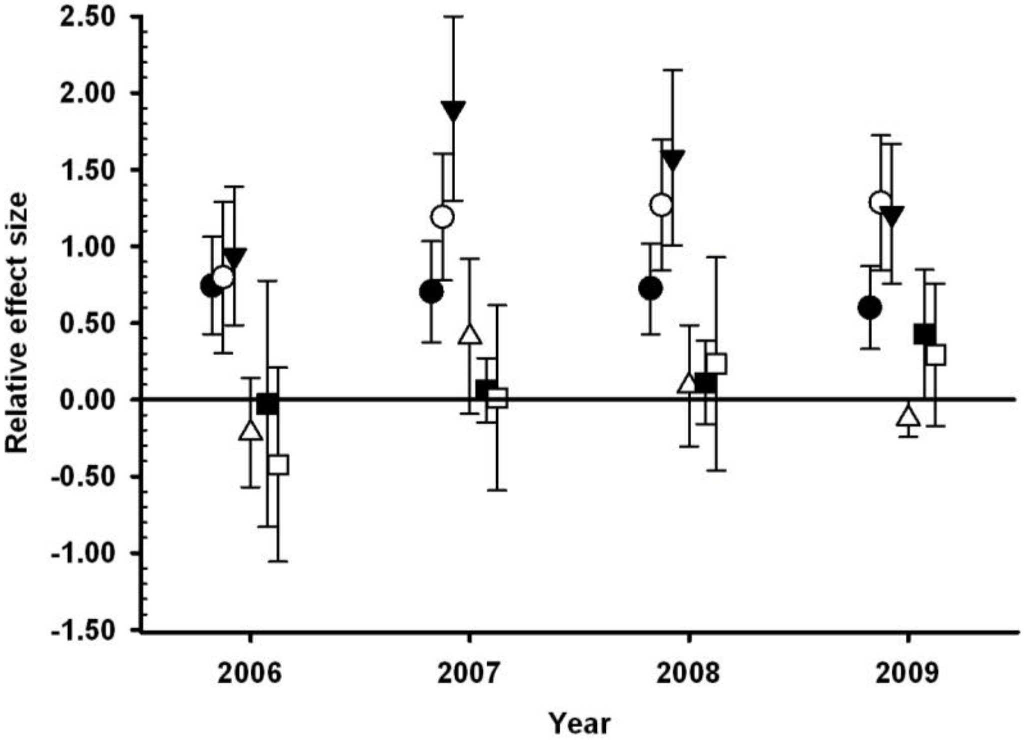

Figure 2.2 Breeding season relative effect size ([$\text{Density}_{\text{buffered}}$-$\text{Density}_{\text{non-buffered}}$]/$\text{Density}_{\text{non-buffered}}$) ± 95% confidence interval of targeted upland bird densities (northern bobwhite [●], dickcissel [○], field sparrow [▼], eastern meadowlark [Δ], grasshopper sparrow [■], eastern kingbird [□]) on paired CP33 buffered and non-buffered row-crop fields across 14 states, 2006-2009.

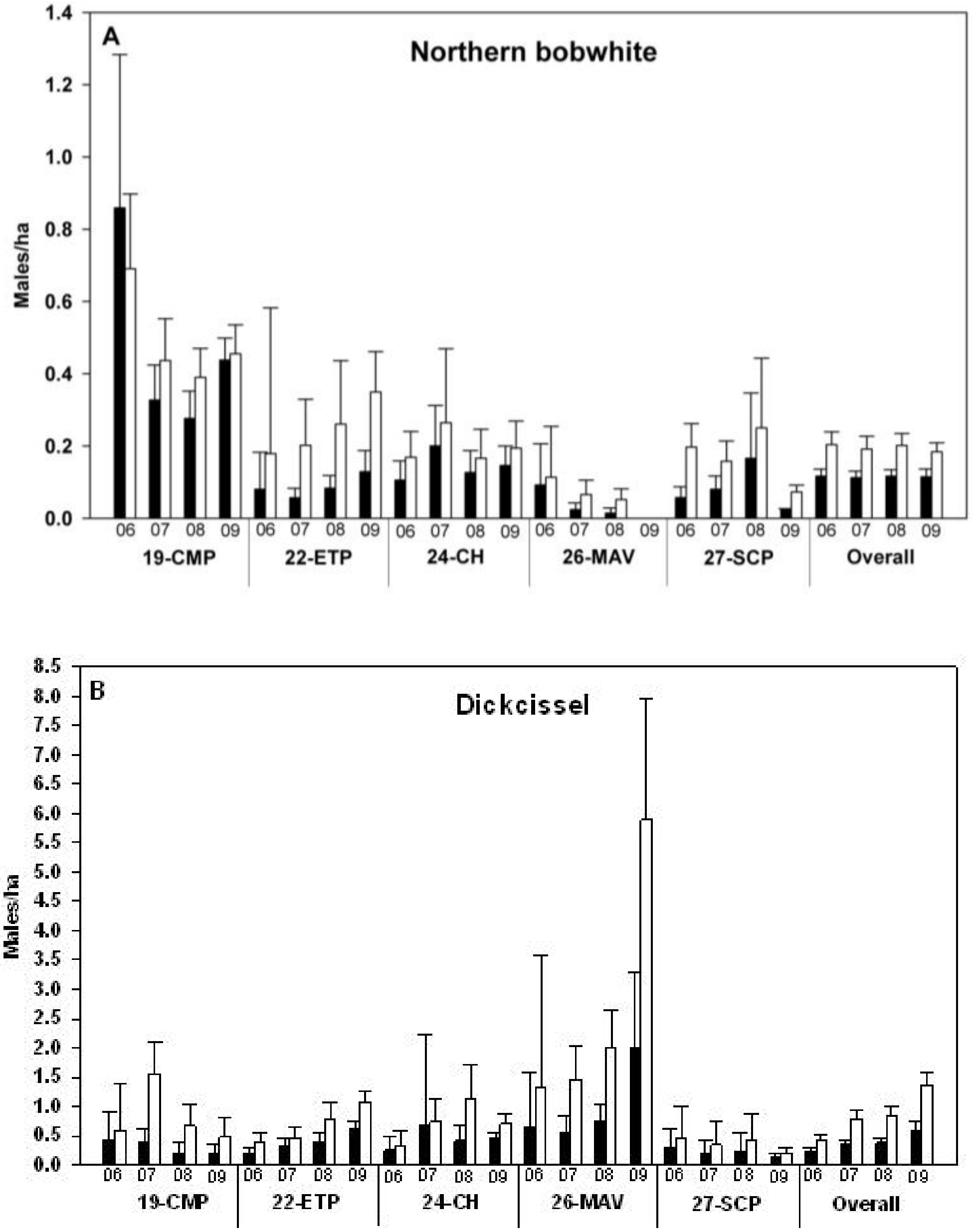

Figure 2.3 Regional and overall breeding season northern bobwhite (A), dickcissel (B), field sparrow (C), eastern meadowlark (D), grasshopper sparrow (E), and eastern kingbird (F) density (males/ha ± 95% confidence interval) on surveyed buffered (□) and non-buffered (■) fields across 14 states, 2006-2009. Regions include the Central Mixed Grass Prairie [19-CMP], Eastern Tallgrass Prairie [22-ETP], Central Hardwoods [24-CH], Mississippi Alluvial Valley [26-MAV], Southeastern Coastal Plain [27-SCP], and Piedmont [29-PIED]. Data from all regions are included in the overall density estimate.

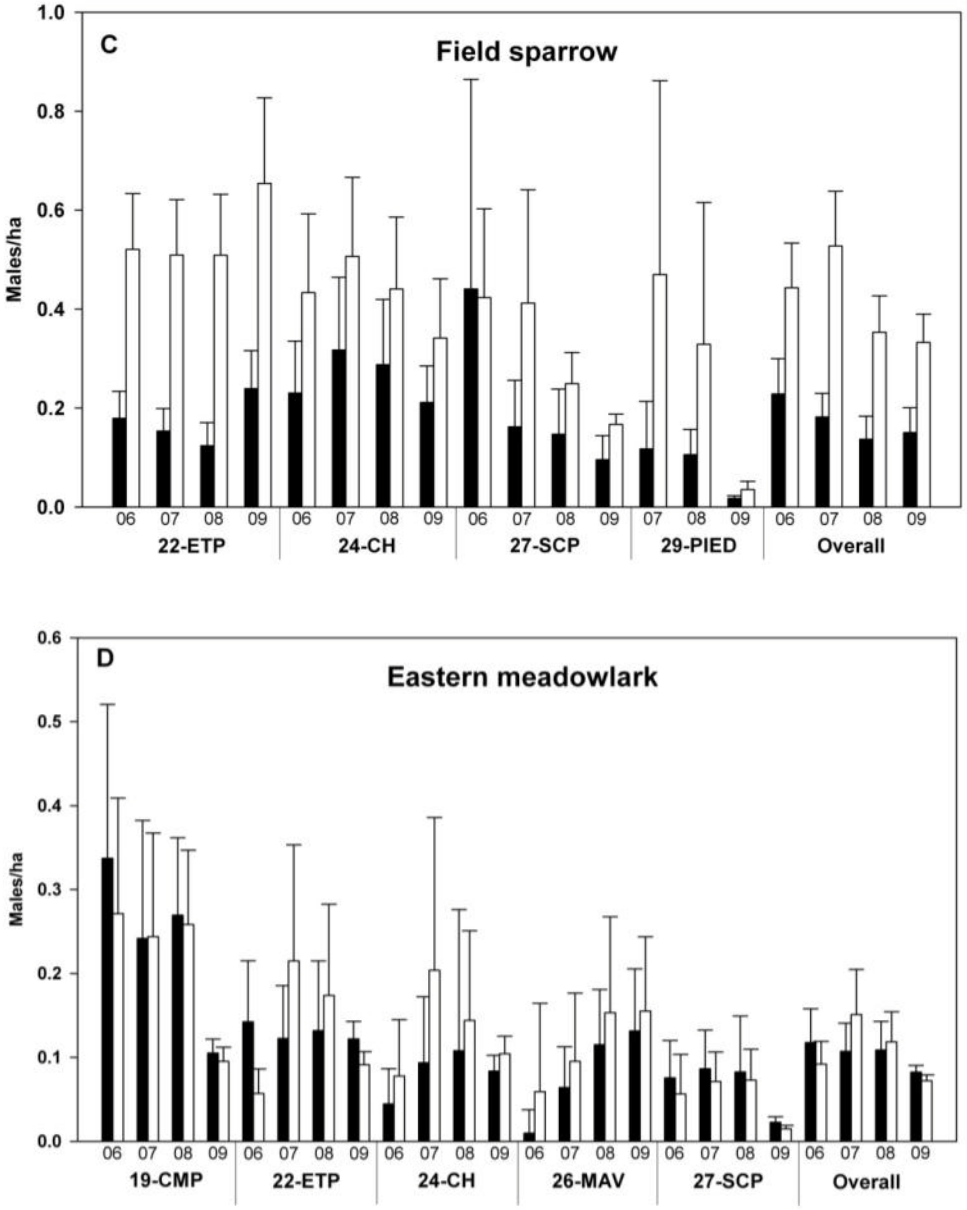

Figure 2.3 (Continued)

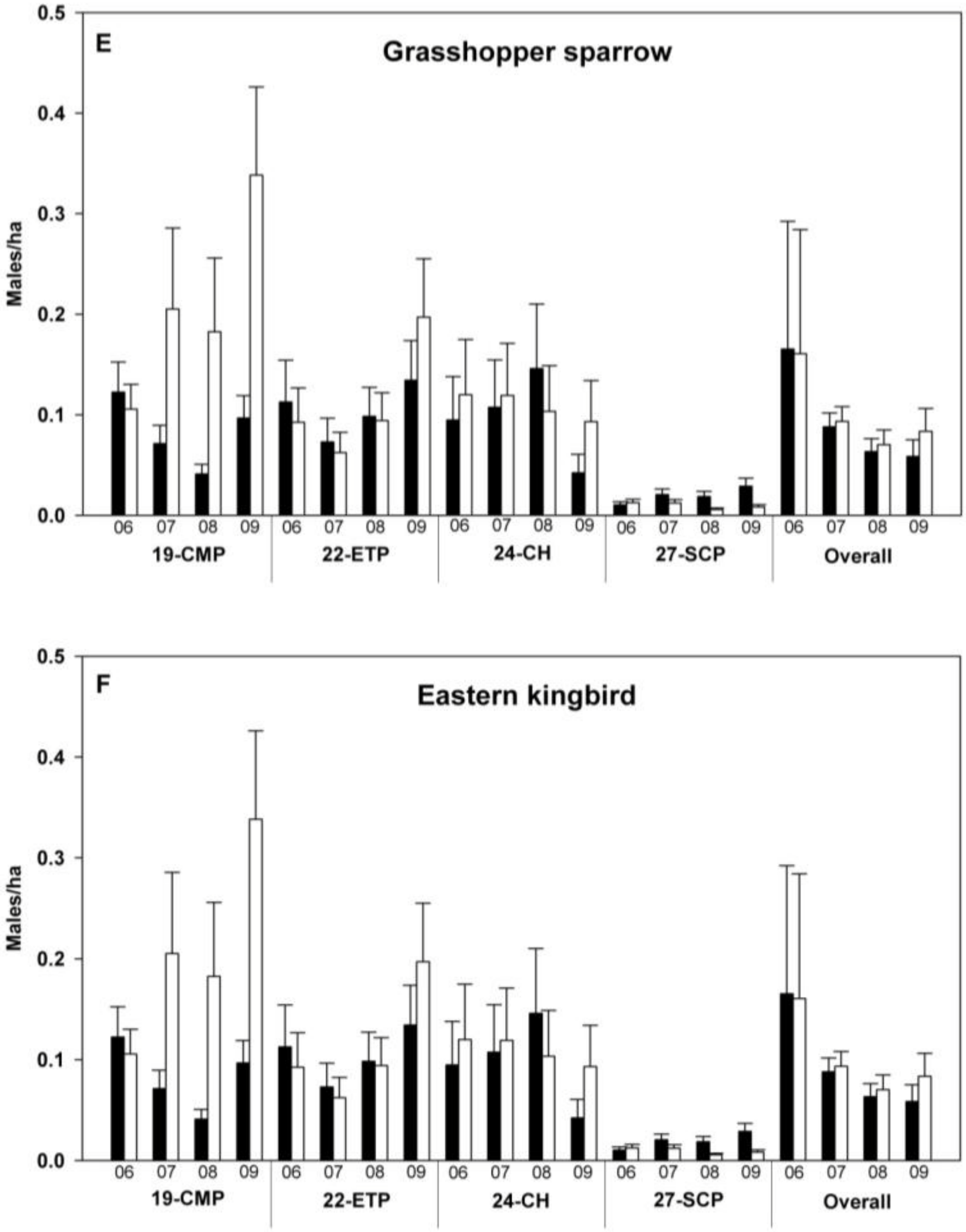

Figure 2.3 (Continued)

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CHAPTER III

REGIONAL DIFFERENCES AMONG MULTI-SCALE EFFECTS OF LANDSCAPE STRUCTURE ON NORTHERN BOBWHITE ABUNDANCE IN AGRICULTURAL LANDSCAPES

Processes that determine patterns of observed wildlife-habitat relationships were once thought to function only at the local (i.e., patch) scale (Dunning et al. 1992). However, there is increasing recognition that surrounding landscape structure influences local wildlife-habitat interactions (Turner 1989, Dunning et al. 1992, Flather and Sauer 1996). The prevailing paradigm that species exist in favorable habitat patches in an otherwise hostile landscape matrix has been challenged with recognition that species use a variety of patch types in complex ways (Fahrig et al. 2011). Hence, a rigid island-biogeographic approach to wildlife-habitat relationships is now shifting toward a "heterogeneous landscape" perspective (Fahrig et al. 2011, Didham et al. 2011). Under this new paradigm, ecological processes believed to occur at the patch level are linked inextricably to the mosaic of patches in the immediate and surrounding landscape (Lindenmayer et al. 2008).

Declines of early-succession bird species are attributed typically to loss and/or fragmentation of habitat (e.g., Brennan and Kuvlesky 2005). However, the current paradigm lacks adequate understanding of interrelationships among structure of the surrounding landscape, usable space, and abundance, trend, and dynamics of species occurring in these habitats (Veech 2006). In landscapes where agriculture represents the dominant land use, composition (e.g., relative proportion) and configuration (e.g., layout and relative placement) of habitat patches affects local distribution and abundance of early-succession bird species (Warner 1994, Clark and Reeder 2005, Herzon and O'Hara 2007, Murray et al. 2008). However, observed patterns tend to be species-specific and often involve a multitude of landscape features and spatial scales (Turner 1996, Murphy 2003).

Northern bobwhites (*Colinus virginianus*; hereafter, bobwhite) use multiple seral stages (e.g., annual weeds, perennial grasses, and shrubs) to meet various seasonal life requisites and thus inhabit a breadth of frequently disturbed habitats including grasslands, agricultural lands, rangelands, and open-canopy forest systems (Brennan 1999). Populations of bobwhite have declined precipitously in the last half-century, with moderate (e.g., -0.4% in the Central Mixed Grass Prairie) to severe (e.g., -4.9% in the Southeastern Coastal Plain) annual declines in most regions (Sauer et al. 2011). These declines are linked to anthropogenic changes in land use which include agricultural and silvicultural intensification, elimination of disturbance such as fire, reforestation, and urbanization (Brennan 1991).

Previous studies that have evaluated bobwhite-landscape associations suggest distribution and abundance is influenced by a combination of landscape composition and configuration, with positive associations with grassland and rangeland composition and mixed relations with forest cover, croplands, and edge density (see Table 3.1). However, most previous studies were conducted within a single state or region, and no clear patterns exist regarding bobwhite-landscape relations across multiple regions or the species' range (Peterson et al. 2002). As bobwhite managers recognize potential influence of landscape structure on bird distribution and abundance, studies evaluating effects of landscape composition and configuration are increasingly prioritized. Yet, though advanced habitat suitability models have been developed for individual regions (e.g., Rittenhouse et al. 2007), there have been no recent definitive studies using advanced computational methods that evaluate effects of landscape structure on bobwhite within multiple regions across the breadth of the range (see Dijak et al. 2007).

I used iterative Markov Chain Monte Carlo [MCMC] resampling methods in a Bayesian hierarchical spatial count model to evaluate effects of landscape composition and configuration on mean predicted abundance of breeding male northern bobwhites in 14 states collected as part of a national monitoring effort to evaluate bobwhite and upland songbird response to Conservation Reserve Program continuous sign-up practice CP33, Habitat Buffers for Upland Birds (Burger et al. 2006). My primary objective involved multi-scale assessment of regional differences in bobwhite-landscape associations while accounting for random temporal and spatial variation. I predicted bobwhite would exhibit substantial regional variation in effects of landscape structure on patterns of abundance, that bobwhite abundances would be driven by processes that occur at larger landscape scales and by degree of landscape heterogeneity, and that abundance in these landscapes would exist operationally within the confines of a row-crop agriculture matrix with limited effects from composition of woody and grass cover and edge density of woody cover. I also predicted composition of native herbaceous cover within upland habitat buffers (CP33) would influence patterns of bobwhite abundance, but would be limited by larger effects of surrounding landscape structure.

Study Area

The study area included survey sites in 14 states participating in the National CP33 Monitoring Program within the core bobwhite range (Table 1.1). A complete description of the study area and multi-stage sampling design is available in Chapter I (Fig. 1.1). Survey sites were located on row-crop fields containing CP33 upland habitat buffers paired with non-buffered row-crop fields 1-3 km from buffered fields. Survey sites were located within 10 Bird Conservation Regions [BCR] (i.e., ecologically defined regions with similar habitat structure and land use that support similar bird communities; North American Bird Conservation Initiative 2000, see Fig. 3.1). However, for purposes of this study, I consolidated sites located in peripheries of 5 BCRs (Prairie Potholes [BCR 11], Oaks and Prairies [BCR 21], Prairie-Hardwood Transition [BCR 23], West Gulf Coastal Plain [BCR 25], Piedmont [BCR 29]) into one of 5 primary, adjacent BCRs as these may influence and complicate analysis and may not be fully representative of the entire range of the BCR (Link et al. 2006). Consolidated survey points then represented 5 primary regions in the study area (Central Mixed-grass Prairie [BCR 19], Eastern Tallgrass Prairie [BCR 22], Central Hardwoods [BCR 24], Mississippi Alluvial Valley [BCR 26], Southeastern Coastal Plain [BCR 27]) (Fig. 3.1).

Methods

Breeding season bird surveys

Breeding season point transect bird surveys were conducted 1-4 times annually by state agency personnel at each survey point (May-July) from 2006-2008 according to the National CP33 Monitoring Protocol (Burger et al. 2006). Whistling and observed male bobwhite were recorded between sunrise and 3 hours following sunrise during a 10-min period at each point during favorable weather conditions (wind < 6.5 kph, cloud cover < 75%, no precipitation, and change in barometric pressure < 0.05 in/Hg). Surveys were conducted on 904 fields (buffered=458; non-buffered=446) in 11 states in 2006, 1,151 fields (buffered=581; non-buffered=570), and 1,124 fields (buffered=564; non-buffered=560) in 14 states in 2007 and 2008, respectively. Variation in sample size across years is due to addition of participating states in 2007 and changes in field accessibility at some sites from 2007-2008.

Land cover survey

I projected spatial locations of all survey points using Albers Equal-Area Conic projection and stored points in file geodatabase format in ArcGIS (ESRI 2009). I buffered each survey point at a 1,500 m radial distance centering on the point using a dissolved buffer. I then overlaid buffers onto 2007 growing-season aerial photography from the USDA NRCS National Agricultural Inventory Program [NAIP] (U.S. Department of Agriculture 2007) in ArcGIS. I chose 2007 NAIP imagery for land cover classification because it was representative of the mid-point of bird monitoring efforts, such that land cover in these landscapes was not expected to vary within a single year from the bird data. I developed a file geodatabase of classified land cover polygons within each dissolved buffer via on-screen digitizing following methods described in Bakker et al. (2002), Cunningham and Johnson (2006), and Murray et al. (2008). I considered hedgerows, ditches, roads or any other discernible break in cover type as a patch boundary. I digitized features as separate polygons only if >5 m in width (minimum mapable unit). Each digitized polygon was assigned to one of 10 land cover/land use categories (CP33, herbaceous-successional, pasture-hay, woody cover, row-crop, CRP grass, open water, barren, urban-developed, rangeland) similar to those assigned by Nielson et al. (2008). Because of inability to ground truth the full extent of dissolved buffers, I grouped all tree and shrub cover into a single woody vegetation category (Cunningham and Johnson 2006). I considered roads >5 m in width and any anthropogenically maintained areas (e.g., yards, neighborhoods, etc.) as urban-developed. I cross-checked my land cover classifications at random with the 2001 National Land Cover Dataset ([NLCD]; Homer et al. 2004) to ensure consistency in classification.

I converted land cover shapefiles to 3 sets of 2.5 x 2.5 m resolution classified raster imagery, based on resolution of land-cover classification. The first raster dataset contained unique attributes for each of 10 digitized land cover classes, whereas the second and third datasets contained generalized classifications for several categories (O'Connor et al. 1999, Bergin et al. 2000, Murray et al. 2008). In the second data set all herbaceous-successional, pasture-hay, and CRP grass were collapsed into a generalized "grass" category. In the third data set CP33, herbaceous-successional, pasture-hay, and CRP grass were collapsed into a generalized "grass" category, and open water, and barren were collapsed into a "natural non-habitat" category. I then clipped each raster dataset at 500 m and 1,500 m spatial scales using a radial buffer around each survey point, which allowed for 2 raster "landscapes" representing immediate (i.e., local) and surrounding land cover attributes to be generated for each bird survey point. I estimated a suite of landscape composition and configuration metrics at 2 spatial scales from bird survey points (500 and 1,500 m circular radii to capture immediate and landscape-level effects) using FRAGSTATS (McGarigal et al. 2002) following Schairer et al. (1999), Riffell et al. (2003), Smith and Burger (2003), Twedt et al. (2007), and Murray et al. (2008). I selected landscape composition and configuration variables based on *a priori* relations of bird-habitat abundance (Thogmartin and Knutson 2007) and previous studies of bobwhite-landscape associations within states or regions encompassed by my study area (Roseberry and Sudkamp 1998, Schairer et al. 1999, Thogmartin 2002, Veech 2006, Twedt et al 2007). For each spatial scale (500 m, 1,500 m), I developed a list of candidate composition (% row-crop, % CP33 buffers, % grass (not including CP33), % woody cover, % urban-developed) and configuration (patch density, total edge density, woody edge density, contagion, and patch richness) metrics (Table 3.1). I included composition of rangeland only for the Central Mixed-grass Prairie region because rangeland, as I defined it, was not present in other regions. For physiognomy metrics, I used density in lieu of metrics such as number of patches, total edge, and total woody edge to allow for variation in spatial scale (McGarigal et al. 2002). I standardized continuous landscape variables (Gilks and Roberts 1996) to assist in convergence of models and enable comparison of slope coefficients relative to composition and configuration metrics (Thogmartin and Knutson 2007).

Bird-landscape analysis

I merged bobwhite observations collected during each survey repetition at each point (2006-2008) with point-specific landscape variables at 500 m and 1,500 m spatial scales. I removed 132 survey points due to either missing landscape or bird data, most which were located in Missouri which re-selected breeding season sampling points in 2007 (i.e., 2006 points and bird data were excluded). After exclusion, 1,188 unique survey points remained, with 5,761 unique breeding season bird surveys conducted over the study period. I ran Spearman correlations to assess multicollinearity among potential explanatory variables and among the same variable assessed at multiple spatial scales.

Multicollinearity is ignored typically in most habitat studies; however, failure to account for it will underestimate precision on parameter estimates and lead to biased inference regarding model parameters (Lawler and Edwards 2006). To reduce potential bias resulting from multicollinearity, I excluded use of potential explanatory variables in the same model if correlation coefficients were > 0.500.

Bayesian hierarchical models

Hierarchical models allow useful application of robust statistical methods to complex multi-level data and are an appropriate quantitative method to evaluate bobwhite-landscape relations among multiple regions (Sauer et al. 2005, Kristan 2006, Kristan and Scott 2006). Most hierarchical modeling of count data is conducted under a Bayesian framework where a hierarchy of fixed and random effects at multiple spatial scales can be modeled within a specified distribution (Link and Sauer 2002, Link et al. 2002, Thogmartin et al. 2004). Bayesian modeling allows for specification of a sampling distribution for the data while allowing concomitantly for specification of probability distributions for unknown parameters (Sauer et al. 2005). Prior distributions are assigned to unknown parameters, from which conditional posterior parameter distributions can be inferred using computationally intensive integration methods such as MCMC (Gilks et al. 1996, Link and Sauer 2002). Parameter estimates are then made from posterior probability distributions conditional on the data and assumed distributions of parameters (Link et al. 2002). If prior distributions are unknown or cannot be assigned, Bayesian modeling allows assignment of non-informative prior distributions to avoid subjectivity in prior distribution assignment (Sauer et al. 2005). Further, hierarchical models can also account for spatial autocorrelation in observed data (Thogmartin et al. 2004), an issue that is ignored frequently in most analyses, but critical to avoid dependency of residual errors (Wintle and Bardos 2006).

Following methods described in Thogmartin et al. (2004), I implemented a Poisson distributed spatial hierarchical count model using MCMC in WinBUGs version 1.4.3 (Lunn et al. 2000) within 5 survey regions (i.e., BCRs). For regional analysis, I treated covariates of landscape composition and configuration as fixed effects, and year, survey point, and unintended excess variation (i.e., noise) as random effects (Thogmartin et al. 2004). I assessed bobwhite-landscape relations at 2 spatial scales (500 m, 1,500 m) around bird survey points. Number of observers and uncertainty in consistency of observer identification across years and sites precluded use of observer as a random effect (Sauer et al. 1994, Link and Sauer 2002).

The region-specific hierarchical model was:

$$\log[\lambda_k] = \sum_{k=1}^{n} \beta_k x_k + \gamma_k + \delta_k + \varepsilon_k \qquad \text{(Equation 3.1)}$$

where year-specific Poisson distributed counts k were indexed with landscape composition and configuration metrics modeled as fixed effects x_k, and random effects of survey point γ_k and year δ_k. I also accounted for extra-Poisson variation by modeling nuisance effects ε_k (Link and Sauer 2002). I used MCMC methods in WinBUGs 4.1.3 (Lunn et al. 2000) to evaluate regional effects of landscape structure on patterns of bird abundance. I assigned non-informative prior distributions to each parameter (Link and Sauer 2002, Link et al. 2002, Gelman 2006) following recommendations defined in Thogmartin et al. (2004). I repeated 60,000 iterations across 3 MCMC chains to better infer posterior parameter distributions and allow for model diagnostics. I thinned parameter outputs to one of every 5 iterations to reduce autocorrelation of MCMC resamples. Because MCMC chains transition from specified initial values to a stationary distribution, I eliminated the first 10,000 iterations (i.e., “burn-in”), determined by visual inspection of MCMC trace plots from analysis (Link and Sauer 2002, Link et al. 2002). I assessed model convergence with the Gelman-Rubin diagnostic, which compares variability within and among MCMC chains (Link and Sauer 2002). I also assessed goodness of model fit over MCMC iterations using a modified Bayesian χ^2 approach [P]

$$P = \sum_k \frac{(y_k - \lambda_k)}{\lambda_k} \qquad \text{(Equation 3.2)}$$

where y_k = observed counts and λ_k = expected counts, by generating a replicated dataset [R] and comparing proportion of iterations where P_R exceeded P_O, of the original dataset [O] (Gelman et al. 1995). A goodness of fit $P = 0.500$ suggests excellent model fit whereas $P < 0.010$ or > 0.990 suggests lack of model fit (Gelman et al. 1995).

I implemented a modified information-theoretic approach (Burnham and Anderson 2002) using 3 modeling stages: 1) screening of variables related to landscape composition and configuration within region to reduce the number of candidate variables; 2) modified forward selection to inform final model selection; and 3) backward selection from “full” models to derive a final candidate model for each region and overall. All candidate models were selected based on biological relevance to bobwhite life history and habitat use, and following evidence in previous bobwhite-landscape studies (Table 3.1). Because region can influence hierarchical bird-landscape models (Sauer et al. 2008), model selection was implemented by region using the Deviance Information Criteria ([DIC]; Spiegelhalter et al. 2002). For initial variable screening (stage one), single-variable models within 5 DIC values of the best approximating model were considered competing, and landscape covariate models >5.0ΔDIC were excluded from remaining stages (Thogmartin et al. 2006). I selected a ΔDIC cutoff >5.0, rather than recommended information theoretic standards of 2.0 or 4.0 (Burnham and Anderson 2002), to allow greater flexibility in model screening processes, and following standards used for model averaging in Thogmartin et al. (2006). I restricted inference to stringent standards of Burnham and Anderson (2002) in subsequent forward and backward selection. Because of extensive cross-scale correlation of landscape variables at 500 and 1,500 m, I selected the spatial scale for a particular landscape covariate which exhibited the least DIC value to move on to remaining stages. In most cases composition and configuration metrics across spatial scales were redundant, thus DIC values were very similar. In the instance that similarly defined or redundant landscape variables (e.g., contagion vs. patch density/patch richness, total edge density vs. woody edge density) were competing at ΔDIC < 5.0, one of the redundant variables was removed to reduce number of model variables. Once landscape covariates were selected through model screening, I implemented forward selection to assess additive effects of landscape variables. I then implemented backward selection from one or a set of representative global models, depending on degree of multicollinearity among model variables. I included a "null model" that included point, year, and extra-Poisson variation without inclusion of landscape variables in forward and backward selection procedures (Thogmartin et al. 2006). Models in forward and backward selection were considered competing if ΔDIC < 4.0 (Burnham and Anderson 2002). If the best approximating model included covariates of % row-crop, %woody cover or woody edge density, I evaluated linear and quadratic forms. I anticipated quadratic relations among bobwhite abundances and these landscape features, with an initial positive or negative linear relationship, followed by a compositional asymptote beyond which bobwhite abundance will decrease or increase (Lindenmayer et al. 2008). Following stage 3 backward selection, I used DIC to calculate model weights and evidence ratios, similar to those described for AIC model selection (Burnham and Anderson 2002), from which I evaluated strength of the top model.

Spatial CAR

Discerning patterns in populations from spatial process is difficult and overlooked frequently in ecological studies (Koenig 1999). Survey sites in my study lacked spatial independence resulting from spatial patterns in buffer enrollment on the landscape and multi-stage nature of the sampling design. Many survey sites were spatially aggregated following spatial distribution of eligible agricultural land within states and further aggregation of CP33 contracts in certain areas. Thus, I assumed bird abundances across survey sites exhibited some degree of spatial autocorrelation. To a lesser degree I accounted for spatial autocorrelation by evaluating region and survey point as random model effects (Thogmartin et al. 2004). To evaluate if I addressed adequately issues of spatial autocorrelation, I compared previously described models to models developed with a Gaussian conditional autoregression [CAR] outlined in Thogmartin et al. (2004, 2006), which assumes counts at a survey point depend spatially on observed counts in the surrounding neighborhood of survey points. I first used a tessellation tool in ArcGIS to create an irregular spatial lattice (clipped at a 50 km^2 extent around each survey point within each region; Fig. 3.1). From this lattice I created a neighborhood structure, from which an adjacency matrix of first-order neighbors (i.e., sharing common boundary) was derived (Thogmartin et al. 2004). The Bayesian hierarchical model was then:

$$\log[\lambda(j)] = \sum_{k=1}^{n} \beta_k x_k(j) + Z_k(j) + \gamma_k(j) + \delta_k(j) + \varepsilon_k$$ (Equation 3.3)

where random effects of spatial neighborhood $Z_k(j)$ were included in the model. I then used DIC to compare the best approximating model within and across regions and with and without incorporation of the spatial CAR to evaluate the need to account for further spatial structuring of data (Thogmartin et al. 2004). Posterior probability estimates on parameters from CAR models were used when determined by DIC. If non-CAR models accounted adequately for spatial structure in the data, posterior probability estimates from non-CAR models were reported.

Results

Regional landscape composition

Regional composition metrics varied across scales for each landscape variable, though were similar in proportion across scales. At the 500 m scale composition of row-crop ranged from 41% (Southeastern Coastal Plain [SCP]) to 67% (Mississippi Alluvial Valley [MAV]) among regions, whereas composition of woody cover ranged from 5% (Central Mixed-grass Prairie [CMP]) to 37% (SCP; Figure 3.2a). Composition of grass (excluding CP33 buffers) ranged from 8% (MAV and CMP) to 12% (SCP and Central Hardwoods [CH]), whereas composition of native herbaceous cover in CP33 buffers was consistently 2-3% among regions (Figure 3.2a). Rangeland, as defined during on-screen digitizing, was only present in the CMP region (16%; Figure 3.2a). Composition of urban-developed classification ranged from 3% (MAV) to 6% (Eastern Tallgrass Prairie [ETP] and SCP) among regions (Figure 3.2a).

At the 1,500 m scale composition of row-crop ranged from 32% (SCP) to 66% (MAV) among regions, whereas composition of woody cover ranged from 5% (CMP) to 46% (SCP) (Figure 3.2b). Composition of grass (excluding CP33 buffers) ranged from 9% (MAV and CMP) to 18% (CH), whereas composition of CP33 upland habitat buffers was consistent (~1%) among regions (Figure 3.2b). Rangeland was again only present, as defined by on-screen digitizing, in the CMP region (20%; Figure 3.2b). Composition of urban-developed classification ranged from 3% (MAV and CMP) to 6% (ETP and SCP) among regions (Figure 3.2b).

Regional northern bobwhite landscape models

Spatial CAR

Incorporation of spatial CAR into top ranking models did not improve model rank in each region (119.76 < ΔDIC > 1644.48). This suggested random effects of survey point and/or explanatory variables included in the model accounted adequately for spatial structure, and hence spatial autocorrelation of bobwhite abundances within each region (Thogmartin et al. 2004).

Central Mixed-grass Prairie (BCR 19)

Stage one model screen for the CMP region revealed 6 landscape variables with ΔDIC < 5.0 (Table 3.2). However, I removed one variable (% CP33 [500]) because of cross-scale (500-1,500 m) correlation ($r^2 = 0.753$), and I added % grass (CP33 excluded [500]) to assess effects of other grass cover in the immediate landscape on bobwhite abundance (Table. 3.2). Correlation coefficients >0.50 were observed between 2 pairs of landscape variables, and correlated variables were excluded in the same candidate model (Table 3.3). Backward selection consisted of 17 candidate models, including a null model comprised of only random effect parameters (Table 3.4). The best approximating model included effects for % grass (CP33 excluded) at 500 m, and % CP33, % urban-developed, and landscape contagion at 1,500 m (Table 3.4; Fig. 3.3-3.4). DIC weight for the top model was 27% and goodness of fit [*P*] = 0.920, suggesting adequate model fit though approaching the upper limit (0.990). Effects of landscape variables on predicted bobwhite abundance included decreasing abundance as % grass (CP33 excluded [500]) increased, increasing abundance as % CP33 (1,500) increased, and decreasing abundance as % urban/developed and contagion (1,500) in the landscape increased (Table 3.5).

Seven models competed with the best approximating model at ΔDIC < 4.0 criteria, and 3 other models competed at the less stringent ΔDIC < 2.0 criteria (Burnham and Anderson 2002; Table 3.4, Appendix A.1-A.3). The evidence ratio between the top model and the second ranked model was 1.59, suggesting weak support for the top ranking approximating model relative to the second ranked model (Burnham and Anderson 2002). The top 4 models had a combined DIC weight of 74%, with all 4 models containing effects of contagion (1,500) and % urban/developed (1,500). The second ranked model removed the effect of % grass (CP33 excluded [500]) from the top model, whereas the third ranking model added % rangeland (1,500) to the second ranked model (Table 3.4).

Eastern Tallgrass Prairie (BCR 22)

Stage one model screen for ETP revealed 9 landscape variables with ΔDIC < 5.0 (Table 3.6). However, I removed 3 variables (total edge density [1,500], contagion [1,500], and % urban-developed [500]) because of variable redundancy (edge density [1,500], contagion [1,500]) and cross-scale (500-1,500 m) correlation ($r^2_{\text{\% urban developed}}$ =

0.611) to further reduce the candidate variable set (Table. 3.6). All candidate landscape variables therefore represented a single scale (1,500 m). Correlation coefficients >0.50 were observed among 6 pairs of landscape variables, and correlated variables were excluded in the same candidate model (Table 3.7). Backward selection consisted of 22 candidate models, including a null model comprised of only random effect parameters (Table 3.8). The best approximating model included % urban-developed, quadratic effects of % row-crop, and patch richness at 1,500 m (Table 3.8; Fig. 3.5-3.6). DIC weight for the top model was 33%, and goodness of fit [*P*] = 0.570, suggesting adequate model fit. Effects of landscape variables on predicted bobwhite abundance included decreasing abundance as % urban-developed (1,500) increased, increasing abundance as patch richness (1,500) landscape increased, and a quadratic relationship with % row-crop (1,500), where bobwhite abundance increased with increasing composition of row-crop up to an asymptote, after which bobwhite abundance decreased (Table 3.9).

Seven models competed with the best approximating model at ΔDIC < 4.0 criteria, and 2 other models competed at less stringent ΔDIC < 2.0 criteria (Burnham and Anderson 2002; Table 3.8, Appendix A.4-A.5). The evidence ratio between the top model and the second ranked model was 1.99 suggesting weak support for the top ranking approximating model relative to the second ranked model (Burnham and Anderson 2002). The top 3 models had a combined DIC weight of 64%, with the second and third ranked model containing patch richness and % urban/developed variables, but removing % row-crop effects and adding effects for patch density in the second model, and quadratic effects of woody edge density in the third model (Table 3.8).

Central Hardwoods (BCR 24)

Stage one model screen for CH revealed all 20 landscape variables exhibited ΔDIC < 5.0 (Table 3.10). I selected scale of landscape variable exhibiting the least DIC to reduce landscape variables in model selection and avoid cross-scale (500-1,500 m) correlations ($r^2_{\text{woody edge density}} = 0.772$; $r^2_{\text{patch density}} = 0.578$; $r^2_{\text{\% CP33}} = 0.708$; $r^2_{\text{\% woody cover}} = 0.780$; $r^2_{\text{\% urban/developed}} = 0.527$) To further reduce number of landscape variables, I also removed variables of total edge density, contagion, % grass (CP33 excluded) and % row-crop at both scales due to redundancy of variables, or ΔDIC > 2.0 (Table. 3.10). Correlation coefficients >0.50 were observed between only 2 pairs of landscape variables, and correlated variables were excluded in the same candidate model (Table 3.11). Backward selection consisted of 28 candidate models, including a null model comprised of only random effect parameters (Table 3.12). The best approximating model included effects for % urban/developed and patch richness at 1,500 m, linear and quadratic effects of % woody cover at 1,500 m, and patch density, % grass (CP33 excluded) and % CP33 at 500 m (Table 3.12; Fig. 3.7-3.8). DIC weight for the top model was only 9% and goodness of fit [*P*] = 0.860, suggesting adequate model fit, though approaching the upper fit limit (0.990). Effects of landscape variables on predicted bobwhite abundance included decreasing abundance as patch density (500) increased, and decreasing abundance and quadratic shape as % woody cover (1,500) increased. The model also suggested increasing abundance as patch richness (1,500) and % grass (CP33 excluded [500]) and % CP33 (500) increased (Table 3.13).

Twenty-one of 28 models competed with the best approximating model at ΔDIC < 4.0 criteria, and 11 models competed at less stringent ΔDIC < 2.0 criteria (Burnham and Anderson 2002; Table 3.12, Appendix A.6-A.16). The evidence ratio between the top model and the second ranked model was 1.04, which suggests very weak support for the top ranking approximating model relative to the second ranked model (Burnham and Anderson 2002). Models competing at ΔDIC < 2.0 had a cumulative DIC weight of 72%, and contained combination of all candidate landscape variables, suggesting little ability to differentiate effects of specific landscape features on bobwhite abundance (Table 3.12).

Mississippi Alluvial Valley (BCR 26)

Stage one model screen for MAV revealed all 20 landscape variables exhibited ΔDIC < 5.0 (Table 3.14). I selected scale of landscape variable exhibiting the least DIC to reduce landscape variables in model selection and avoid cross-scale (500-1,500 m) correlations ($r^2_{\text{woody edge density}} = 0.713$; $r^2_{\text{\% woody cover}} = 0.679$; $r^2_{\text{\% grass}} = 0.789$; $r^2_{\text{\% CP33}} = 0.622$; $r^2_{\text{\% row-crop}} = 0.674$; $r^2_{\text{patch richness}} = 0.558$; $r^2_{\text{\% urban/developed}} = 0.571$; $r^2_{\text{patch density}} = 0.669$). To further reduce number of landscape variables, I also removed variables of total edge density and contagion at both scales due to redundancy of variables (Table. 3.14). Correlation coefficients >0.50 were observed among 10 pairs of landscape variables, and correlated variables were excluded in the same candidate model (Table 3.15). Percentage of row-crop (1,500) was correlated with every other landscape variable and was thus excluded from multi-variable analysis (Table 3.15). Backward selection consisted of 32 candidate models, including a null model comprised of only random effect parameters (Table 3.16). The best approximating model included linear and quadratic effects for woody edge density and linear effects of patch richness at 1,500 m (Table 3.16; Fig. 3.9-3.10). DIC weight for the top model was only 13% and goodness of fit [*P*] = 0.670, suggesting adequate model fit. Effects of landscape variables on predicted bobwhite abundance included decreasing abundance as patch richness (1,500) increased, and a quadratic relationship with % woody cover (1,500), where abundance increased as % woody cover (1,500) increased to an asymptote, beyond which increases in woody cover caused decreases in bobwhite abundance (Table 3.17).

Twenty-five of 32 models competed with the best approximating model at ΔDIC < 4.0 criteria, and 3 models competed at less stringent ΔDIC < 2.0 criteria (Burnham and Anderson 2002; Table 3.16, Appendix A.17-A.19). The evidence ratio between the top model and the second ranked model was 2.60, which suggests minimal support for the top ranking approximating model relative to the second ranked model (Burnham and Anderson 2002). Models competing at ΔDIC < 2.0 had a cumulative DIC weight of only 28%, and primarily contained landscape variables of woody edge density (1,500) and patch richness (1,500), with one model including % CP33 (500; Table 3.16).

Southeastern Coastal Plain (BCR 27)

Stage one model screen for SCP revealed all 20 landscape variables exhibited ΔDIC < 5.0 (Table 3.18). I selected the scale of landscape variable exhibiting the least DIC to reduce landscape variables in model selection and avoid cross-scale (500-1,500 m) correlations ($r^2_{\text{\% woody cover}} = 0.720$; $r^2_{\text{\% urban/developed}} = 0.575$; $r^2_{\text{woody edge density}} = 0.702$; $r^2_{\text{patch density}} = 0.735$; $r^2_{\text{\% row-crop}} = 0.756$; $r^2_{\text{\% grass}} = 0.607$; $r^2_{\text{\% CP33}} = 0.742$). To further reduce number of landscape variables, I also removed variables of total edge density and contagion at both scales due to redundancy of variables (Table. 3.18). Correlation coefficients >0.50 were observed between only one pair of landscape variables (% woody cover [500], % row-crop [500]), and these 2 correlated variables were excluded in the same candidate model (Table 3.19). Backward selection consisted of 22 candidate models, including a null model comprised of only random effect parameters (Table 3.20). The best approximating model included linear and quadratic effects for % row-crop at 500 m and woody edge density at 1,500 m, linear effects of % CP33 and % urban/developed at 1,500 m, and linear effects of % grass (CP33 excluded), patch density, and patch richness at 500 m (Table 3.20; Fig. 3.11-3.12). DIC weight for the top model was only 19% and goodness of fit [*P*] = 0.990, suggesting borderline inadequate model fit to the data (also observed in competing models). Effects of landscape variables on predicted bobwhite abundance included decreasing abundance as % urban/developed and woody edge density (1,500) increased, increasing abundance as % CP33 (1,500), and % grass (CP33 excluded [500]), patch density (500) and patch richness (500) increased, and an increased abundance with % row-crop (500) up to an asymptote, beyond which increases in row-crop caused decreases in bobwhite abundance (Table 3.21).

Eight of 22 models competed with the best approximating model at ΔDIC < 4.0 and more stringent ΔDIC < 2.0 criteria (Burnham and Anderson 2002; Table 3.20, Appendix A.20-A.27). The evidence ratio between the top model and the second ranked model was 1.22, which suggests minimal support for the top ranking approximating model relative to the second ranked model (Burnham and Anderson 2002). Models competing at ΔDIC < 2.0 had a cumulative DIC weight of 94%, and primarily contained multi-variable combinations of landscape variables selected from model screening (Table 3.20).

Discussion

Failure to recognize regional variability in avian response to landscape structure may impair inference regarding bobwhite-landscape relations as patterns may be confounded and true causal mechanisms blurred (Wiens et al. 1987, Peterson et al. 2002, Peterjohn 2003, Thogmartin 2007). Composition and configuration differences in land cover and land use observed among 5 regions in this study warranted a regionally-explicit investigation into bobwhite-landscape associations. Whether due to differences in composition/configuration, land management or species habitat selection preferences, bobwhite-landscape associations and scale of those associations varied among ecological regions. This was predicted by Peterson et al. (2002) who found no range-wide patterns of bobwhite-landscape relations using BBS data (see also Riffell et al. 2008), similar to other farmland (Davey et al. 2010) and neotropical migrant bird species (Flather and Sauer 1996).

Though immediate (i.e., 500 m) landscape variables were included in 3 out of 5 regions, features of landscape structure at 1,500 m from survey points dominated bobwhite-landscape associations in all regions but the Southeastern Coastal Plain, suggesting bobwhite abundances are affected by composition and configuration of the adjacent surrounding landscape in most of their range. These findings are not limited solely to bobwhite, as increasing evidence suggests features of surrounding landscape composition and configuration have far greater effects on forest (e.g., Thogmartin and Knutson 2007) and early-succession (e.g., Siriwardena et al. 2011) bird communities than suspected previously. In the Prairie Hardwood Transition region (BCR 23), Thogmartin and Knutson (2007) found breeding populations of 2 forest species (black-billed cuckoo [*Coccyzus erythropthalmus*], wood thrush [*Hylocichla mustelina*]) to respond to landscape features with greater association at 1.0 km than at 0.1 or 10 km scales. Yet competing models suggested effects of 0.1 and 10 km may also influence bird-habitat associations (Thogmartin and Knutson 2007). In the U.K., models assessing landscape features at 1 km spatial scales were ranked best in 21 of 31 bird species (Siriwardena et al. 2011). This included effects for grey partridge (*Perdix perdix*), a species with similar habitat requirements and population trajectories as bobwhite (Siriwardena et al. 2011). In Europe nearly 80% of bird species inhabiting agricultural landscapes exhibit relations with surrounding landscape structure at a 1 km scale (Soderstrom and Part 2000). Similarly, breeding season bobwhite abundances and responses to agricultural conservation practices were dominated by composition of agriculture and forest at 2.5 km scales in North Carolina (Riddle et al. 2008).

Features associated with surrounding landscape heterogeneity were also important predictors of bobwhite abundance in all 5 regions in my study, suggesting configuration of habitat patches in combination with patch composition, particularly at the 1,500 m-scale, may be important for population persistence. Bobwhites were associated positively with patch richness (i.e., number of different patch types in the landscape) in Eastern Tallgrass Prairie and Central Hardwoods, associated positively with patch richness and patch density (i.e., number of patches per unit area) in the Southeastern Coastal Plain, and associated negatively with contagion (a measure of aggregation of patch types) in Central Mixed-grass Prairie. This suggests heterogeneity of cover types, representing variability in habitat types, may meet greater resource requirements (Siriwardena et al. 2011).

Studies in Illinois and Virginia suggest bobwhite abundances are influenced by configuration of habitat patches (Thogmartin 2002) and are associated strongly with heterogeneous and patchy landscapes dominated by 30-70% row-crop agriculture, 12-30% grassland, and a component of woody edge density (Roseberry and Sudkamp 1998, Schairer et al. 1999). In Mississippi, bobwhites were associated negatively with landscape contagion (Conover 2009). In contrast, bobwhite abundances in Oklahoma and the West Gulf Coastal Plain were associated negatively with patch diversity and positively with aggregation of row-crop (Guthery et al. 2001, Twedt et al. 2007). These results led Guthery et al. (2001) to suggest bobwhite responded more strongly to position of land cover classes than to configuration of those classes, which is in direct contrast to results presented here. However, in Oklahoma, replacement of native rangeland habitats with row-crop may have influenced Guthery et al (2001)'s results, as native rangeland habitat likely formerly met all resource requirements necessary to bobwhite such that composition would dominate bobwhite-landscape associations in this region. In the West Gulf Coastal Plain, bobwhite response to aggregation of row-crop may be attributed to limited availability of other alternative early successional habitat (Twedt et al. 2007).

Compositional associations were also evident within regions and at different spatial scales. Percentage of urbanized or developed land area (1,500) was associated negatively with bobwhite abundance in 3 out of 5 regions (Eastern Tallgrass Prairie, Central Mixed-grass Prairie, and Southeastern Coastal Plain). Though bobwhite may be elastic to a diversity of cover types, my results present evidence that bobwhites may be disproportionately averse to urbanized and developed landscapes (see also Conover [2009] in Mississippi). Further, strong associations with row-crop were found only in the Eastern Tallgrass Prairie (a quadratic relationship), though a weaker quadratic association with % row-crop was also observed in the Southeastern Coastal Plain. Row-crop has been shown previously to exhibit strong associations with bobwhite abundance in Oklahoma (Brady et al. 1993, Guthery et al. 2001), Mississippi and the West Gulf Coastal Plain region (Twedt et al. 2007, Conover 2009), Illinois (Roseberry and Sudkamp 1998), Virginia (Schairer et al. 1999), and across the Eastern U.S. (Murphy 2003). However these relationships varied in direction, with studies demonstrating positive and negative row-crop associations in different areas and at varying scales (see summary in Table 3.1).

Amount of woody cover and woody edge density in excess of some threshold quantity may also influence negatively bobwhite abundance in agricultural landscapes (Schairer et al. 1999, Guthery et al. 2001, Seckinger et al. 2008, Conover 2009). I observed negative relations with woody cover in the Central Hardwoods (30% woody cover), and with woody cover and woody edge density in the Southeastern Coastal Plains (where woody cover exceeds 45% at 1,500 m). The 2 regions with greatest amount of woody cover demonstrated the strongest negative relations between woody cover and bobwhite abundance. Bobwhite abundance was also related quadratically to woody edge density in the Mississippi Alluvial Valley, a historically forested, but presently agriculture-dominated region. Similarly, Riddle et al. (2008) demonstrated bobwhite abundance and response to conservation practices were influenced negatively by amount of forest cover in the surrounding landscape in North Carolina. However, bobwhites occur frequently in open-canopy, disturbance maintained forest lands, where combinations of native annual and perennial herbaceous ground cover and shrubs provide appropriate habitat to sustain substantial population densities, primarily in the Southeast (Burger 2001). Negative associations with woody cover observed in the Central Hardwoods and Southeastern Coastal Plain are likely related to modern forest management practices that involve fire exclusion, dominated by closed-canopy forest structure and not forested systems in general.

As bobwhites depend on grass cover for nesting, amount of grass habitat is often associated positively with bobwhite abundance in agricultural landscapes (e.g., Brady et al. 1993, Twedt et al. 2007, Conover 2009). Amount of grass (excluding that available in

CP33 buffers) was related positively with abundance at 500 m in the Southeastern Coastal Plain and Central Hardwoods, but associated negatively in the Central Mixed-grass Prairie, further supporting evidence of regional variation in bird-habitat associations (Whittingham et al. 2007). Potential causal mechanisms behind negative effects of grass in CMP include sufficient alternative habitats in rangeland areas. Alternatively, perhaps on-screen digitizing of grasslands in this region were limited to exotic grass pastures, with remaining grass habitats characterized into rangeland classification. Native grass habitat provided by CP33 upland habitat buffers showed positive, but weak associations in Central Mixed-grass Prairie, Central Hardwoods, and the Southeastern Coastal Plain, which may be attributed to limited proportion of native herbaceous cover in CP33 buffers within the landscape (e.g., ~1% at 1,500 m).

Though results of this study demonstrate regionally-specific associations among bobwhite abundances and composition and configuration of the local and surrounding landscape, there is no guarantee that landscape metrics are not confounded with other, unmeasured, ecological processes (Thogmartin et al. 2004). For example, relationships with woody cover may be spurious products of biological processes of predation. This study cannot draw inference regarding ecological processes driving observed landscape associations (Dunning et al. 2002, Lindenmayer et al. 2008), but does establish a framework for further investigation into regionally-explicit ecological processes from observed patterns. Further, I only assessed structural and not functional heterogeneity of landscapes (Fahrig et al. 2011). Bobwhites likely perceive landscapes differently than expected such that land cover classification is not necessarily synonymous with habitat (Lindenmayer et al. 2008). Finally, I was also limited in this data set to a fixed single-year land cover representative of a "cross-section" of the range of 2006-2008 bird data

(Flather and Sauer 1996). Thus I could not assess change in bird abundance across time in relation to changing landscape variables, nor could I evaluate cumulative effects of crop succession or rotation across years. However, NAIP imagery used in my study represented a mid-point in the 3-year bird monitoring effort (2007), such that bird data was at most only one year removed from classified land cover. Thus, I would not expect major changes in land cover or land use to occur within the time frame of bird data collection.

This study demonstrates the importance of approaching bobwhite conservation from a regional perspective and emphasizes the necessity to assess local habitat and surrounding landscape context during conservation planning (Dallimer et al. 2010). This study also demonstrates that conservation at the patch level must be implemented within context of the adjacent landscape mosaic (Lindenmayer et al. 2008). Management within a single patch will likely fail if the adjacent landscape mosaic is not accounted for or managed (Lindenmayer et al. 2008). Broadening conservation to a landscape context as is being currently implemented in many states via the "focus area" approach, may elicit much greater net population benefits for declining species such as bobwhite (Benton et al. 2003). Because heterogeneity of habitat types may be critical to bobwhite success in each region, managers should focus on "softening" agricultural landscapes via integration of conservation within production systems when possible.

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Table 3.1 Description of landscape composition and configuration metrics used to evaluate northern bobwhite-landscape associations at 500 and 1,500 m spatial scales across a 14 state study area, 2006-2008. Metrics were selected based on findings of previous studies or biological relevance based on life-history characteristics.

Landscape metric	Description	Previous research
% Row-crop	Percentage of area in row-crop agriculture relative to total landscape area.	+ Roseberry and Sudkamp (1998) + Schairer et al. (1999) + Thogmartin (2002) + Murphy (2003) + Flock (2006) - Brady et al. (1993) - Guthery et al. (2001) - Conover (2009)
% CP33	Percentage of area in CP33 native herbaceous buffers relative to total landscape area.	Evans (this document)
% Woody cover	Percentage of area in early-mature forest cover relative to total landscape area.	+ Brady et al. (1993) + Thogmartin (2002) + Flock (2006) - Schairer et al. (1999) - Conover (2009)
% Urban-developed	Percentage of area subject to urbanization/human development relative to total landscape area. Includes roads > 5m in width, housing developments, mowed yards, and industrial areas.	- Conover (2009)
% Grass	Percentage of area in grass cover relative to total landscape area. Excludes CP33 buffer cover. Includes pasture and hay and other herbaceous cover. Does not separate native vs. introduced grass species.	+ Exum et al. (1982) + Brady et al. (1993) + Roseberry and Sudkamp (1998) + Twedt et al. (2007) + Conover (2009)
% Rangeland (CMP)	Percentage of area in rangeland relative to total landscape area. Excludes pasture and hay fields and other herbaceous cover. Limited to the Central Mixed-grass Prairie region only.	

Table 3.1 (Continued)

Patch richness	Number of different habitat patch types within landscape area.	+ Roseberry and Sudkamp (1998) (patch diversity) - Guthery et al. (2001) (patch diversity) - Thogmartin (2002) (evenness)
Contagion	Spatial aggregation of habitat patch types within landscape area.	+ Twedt et al. (2007) (ag clumpiness) - Conover (2009)
Patch density	Number of patches (regardless of type) divided by landscape area.	+ Roseberry and Sudkamp (1998)
Total edge density	Sum of all edge divided by landscape area. Edge defined as juxtaposition between 2 cover types.	- Twedt et al. (2007) (total edge)
Woody edge density	Sum of all woody edge divided by landscape area. Edge defined as juxtaposition between woody cover and an alternative cover type.	+ Roseberry and Sudkamp (1998) + Schairer et al. (1999) + Twedt et al. (2007) (forest edge) - Guthery et al. (2001) - Seckinger et al. (2008)

Table 3.2 Results from stage one model screen for hierarchical modeling of northern bobwhite-landscape associations within the Central Mixed-grass Prairie region (BCR 19), 2006-2008. Models with change in Deviance Information Criteria [ΔDIC] > 5.0 were excluded. Percentage of CP33 (500) exhibited ΔDIC < 5.0 but was removed from subsequent models due cross-scale correlation with % CP33 (1,500). Percentage of grass (CP33 excluded) (500) was included in model selection. Variables in italics were retained in subsequent model selection.

Landscape variable	Scale (m)	DIC	ΔDIC
% CP33	1,500	2,900.32	0
Patch richness	1,500	2,900.43	0.11
% CP33	500	2,903.11	2.79
Contagion	1,500	2,904.06	3.74
%Urban/developed	1,500	2,904.84	4.52
% Rangeland	1,500	2,904.97	4.65
% Grass (CP33 excluded)	500	2,905.42	5.10
Contagion	500	2,905.45	5.13
% Row-crop	1,500	2,905.46	5.14
Patch richness	500	2,905.62	5.30
% Row-crop	500	2,905.64	5.32
% Rangeland	500	2,905.68	5.36
Patch density	1,500	2,906.30	5.98
Woody edge density	500	2,906.49	6.17
% Woody cover	500	2,906.51	6.19
Total edge density	1,500	2,906.62	6.30
% Woody cover	1,500	2,906.83	6.51
Woody edge density	1,500	2,906.83	6.51
Total edge density	500	2,906.84	6.52
%Urban/developed	500	2,907.19	6.87
% Grass (CP33 excluded)	1,500	2,907.45	7.13
Patch density	500	2,907.47	7.15

Table 3.3 Spearman correlations for the Central Mixed-grass Prairie region (BCR 19) for variables selected in stage one model screen analysis of northern bobwhite landscape associations at 500 and 1,500 m scales, 2007.

	% Grass (500)	% CP33 (1,500)	% Urban/developed (1,500)	% Rangeland (1,500)	Contagion (1,500)
% CP33 (1,500)	-0.112				
% Urban/developed (1,500)	0.027	0.035			
% Rangeland (1,500)	-0.508*	0.249	0.023		
Contagion (1,500)	-0.166	-0.131	-0.156	-0.280	
Patch richness (1,500)	0.114	0.545*	-0.019	0.095	-0.135

*Variables with correlation coefficients > 0.500 were not included in the same model.

Table 3.4 Model rank, based on change in Deviance Information Criteria [ΔDIC], and DIC weight for models developed via stage 3 backward selection for hierarchical modeling of northern bobwhite landscape associations at 500 and 1,500 m scales within the Central Mixed-grass Prairie region (BCR 19), 2006-2008.

Rank	Model	DIC	ΔDIC	DIC weight
1	%Grass^{500} + %CP33^{1,500} + Contagion^{1,500} + %Urban/developed^{1,500}	2,894.66	0	0.270
2	%CP33^{1,500} + Contagion^{1,500} + %Urban/developed^{1,500}	2,895.59	0.93	0.170
3	%CP33^{1,500} + Contagion^{1,500} + %Urban/developed^{1,500} + %Rangeland^{1,500}	2,895.7	1.04	0.161
4	%Grass^{500} + Patch Richness^{1,500} + Contagion^{1,500} + %Urban/developed^{1,500}	2,896.22	1.56	0.124
5	%CP33^{1,500} + %Urban/developed^{1,500}	2,897.23	2.57	0.075
6	Patch richness^{1,500} + Contagion^{1,500} + %Urban/developed^{1,500} + %Rangeland^{1,500}	2,897.47	2.81	0.066
7	Patch richness^{1,500} + Contagion^{1,500} + %Urban/developed^{1,500}	2,898.39	3.73	0.042
8	%Grass^{500} + Contagion^{1,500} + %Urban/developed^{1,500}	2,898.40	3.74	0.042
9	%CP33^{1,500}	2,900.32	5.66	0.016
10	Patch Richness^{1,500}	2,900.69	6.03	0.013
11	Contagion^{1,500} + %Urban/developed^{1,500}	2,901.28	6.62	0.010
12	%Grass^{500}+ %Urban/developed^{1,500}	2,903.34	8.68	0.004
13	Contagion^{1,500}	2,904.01	9.35	0.003
14	%Urban/developed^{1,500}	2,904.59	9.93	0.002
15	%Rangeland^{1,500}	2,904.97	10.31	0.002
16	%Grass^{500}	2,905.82	11.16	0.001
17	Null	2,907.02	12.36	0.001

Table 3.5 Mean posterior probability estimates, standard deviation (SD), Monte Carlo error (MCE), 95% percentiles, and median posterior probability estimates for the best approximating model of northern bobwhite abundance in the Central Mixed-grass Prairie region (BCR 19), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	-5.375	2.428	0.133	-9.373	-0.447	-5.431
% Grass^{500}	beta1	-0.088	0.052	0.000	-0.191	0.012	-0.087
% CP33^{1,500}	beta2	0.107	0.036	0.000	0.037	0.178	0.107
Contagion^{1,500}	beta3	-0.116	0.047	0.000	-0.208	-0.025	-0.115
% Urban/developed^{1,500}	beta4	-0.156	0.048	0.000	-0.251	-0.065	-0.156

Table 3.6 Results from stage one model screen for hierarchical modeling of northern bobwhite landscape associations within the Eastern Tallgrass Prairie region (BCR 22), 2006-2008. Models with change in Deviance Information Criteria [ΔDIC] > 5.0 were excluded. Total edge density (1,500), contagion (1,500), and % urban/developed (500) exhibited ΔDIC < 5.0 but were removed from subsequent models due to redundancy (total edge density, contagion) or cross-scale correlation (urban/developed). Variables in italics were retained in subsequent model selection.

Landscape Variable	Scale (m)	DIC	ΔDIC
Patch density	1,500	4,578.76	0.000
Total edge density	1,500	4,578.96	0.200
% Grass (CP33 excluded)	1,500	4,580.75	1.990
% Urban/developed	1,500	4,581.6	2.840
Woody edge density	1,500	4,581.95	3.190
Patch richness	1,500	4,582.72	3.960
Contagion	1,500	4,582.73	3.970
% Urban/developed	500	4,583.02	4.260
% Row-crop	1,500	4,583.76	5.000
% Grass (CP33 excluded)	500	4,584.61	5.850
Patch richness	500	4,584.87	6.110
Patch density	500	4,585.2	6.440
Total edge density	500	4,585.27	6.510
% Woody cover	1,500	4,586.46	7.700
Woody edge density	500	4,586.93	8.170
% Row-crop	500	4,587.52	8.760
Contagion	500	4,588.29	9.530
% Woody cover	500	4,589.65	10.890
% CP33	1,500	4,590.16	11.400
% CP33	500	4,590.44	11.680

Table 3.7 Spearman correlations the Eastern Tallgrass Prairie region (BCR 22) for variables selected in stage one model screen analysis of northern bobwhite landscape associations at 500 and 1,500 m scales, 2007.

	% Row-crop (1,500)	Woody edge density (1,500)	% Urban/developed (1,500)	Patch density (1,500)	Patch richness (1,500)
Woody edge density (1,500)	-0.860*				
% Urban/developed (1,500)	-0.184	0.063			
Patch density (1,500)	-0.683*	0.764*	-0.051		
Patch richness (1,500)	-0.388	0.401	-0.021	0.418	
% Grass (CP33 excluded) (1,500)	-0.741*	0.624*	-0.135	0.722*	0.307

*Variables with correlation coefficients >0.500 were not included in the same model.

Table 3.8 Model rank, based on change in Deviance Information Criteria [ΔDIC], and DIC weight for models developed via stage 3 backward selection for hierarchical modeling of northern bobwhite landscape associations at 500 and 1,500 m scales within the Eastern Tallgrass Prairie region (BCR 22), 2006-2008.

Rank	Model	DIC	ΔDIC	DIC weight
1	%Urban/developed^{1,500} + %Row-crop^{1,500} + (Rowcrop^{1,500})^{2} + Patch Richness^{1,500}	4,565.50	0	0.332
2	Patch Density^{1,500} + Patch Richness^{1,500} + %Urban/Developed ^{1,500}	4,566.88	1.38	0.167
3	%Urban/Developed^{1,500} + Woody Edge Density^{1,500} + (Woody edge density^{1,500})^{2} + Patch Richness^{1,500}	4,567.21	1.71	0.141
4	%Urban/developed^{1,500} + %Row-crop^{1,500} + Patch Richness^{1,500}	4,567.82	2.32	0.104
5	%Grass^{1,500} + Patch Richness^{1,500} + %Urban/developed^{1,500}	4,568.32	2.82	0.081
6	%Urban/developed^{1,500} + Woody Edge Density^{1,500} + Patch Richness^{1,500}	4,568.40	2.90	0.078
7	Patch Density^{1,500} + %Urban/developed^{1,500}	4,569.22	3.72	0.052
8	%Urban/developed^{1,500} + %Row-crop^{1,500}	4,571.32	5.82	0.018
9	%Urban/developed^{1,500} + Woody Edge Density^{1,500}	4,572.30	6.80	0.011
10	%Grass^{1,500} + %Urban/developed^{1,500}	4,573.64	8.14	0.006
11	Patch Richness^{1,500} + %Urban/developed^{1,500}	4,573.68	8.18	0.006
12	Patch Density^{1,500} + Patch Richness^{1,500}	4,576.13	10.63	0.002
13	%Grass^{1,500} + Patch Richness^{1,500}	4,576.18	10.68	0.002
14	Woody Edge Density^{1,500} + Patch Richness^{1,500}	4,578.67	13.17	0.0005
15	Patch Density^{1,500}	4,579.00	13.5	0.0004
16	%Row-crop^{1,500} + Patch Richness^{1,500}	4,579.92	14.42	0.0002
17	%Grass^{1,500}	4,580.45	14.95	0.0002
18	% Urban/developed^{1,500}	4,581.39	15.89	0.0001
19	Woody Edge Density^{1,500}	4,581.63	16.13	0.0001
20	Patch Richness^{1,500}	4,582.65	17.15	0.00006
21	%Row-crop^{1,500}	4,583.69	18.19	0.00004
22	Null	4,590.27	24.77	0.000001

Table 3.9 Mean posterior probability estimates, standard deviation (SD), Monte Carlo error (MCE), 95% percentiles, and median posterior probability estimates for the best approximating model of northern bobwhite abundance in the Eastern Tallgrass Prairie region (BCR 22), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	-4.801	8.252	0.455	-18.780	12.290	-6.628
% Urban/ developed ^{1,500}	beta1	-0.716	0.119	0.001	-0.953	-0.488	-0.714
% Row-crop^{1,500}	beta2	1.023	0.732	0.028	-0.395	2.430	1.025
(% Row-crop^{1,500})^2	beta3	-1.401	0.676	0.026	-2.706	-0.090	-1.401
Patch richness^{1,500}	beta4	0.286	0.135	0.002	0.022	0.552	0.285

Table 3.10 Results from stage one model screen for hierarchical modeling of northern bobwhite landscape associations within the Central Hardwoods region (BCR 24), 2006-2008. All candidate landscape variables exhibited change in Deviance Information Criteria [ΔDIC] > 5.0. Scale of landscape variable was chosen based on least DIC. Variables in italics were retained in subsequent model selection.

Landscape Variable	Scale	DIC	ΔDIC
Patch richness	1,500	2,313.17	0
Woody edge density	500	2,314.13	0.96
Patch richness	500	2,314.19	1.02
Patch density	500	2,314.62	1.45
Edge density	500	2,314.77	1.60
% CP33	500	2,314.79	1.62
% Woody cover	1,500	2,315.01	1.84
Patch density	1,500	2,315.13	1.96
% Urban/developed	1,500	2,315.30	2.13
% Urban/developed	500	2,315.32	2.15
Edge density	1,500	2,315.34	2.17
% Woody cover	500	2,315.38	2.21
Woody edge density	1,500	2,315.43	2.26
% Grass (CP33 excluded)	500	2,315.49	2.32
% CP33	1,500	2,315.51	2.34
% Grass (CP33 excluded)	1,500	2,315.83	2.66
Contagion	500	2,315.88	2.71
Contagion	1,500	2,315.89	2.72
% Row-crop	500	2,316.07	2.90
% Row-crop	1,500	2,316.46	3.29

Table 3.11 Spearman correlations for the Central Hardwoods region (BCR 24) for variables selected in stage one model screen analysis of northern bobwhite landscape associations at 500 and 1,500 m scales, 2007.

	% CP33 (500)	Woody edge density (500)	Patch density (500)	% Woody cover (1,500)	% Urban/developed (1,500)
Woody edge density (500)	0.055				
Patch density (500)	0.316	0.536*			
% Woody cover (1,500)	0.013	0.678*	0.331		
% Urban/developed (1,500)	0.010	-0.210	0.202	-0.375	
Patch richness (1,500)	0.439	-0.097	0.094	-0.083	0.076

*Variables with correlation coefficients >0.500 were not included in the same model.

Table 3.12 Model rank, based on change in Deviance Information Criteria [ΔDIC], and DIC weight for models developed via stage 3 backward selection for hierarchical modeling of northern bobwhite landscape associations at 500 and 1,500 m scales within the Central Hardwoods region (BCR 24), 2006-2008.

Rank	Model	DIC	ΔDIC	DIC weight
1	Patch richness^{1,500} + %Woody cover^{1,500} + (%Woody cover^{1,500})^{2} + Patch density^{500} + % Grass^{500} + %CP33^{500}	2,310.78	0	0.101
2	Patch richness^{1,500} + %Woody cover^{1,500} + Patch density^{500} + %Grass^{500} + %CP33^{500}	2,310.85	0.07	0.098
3	Patch richness^{1,500} + %Woody cover^{1,500} + Patch density^{500}+ %Grass^{500} + %CP33^{500} + Urban/developed^{1,500}	2,311.16	0.38	0.084
4	Woody edge density^{500} + %Grass^{500} + %CP33^{500} + Patch richness^{1,500}	2,311.29	0.51	0.078
5	Woody edge density^{500} + %Urban/developed^{1,500} + %Grass ^{500} + %CP33^{500} + Patch richness^{1,500}	2,311.50	0.72	0.070
6	Woody edge density^{500} + Patch richness^{1,500}	2,311.87	1.09	0.059
7	Woody edge density^{500} + %CP33^{500} + Patch richness^{1,500}	2,312.01	1.23	0.055
8	Patch richness^{1,500} + %Woody cover^{1,500} + Patch density^{500}	2,312.08	1.3	0.053
9	Patch richness^{1,500} + %Woody cover^{1,500} + Patch density^{500} + %CP33^{500}	2,312.16	1.38	0.051
10	Patch density^{500} + %Woody cover^{1,500} + %Grass^{500}+ %CP33^{500}	2,312.34	1.56	0.046
11	Patch richness^{1,500} + %Woody cover^{1,500}	2,312.64	1.86	0.040
12	Patch density^{500} + %Woody cover^{1,500} + %Urban/developed^{1,500} + %Grass^{500} + %CP33^{500}	2,312.73	1.95	0.038
13	Patch richness^{1,500}	2,312.87	2.09	0.036
14	Patch density^{500} + %Woody cover^{1,500}+ %CP33^{500}	2,313.80	3.02	0.022
15	%Row-crop^{500} + Patch richness^{1,500}	2,313.90	3.12	0.021
16	%Row-crop^{500} + %CP33^{500} + Patch richness^{1,500}	2,314.00	3.22	0.020
17	%Row-crop^{500} + %CP33^{500} + %Urban/developed^{1,500} + Patch richness^{1,500}	2,314.07	3.29	0.019
18	Woody edge density^{500}	2,314.23	3.45	0.018
19	%Woody cover^{1,500}+ %CP33^{500}	2,314.46	3.68	0.016
20	Patch density^{500}	2,314.77	3.99	0.014
21	%Woody cover^{1,500}	2,314.88	4.1	0.013

Table 3.12 (Continued)

22	%CP33^{500}	2,314.96	4.18	0.012
23	%Urban/developed^{1,500}	2,315.29	4.51	0.011
24	%Grass^{500}	2,315.44	4.66	0.010
25	Null	2,315.44	4.66	0.010
26	%Row-crop^{500}	2,316.40	5.62	0.006

Table 3.13 Mean posterior probability estimates, standard deviation (SD), Monte Carlo error (MCE), 95% percentiles, and median posterior probability estimates for the best approximating model of northern bobwhite abundance in the Central Hardwoods region (BCR 24), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	-16.650	12.550	0.692	-43.170	0.871	-13.420
Patch richness^{1,500}	beta1	0.310	0.179	0.001	-0.039	0.663	0.310
% Woody cover^{1,500}	beta2	-0.252	0.530	0.011	-1.294	0.798	-0.250
(% Woody cover^{1,500})^2	beta3	-0.100	0.488	0.010	-1.070	0.850	-0.101
Patch density^{500}	beta4	-0.337	0.163	0.002	-0.659	-0.024	-0.334
% Grass^{500}	beta5	0.165	0.130	0.001	-0.089	0.421	0.164
% CP33^{500}	beta6	0.259	0.109	0.001	0.044	0.474	0.258

Table 3.14 Results from stage one model screen for hierarchical modeling of northern bobwhite landscape associations within the Mississippi Alluvial Valley region (BCR 26), 2006-2008. No models exhibited change in Deviance Information Criteria [ΔDIC] > 5.0, thus screening was conducted by removing cross-scale variables with the greatest DIC. Total edge density and contagion were also removed from subsequent models due to redundancy. Variables in italics were retained in subsequent model selection.

Landscape Variable	Scale	DIC	ΔDIC
Woody edge density	1,500	800.96	0
% Woody cover	1,500	801.96	1.01
% Woody cover	500	802.49	1.53
Woody edge density	500	802.51	1.55
% Grass (CP33 excluded)	1,500	802.55	1.59
% CP33	500	802.62	1.66
% Row-crop	1,500	802.77	1.81
Contagion	1,500	802.77	1.81
Patch richness	1,500	802.86	1.90
Patch richness	500	802.93	1.97
Edge density	1,500	803.10	2.14
% Urban/developed	500	803.14	2.18
% CP33	1,500	803.15	2.19
Patch density	1,500	803.25	2.29
Contagion	500	803.63	2.67
% Grass (CP33 excluded)	500	803.65	2.70
% Row-crop	500	803.79	2.84
Patch density	500	803.95	3.00
Edge density	500	804.05	3.09
% Urban/developed	1,500	804.08	3.12

Table 3.15 Spearman correlations for the Mississippi Alluvial Valley region (BCR 26) for variables selected in stage one model screen analysis of northern bobwhite landscape associations at 500 and 1,500 m scales, 2007.

	% CP33 (500)	% Urban/ developed (500)	% Row-crop (1,500)	% Woody cover (1,500)	Woody edge density (1,500)	Patch density (1,500)	Patch richness (1,500)
% Urban/ developed (500)	-0.057						
% Row-crop (1,500)	-0.213	-0.034					
% Woody cover (1,500)	0.053	-0.108	-0.840*				
Woody edge density (1,500)	0.169	-0.034	-0.645*	0.652*			
Patch density (1,500)	0.301	0.310	-0.543*	0.247	0.621*		
Patch richness (1,500)	0.298	0.110	-0.555*	0.331	0.392	0.593*	
% Grass (CP33 excluded) (1,500)	0.257	0.200	-0.664*	0.354	0.497	0.711*	0.634*

*Variables with correlation coefficients > 0.500 were not included in the same model.

Table 3.16 Model rank, based on change in Deviance Information Criteria [ΔDIC], and DIC weight for models developed via stage 3 backward selection for hierarchical modeling of northern bobwhite landscape associations at 500 and 1,500 m scales within the Mississippi Alluvial Valley region (BCR 26), 2006-2008.

Rank	Model	DIC	ΔDIC	DIC Weight
1	Woody edge density^{1,500} + (Woody edge density1,500)^{2} + Patch richness^{1,500}	798.91	0.00	0.133
2	Woody edge density^{1,500} + Patch richness^{1,500}	800.83	1.91	0.051
3	Woody edge density^{1,500} + Patch richness^{1,500} + %CP33^{500}	800.88	1.96	0.050
4	Woody edge density^{1,500}	800.88	1.97	0.050
5	Woody edge density^{1,500} + %CP33^{500}	800.93	2.01	0.049
6	Woody edge density^{1,500} + Patch richness^{1,500} + %Urban/developed^{500} + %CP33^{500}	801.03	2.12	0.046
7	Woody edge density^{1,500} + Patch richness^{1,500} + %Urban/developed^{500}	801.22	2.31	0.042
8	Woody edge density^{1,500} + %Urban/developed^{500}	801.23	2.31	0.042
9	Woody edge density^{1,500} + %Urban/developed ^{500} + %CP33^{500}	801.27	2.36	0.041
10	%CP33^{500} + Patch richness^{1,500} + %Woody cover^{1,500}	801.81	2.90	0.031
11	Woody edge density^{1,500} + %Grass^{1,500} + %Urban/developed^{500}	801.98	3.07	0.029
12	Woody edge density^{1,500} + %Grass^{1,500}	802.03	3.11	0.028
13	%Woody cover^{1,500}	802.06	3.15	0.028
14	Woody edge density^{1,500} + %Grass^{1,500} + %Urban/developed^{500} + %CP33^{500}	802.24	3.33	0.025
15	%Urban/developed^{500} + Patch richness^{1,500} + %Woody cover^{1,500}	802.35	3.44	0.024
16	%Urban/developed^{500} + %Woody cover^{1,500}	802.42	3.50	0.023
17	%CP33^{500} + %Urban/developed^{500} + Patch richness^{1,500} + %Woody cover^{1,500}	802.43	3.52	0.023
18	Null	802.43	3.52	0.023
19	%Grass^{1,500}	802.47	3.55	0.023
20	%Woody cover^{1,500} + Patch density^{1,500}	802.48	3.56	0.022
21	% CP33^{500}	802.63	3.71	0.021

Table 3.16 (Continued)

22	%Woody cover^{1,500} + %Grass^{1,500} + %Urban/developed^{500}	802.64	3.73	0.021
23	%Woody cover^{1,500} + Patch density^{1,500} + %Urban/developed^{500} + %CP33^{500}	802.68	3.76	0.020
24	%Woody cover^{1,500} + %Grass^{1,500} + %Urban/developed^{500} + %CP33^{500}	802.68	3.76	0.020
25	%Row-crop^{1,500}	802.70	3.78	0.020
26	%Woody cover^{1,500} + Patch density^{1,500} + %Urban/developed^{500}	802.79	3.88	0.019
27	%CP33^{500} + %Urban/developed^{500}	803.05	4.13	0.017
28	Patch richness^{1,500}	803.05	4.14	0.017
29	%CP33^{500} + %Row-crop^{1,500} + %Urban/developed^{500}	803.07	4.16	0.017
30	%Row-crop^{1,500} + %Urban/developed^{500}	803.10	4.19	0.016
31	%Urban/developed^{500}	803.19	4.27	0.016
32	Patch density^{1,500}	803.39	4.48	0.014

Table 3.17 Mean posterior probability estimates, standard deviation (SD), Monte Carlo error (MCE), 95% percentiles, and median posterior probability estimates for the best approximating model of bobwhite abundance in the Mississippi Alluvial Valley region (BCR 26), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	-14.380	15.590	0.858	-46.610	10.420	-12.150
Woody edge density^{1,500}	beta1	1.398	0.604	0.008	0.238	2.610	1.388
(Woody edge density^{1,500})^2	beta2	-0.949	0.518	0.007	-1.993	0.041	-0.937
Patch richness^{1,500}	beta3	-0.300	0.140	0.001	-0.579	-0.030	-0.299

Table 3.18 Results from stage one model screen for hierarchical modeling of northern bobwhite landscape associations within the Southeastern Coastal Plain region (BCR 27), 2006-2008. Models with change in Deviance Information Criteria [ΔDIC] > 5.0 were excluded. Total edge density and contagion at both scales exhibited ΔDIC < 5.0 but were removed from subsequent models due to variable redundancy. Variables in bold italics were retained in subsequent model selection.

Landscape variable	Scale (m)	DIC	ΔDIC
% Woody cover	500	4,663.79	0
% Urban/developed	1,500	4,665.68	1.89
Woody edge density	1,500	4,665.84	2.05
Woody edge density	500	4,666.09	2.30
Patch density	500	4,666.36	2.57
% Row-crop	500	4,666.46	2.67
Edge density	500	4,666.46	2.67
% Row-crop	1,500	4,666.53	2.74
% Grass (no CP33)	500	4,666.62	2.83
% Urban/developed	500	4,666.67	2.88
% Grass (no CP33)	1,500	4,666.69	2.90
Patch richness	500	4,666.80	3.01
% Woody cover	1,500	4,666.99	3.20
Patch richness	1,500	4,667.08	3.29
% CP33	1,500	4,667.23	3.44
% CP33	500	4,667.27	3.48
Patch density	1,500	4,667.33	3.54
Edge density	1,500	4,667.4	3.61
Contagion	1,500	4,667.43	3.64
Contagion	500	4,667.56	3.77

Table 3.19 Spearman correlations Southeastern Coastal Plain region (BCR 27) for variables selected in stage one model screen analysis of northern bobwhite landscape associations at 500 and 1,500 m scales, 2007.

	% Woody Cover (500)	% Row-crop (500)	Patch density (500)	Patch richness (500)	% Grass (CP33 excluded) (500)	% CP33 (1,500)	Woody edge density (1,500)
% Row-crop (500)	-0.712*						
Patch density (500)	-0.081	-0.106					
Patch richness (500)	0.060	-0.352	0.485				
% Grass (CP33 excluded) (500)	-0.157	-0.412	0.359	0.439			
% CP33 (1,500)	0.071	-0.261	0.052	0.275	0.084		
Woody edge density (1,500)	0.159	-0.224	0.354	0.364	0.266	0.078	
% Urban/ developed (1,500)	0.014	-0.195	0.211	0.157	0.130	-0.152	0.140

*Variables with correlation coefficients >0.50 were not included in the same model.

Table 3.20 Model rank, based on change in Deviance Information Criteria [ΔDIC], and DIC weight for models developed via stage 3 backward selection for hierarchical modeling of northern bobwhite landscape associations at 500 and 1,500 m scales within the Southeastern Coastal Plain region (BCR 27), 2006-2008.

Rank	Landscape Model	DIC	ΔDIC	DIC weight
1	%CP33^{1,500} + %Urban/developed^{1,500} + %Row-crop^{500} + (%Row-crop500)^{2}+ Woody edge density^{1,500} + (Woody edge density^{1,500})^{2}+ Patch density^{500} + %Grass^{500} + Patch richness^{500}	4,657.12	0	0.193
2	%CP33^{1,500} + %Urban/developed^{1,500} + %Row-crop^{500} + Woody edge density^{1,500} + Patch density^{500} + %Grass^{500} + Patch richness^{500}	4,657.52	0.40	0.158
3	%CP33^{1,500} + %Urban/developed^{1,500} + %Woody cover^{500} + Woody edge denisty^{1,500} + Patch density^{500} + Patch richness^{500}	4,657.71	0.59	0.144
4	%CP33^{1,500} + %Urban/developed^{1,500} + %Woody cover^{500} + Woody edge denisty^{1,500} + Patch density^{500} + %Grass^{500} + Patch richness^{500}	4,658.12	1.00	0.117
5	%CP33^{1,500} + %Urban/developed^{1,500} + %Row-crop^{500} + Woody edge density^{1,500} + %Grass^{500} + Patch richness^{500}	4,658.21	1.09	0.112
6	%Urban/developed^{1,500} + %Row-crop^{500} + Woody edge density^{1,500} + %Grass^{500} + Patch richness^{500}	4,659.07	1.95	0.073
7	%CP33^{1,500} + %Urban/developed^{1,500} + %Woody cover^{500} + Woody edge denisty^{1,500} + Patch richness^{500}	4,659.10	1.98	0.072
8	%Urban/developed^{1,500} + %Woody cover^{500} + Woody edge denisty^{1,500} + Patch richness^{500}	4,659.12	2.00	0.071
9	%Urban/developed^{1,500} + Woody edge density^{1,500} + %Grass^{500} + Patch richness^{500}	4,661.73	4.61	0.019
10	%Urban/developed^{1,500} + Woody edge density^{1,500} + %Grass^{500}	4,662.63	5.51	0.012
11	%Urban/developed^{1,500} + Woody edge denisty^{1,500} + Patch richness^{500}	4,663.06	5.94	0.010

Table 3.20 (Continued)

12	%Woody cover^{500}	4,663.67	6.55	0.007
13	Woody edge density^{1,500} + %Grass^{500}	4,664.46	7.34	0.005
14	Woody edge denisty^{1,500} + Patch richness^{500}	4,664.88	7.76	0.004
15	%Urban/developed^{1,500}	4,665.63	8.51	0.003
16	Woody edge denisty^{1,500}	4,665.74	8.62	0.003
17	Patch density^{500}	4,665.98	8.86	0.002
18	%Grass^{500}	4,666.33	9.21	0.002
19	%Row-crop^{500}	4,666.47	9.35	0.002
20	Patch richness^{500}	4,666.61	9.49	0.002
21	null	4,666.97	9.85	0.001
22	%CP33^{1,500}	4,667.27	10.15	0.001

Table 3.21 Mean posterior probability estimates, standard deviation (SD), Monte Carlo error (MCE), 95% percentiles, and median posterior probability estimates for the best approximating model of northern bobwhite abundance in the Southeastern Coastal Plain region (BCR 27), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	-10.470	7.218	0.398	-22.810	4.451	-11.300
% CP33^{1,500}	beta1	0.106	0.060	0.000	-0.012	0.223	0.106
% Urban/ developed^{1,500}	beta2	-0.169	0.072	0.000	-0.311	-0.030	-0.169
% Row-crop^{500}	beta3	0.530	0.306	0.006	-0.075	1.133	0.527
(% Row-crop^{500})^2	beta4	-0.430	0.354	0.007	-1.127	0.272	-0.428
Woody edge density^{1,500}	beta5	-0.312	0.528	0.014	-1.359	0.713	-0.309
(Woody edge density^{1,500})^2	beta6	-0.035	0.387	0.010	-0.789	0.725	-0.035
Patch density^{500}	beta7	0.042	0.065	0.001	-0.086	0.171	0.042
% Grass^{500}	beta8	0.303	0.077	0.001	0.153	0.456	0.303
Patch richness^{500}	beta9	0.167	0.094	0.001	-0.016	0.353	0.167

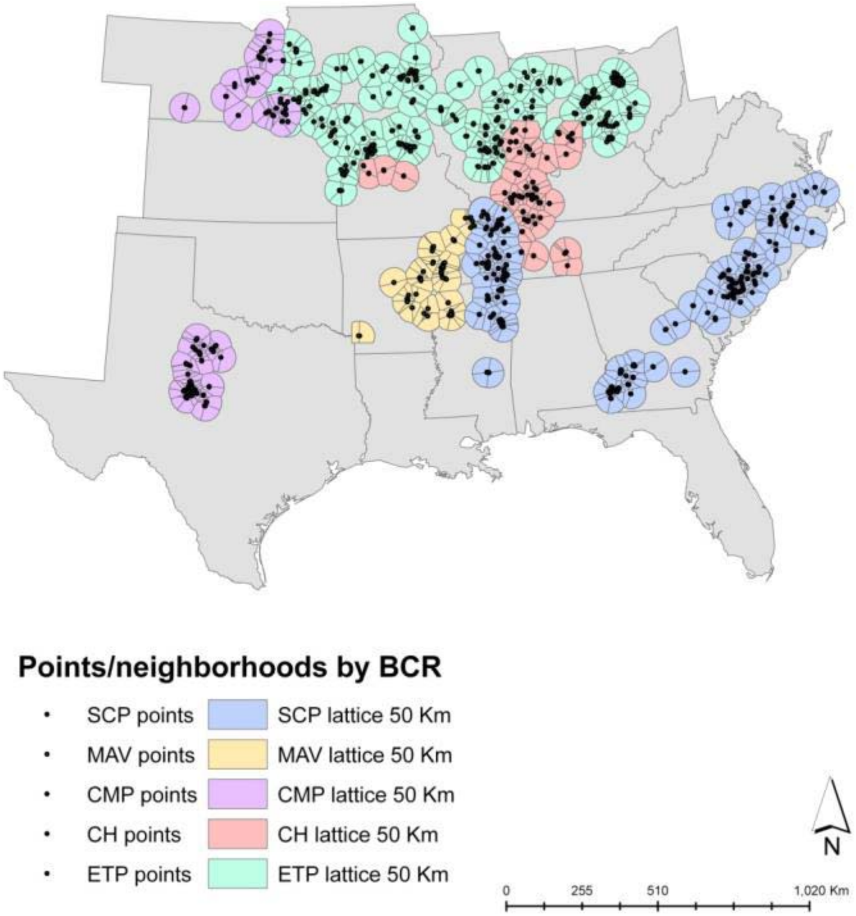
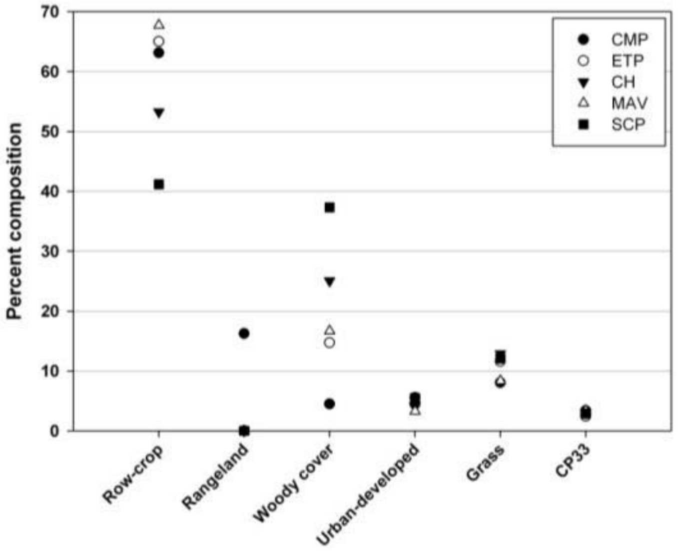


Figure 3.1 Bird survey point locations and irregular lattice of 50 km^{2}spatial neighborhoods around bird survey points within each of 5 Bird Conservation Regions [BCR] (Central Mixed-grass Prairie (BCR 19) [CMP], Eastern Tallgrass Prairie (BCR 22) [ETP], Central Hardwoods (BCR 24) [CH], Mississippi Alluvial Valley (BCR 26) [MAV], and Southeastern Coastal Plain (BCR 27) [SCP] in 14 states within the core northern bobwhite range, surveyed from 2006-2008.

A



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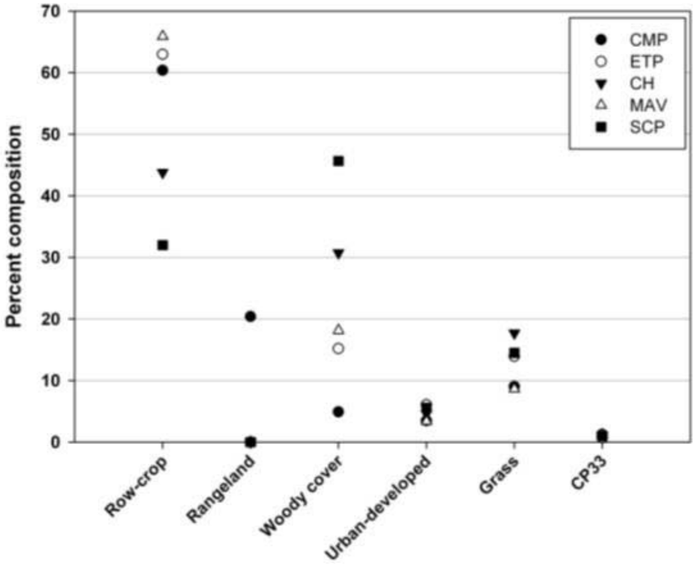

Figure 3.2 Percentage of land cover types in the (A) 500 m and (B) 1,500 m landscape surrounding bird survey points in the Central Mixed-grass Prairie (BCR 19) [CMP], Eastern Tallgrass Prairie (BCR 22) [ETP], Central Hardwoods (BCR 24) [CH], Mississippi Alluvial Valley (BCR 26) [MAV], and Southeastern Coastal Plain (BCR 27) [SCP] regions in the core northern bobwhite range, 2007.

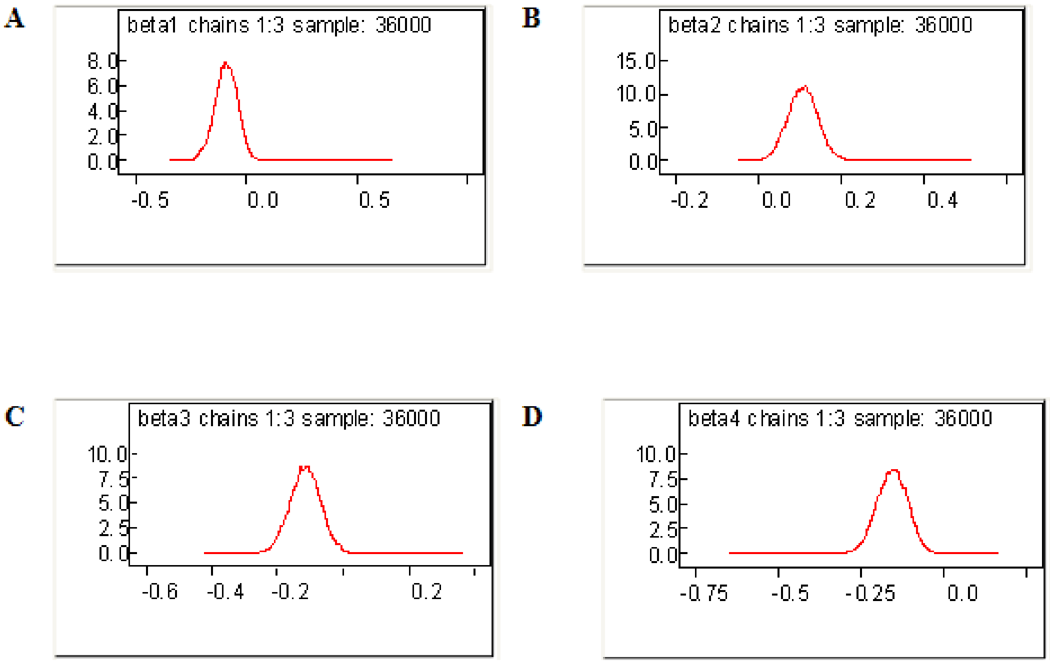

Figure 3.3 Posterior probabilities for model parameters A) % grass (CP33 excluded) (500), B) % CP33 (1,500), C) contagion (1,500), D) % urban/developed (1,500) for the best approximating model of northern bobwhite abundance in the Central Mixed-grass Prairie region (BCR 19), 2006-2008.

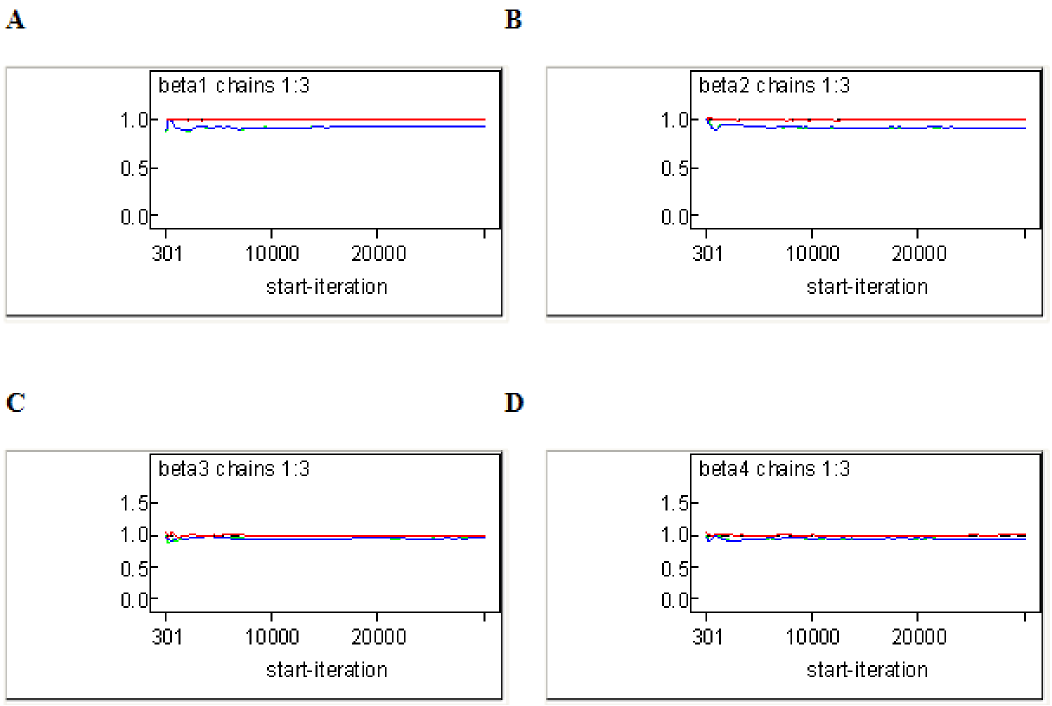

Figure 3.4 Gelman-Rubin diagnostics to assess fit of model parameters A) % grass (CP33 excluded) (500), B) % CP33 (1,500), C) contagion (1,500), D) % urban/developed (1,500) for the best approximating model of northern bobwhite abundance in the Central Mixed-grass Prairie region (BCR 19), 2006-2008.

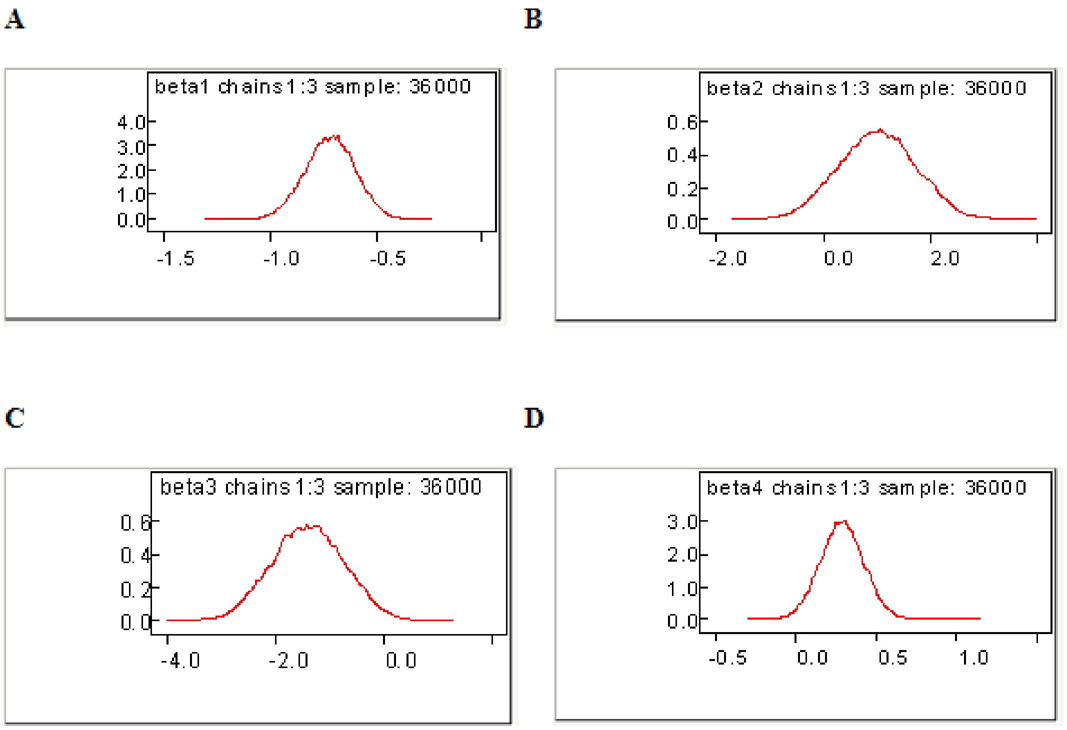

Figure 3.5 Posterior probabilities for model parameters A) % urban/developed (1,500), B) % row-crop (1,500; linear), C) % row-crop (1,500; quadratic), D) patch richness (1,500) for the best approximating model of northern bobwhite abundance in the Eastern Tallgrass Prairie region (BCR 22), 2006-2008.

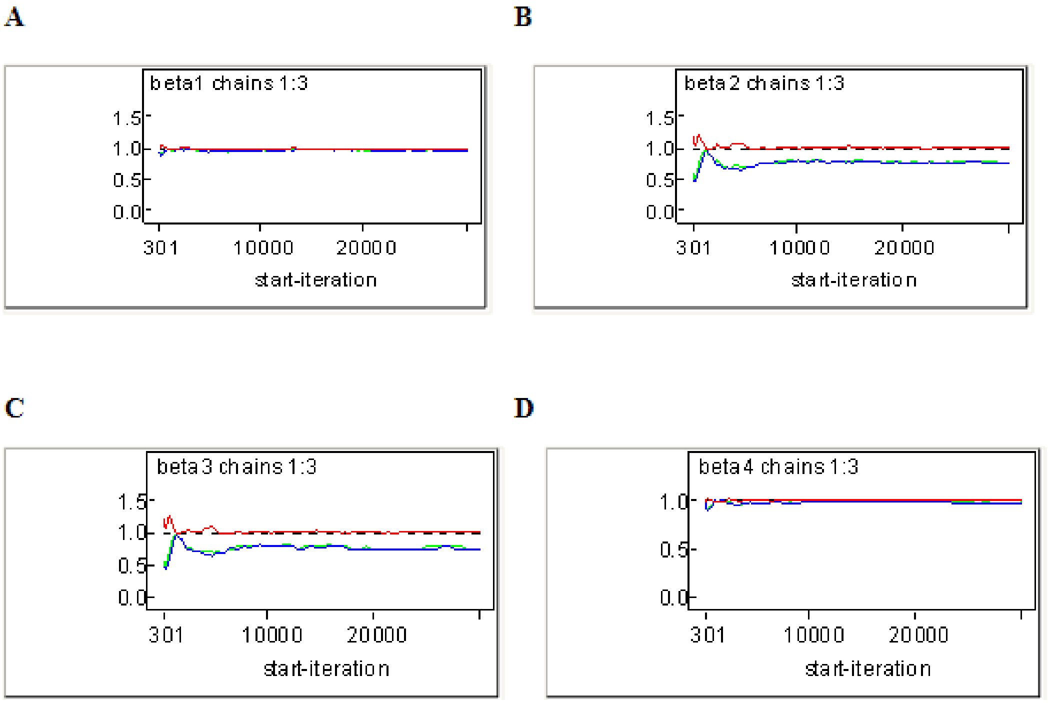

Figure 3.6 Gelman-Rubin diagnostics to assess fit of model parameters A) % urban/developed (1,500), B) % row-crop (1,500; linear), C) % row-crop (1,500; quadratic), D) patch richness (1,500) for the best approximating model of northern bobwhite abundance in the Eastern Tallgrass Prairie region (BCR 22), 2006-2008.

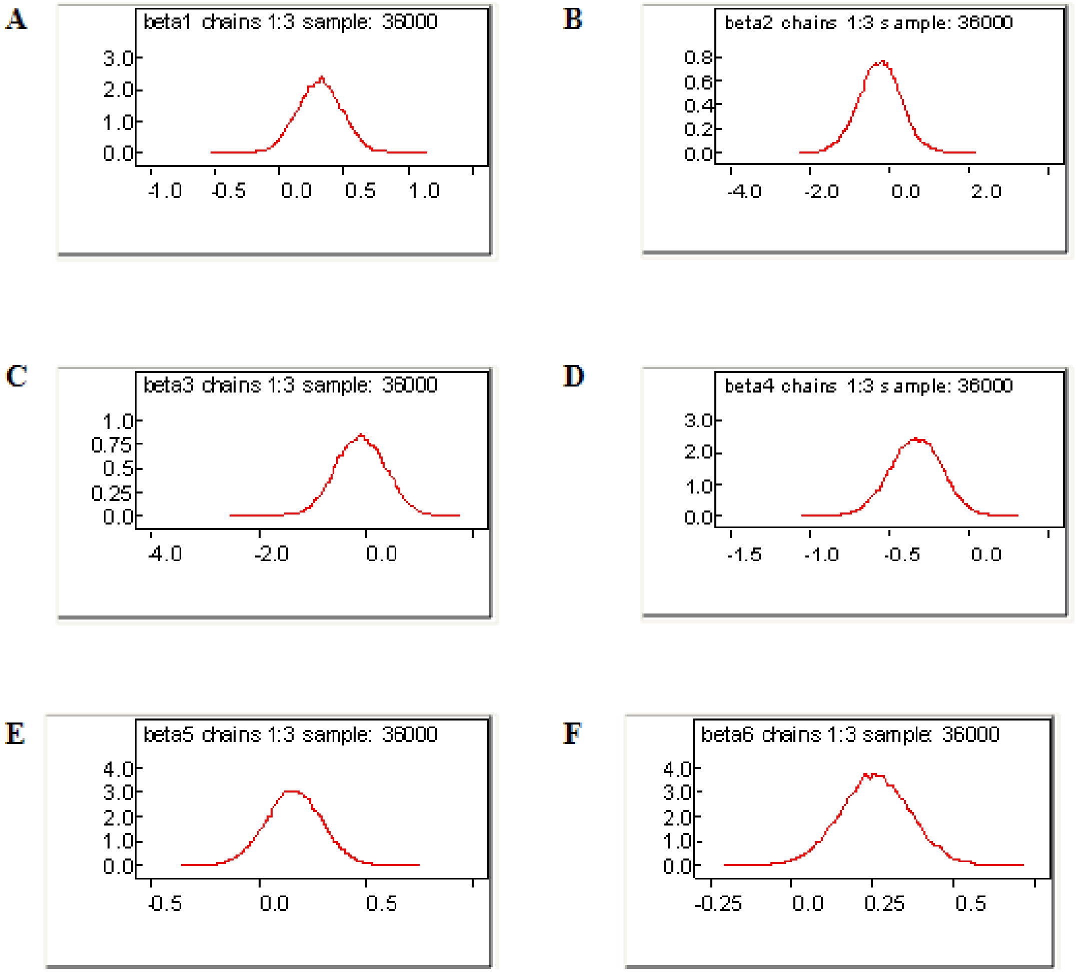

Figure 3.7 Posterior probabilities for model parameters A) patch richness (1,500), B) % woody cover (1,500; linear), C) % woody cover (1,500; quadratic), D) patch density (500), E) % grass (CP33 excluded) (500), F) % CP33 (500) for the best approximating model of bobwhite abundance in the Central Hardwoods region (BCR 24), 2006-2008.

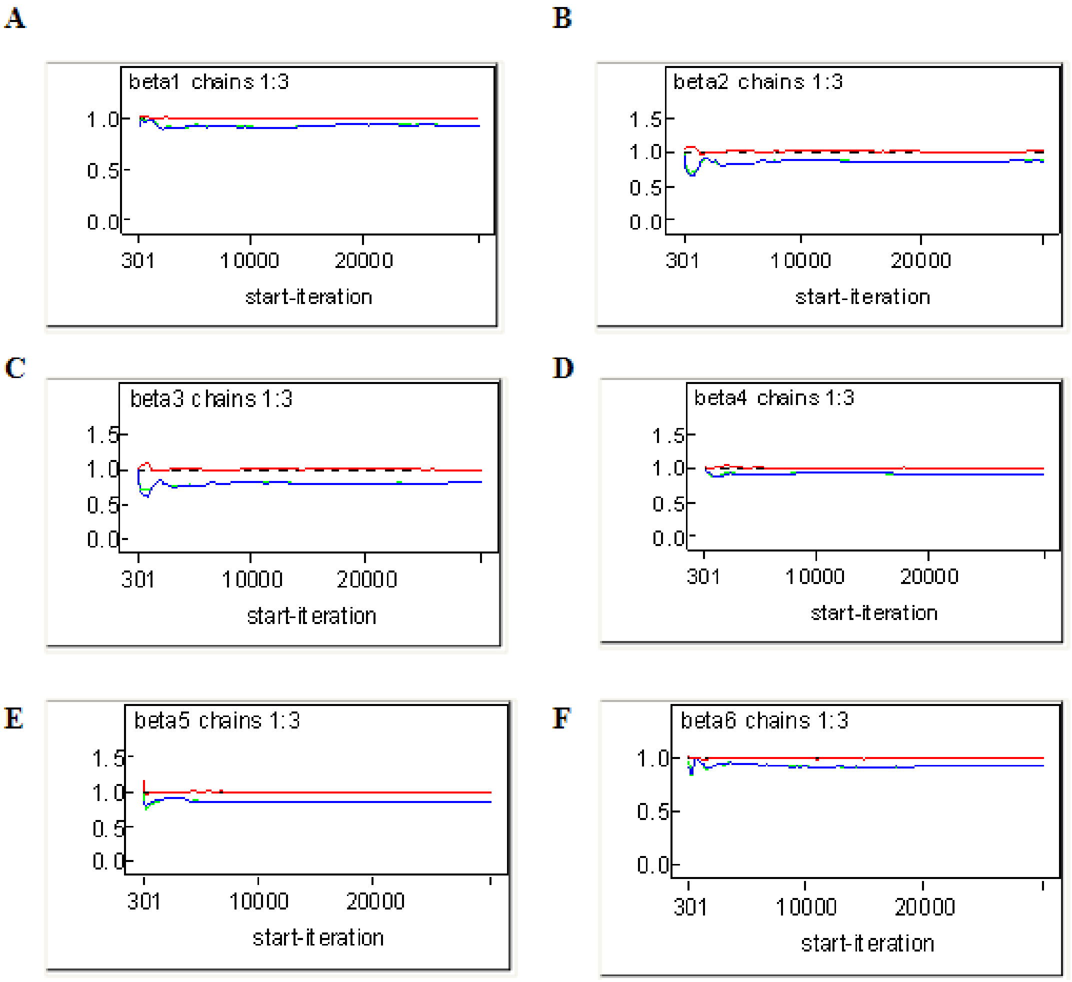

Figure 3.8 Gelman-Rubin diagnostics to assess fit of model parameters A) patch richness (1,500), B) % woody cover (1,500; linear), C) % woody cover (1,500; quadratic), D) patch density (500), E) % grass (CP33 excluded) (500), F) % CP33 (500) for the best approximating model of northern bobwhite abundance in the Central Hardwoods region (BCR 24), 2006-2008.

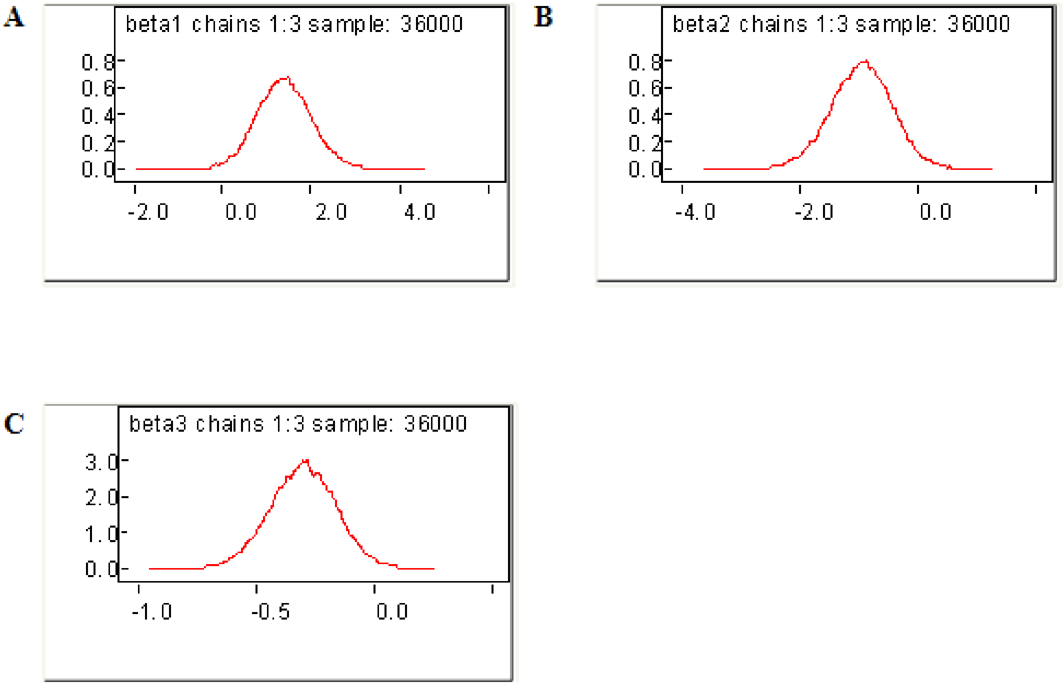

Figure 3.9 Posterior probabilities for model parameters A) woody edge density 1,500; linear), B) woody edge density (quadratic; 1,500), C) patch richness (1,500) for the best approximating model of bobwhite abundance in the Mississippi Alluvial Valley region (BCR 26), 2006-2008.

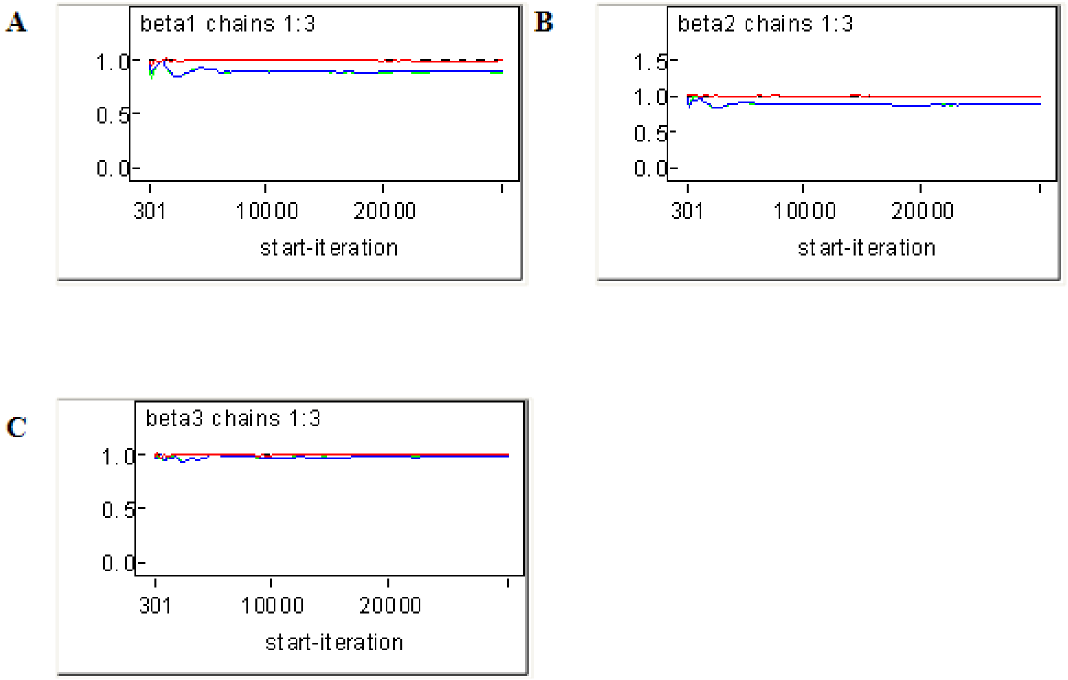

Figure 3.10 Gelman-Rubin diagnostics to assess fit of model parameters A) woody edge density (1,500; linear), B) woody edge density (1,500; quadratic), C) patch richness (1,500) for the best approximating model of bobwhite abundance in the Mississippi Alluvial Valley region (BCR 26), 2006-2008.

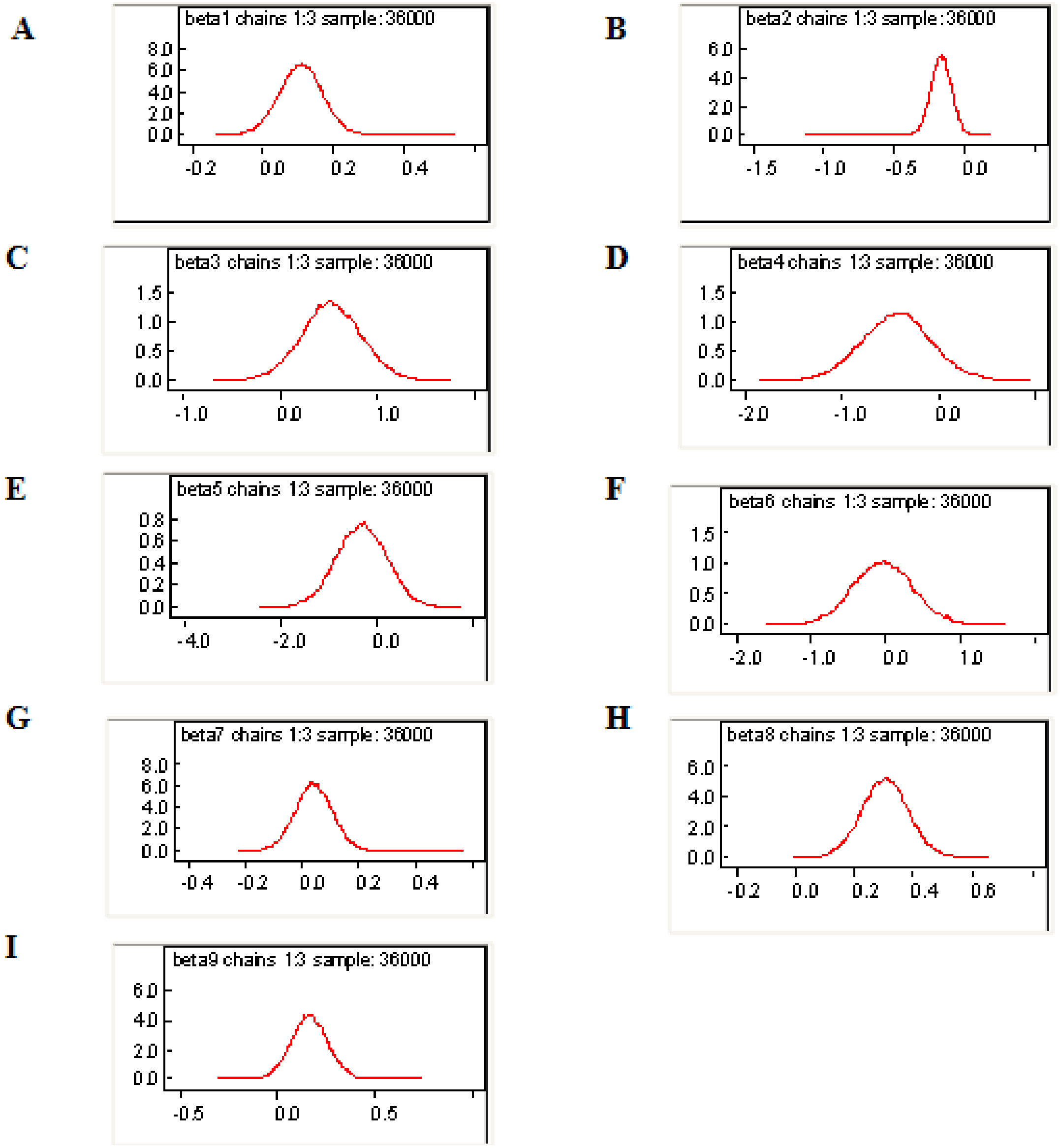

Figure 3.11 Posterior probabilities for model parameters A) % CP33 (1,500), B) % urban/developed (1,500), C) % row-crop (500; linear), D) % row-crop (500; quadratic), E) woody edge density (1,500; linear), F) woody edge density (1,500; quadratic), G) patch density (500), H) % grass (CP33 excluded) (500), I) patch richness (500) for the best approximating model of northern bobwhite abundance in the Southeastern Coastal Plain region (BCR 27), 2006-2008.

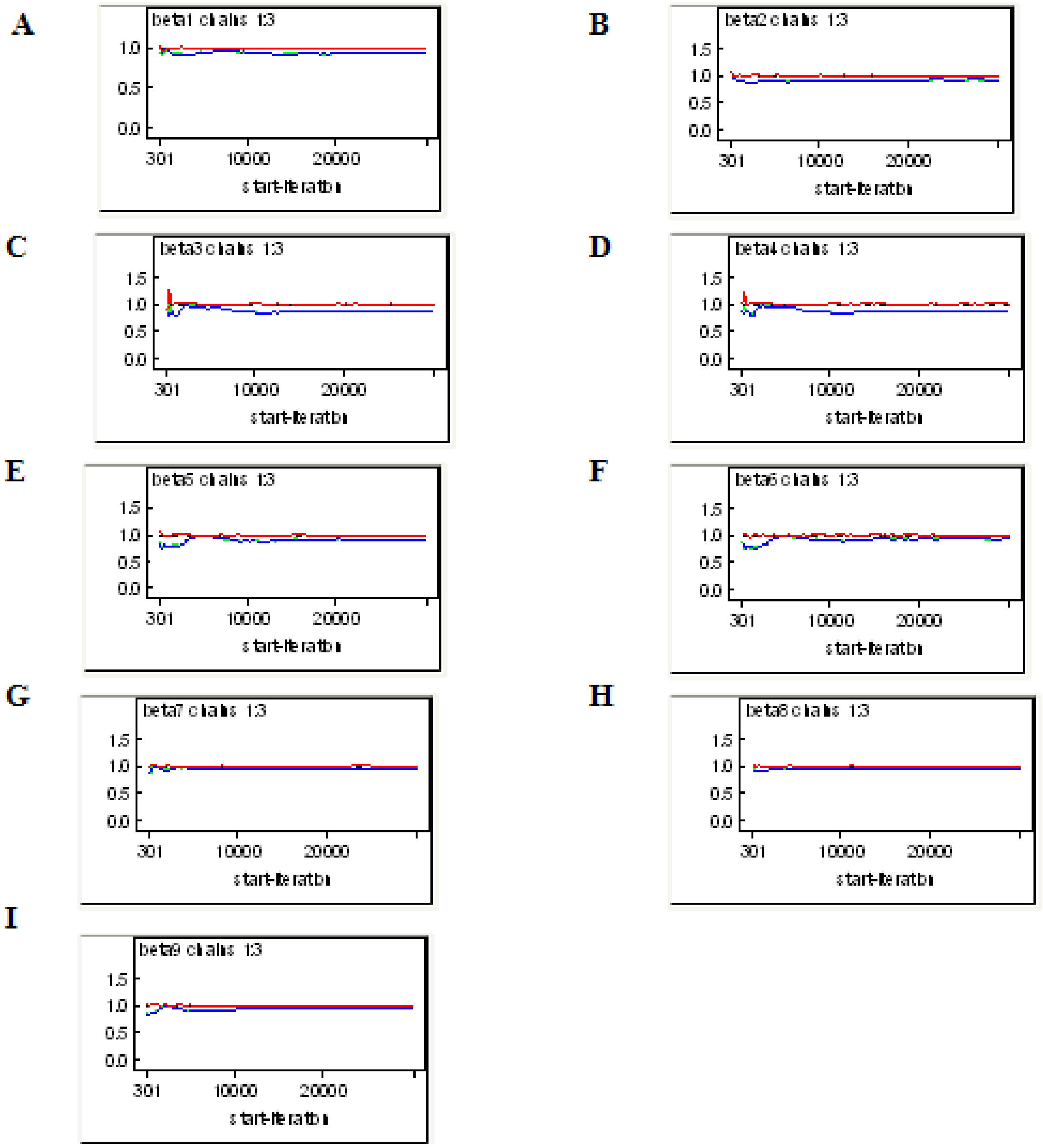

Figure 3.12 Gelman-Rubin diagnostics to assess fit of model parameters A) % CP33 (1,500), B) % urban/developed (1,500), C) % row-crop (500; linear), D) % row-crop (500; quadratic), E) woody edge density (1,500; linear), F) woody edge density (1,500; quadratic), G) patch density (500), H) % grass (CP33 excluded) (500), I) patch richness (500) for the best approximating model of northern bobwhite abundance in the Southeastern Coastal Plain region (BCR 27), 2006-2008.

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CHAPTER IV

MULTI-SCALE RESPONSE OF AUTUMN NORTHERN BOBWHITE COVEYS TO TARGETED CONSERVATION BUFFERS

Large-scale changes in agriculture, forestry, and grassland management practices to accommodate production needs have spawned a global trend in habitat loss and subsequent population declines in early-succession bird species (Peterjohn 2003, Green et al. 2005). Because of their inextricable linkage to human land use, northern bobwhites (*Colinus virginianus*; hereafter, bobwhite) have endured some of the worst of these population losses across their natural range (Klimstra 1982, Brennan 1991). For nearly a century, researchers have agreed that habitat loss is the “fundamental issue” affecting bobwhite populations (Klimstra 1982), yet complexities of what defines “habitat” (i.e., usable space; Guthery1997) have led to no single solution for successful range-wide bobwhite recovery. Insofar as the bobwhite is a flagship species for agro-ecological conservation and a treasured icon of rural Americana (Brennan 1991, Burger et al. 1999), major efforts are underway to recover range-wide populations. These efforts were spearheaded by creation and subsequent revision of the National Bobwhite Conservation Initiative [NBCI] which suggested an additional 2.4-2.7 million coveys could be added to existing populations with only a 6-7% change in primary land use in prioritized landscapes (Dimmick et al. 2002, National Bobwhite Technical Committee 2011). The NBCI recognizes that successful restoration of bobwhite populations can only be addressed through multi-dimensional habitat solutions that vary by landscape and region

(Dimmick et al. 2002, National Bobwhite Technical Committee 2011), and suggests agricultural field-edge and in-field management accounts for up to 20% of prioritized land area for bobwhite recovery (National Bobwhite Technical Committee 2011).

Establishment and management of native herbaceous field margins along agricultural field edges are broadly applicable tools that could affect large-scale habitat and population recovery goals of the NBCI plan (Dimmick et al. 2002). Targeting agricultural field margins for bobwhites has been suggested since the 1930's (Stoddard 1931, Davison 1941), and benefit upland bird communities during breeding (Smith et al. 2005*a*, Jones et al. 2006, Conover et al. 2009) and non-breeding season (Marcus et al. 2000, Smith et al. 2005*b*, Conover et al. 2007, Blank et al. 2011). These observed population benefits are presumably a direct result of enhanced reproductive success resulting from increased habitat amount, heterogeneity and connectivity provided by field margins (Wiens 1995, Fahrig 2003). However, utility of field margins (i.e., buffers) for bobwhite restoration remains debated, particularly during non-breeding season. The few studies that have evaluated response to field margin habitats by non-breeding bobwhite populations demonstrated mixed results (e.g., Moorman and Riddle 2009, Smith and Burger 2009). One plausible explanation is that bobwhite exhibit typically "slack" in habitat configuration requirements, suggesting a flexible habitat selection strategy (Guthery 1999). Studies of preferential habitat selection during non-breeding season are often contradictory. Some suggest bobwhite coveys are non-specific, even ubiquitous, in habitat choices (Roseberry and Klimstra 1984), whereas others suggest coveys select for linear habitat patches (Terhune et al. 2009), agricultural fields (Dixon et al. 1996) or grasslands (Lohr et al. 2011) over alternative habitat types. These reported differences in habitat requirements and use of linear field margin habitats by overwintering bobwhite populations demonstrate a need for a comprehensive multi-scale evaluation of bobwhite response to herbaceous field margin habitats across multiple physiographic regions.

Continuous Conservation Reserve Program practice 33, Habitat Buffers for Upland Birds [CP33], was the first federal Farm Bill conservation practice designed to target habitat and recovery objectives of a large-scale wildlife conservation initiative, the NBCI (Burger et al. 2006*a*) and provides landowners with incentives to establish of 9-37 m native herbaceous buffers along row-crop field margins to provide temporary habitat for bobwhite and other upland bird species (U. S. Department of Agriculture 2004). I evaluated multi-scale effects of CP33 habitat buffers on autumn bobwhite covey densities across 9 physiographic regions and 13 states using a novel 2-stage analytical approach that incorporates probability of detection into random effects modeling (Buckland et al. 2009). Presuming native herbaceous cover is limiting to bobwhite in agricultural landscapes during non-breeding season, I hypothesized autumn bobwhite coveys would exhibit a disproportionate positive population response to habitat provided by CP33 buffers as predicted by the NBCI recovery plan. However, I expected autumn bobwhite coveys to exhibit regional differences in response to native herbaceous buffer establishment, with response in northern regions influenced to a greater degree by ability of buffers to provide thermoregulatory cover during unfavorable weather conditions than other regions.

Study Area

The study area for autumn bobwhite covey monitoring included 13 of 14 states participating in the coordinated National CP33 Monitoring Program described in detail in Chapter I (Table 1.1, Fig. 2.1). CP33 contracts and survey points were selected randomly according to a modified multi-stage sampling design described in Chapter I. Sample size for autumn surveys was determined using pilot study information from Smith et al. (2009), which determined that a coefficient of variation [CV] < 15% could be achieved with 40-50 survey points/state if a mean of one covey/point were detected (Burger et al. 2006*b*). Autumn covey survey points were located subsequently on 546 and 542 buffered and paired non-buffered row-crop fields, respectively, in 13 states (Fig. 4.1). Autumn covey survey points were identical to those surveyed during breeding season in the 13-state study area. Although buffered fields were paired with non-buffered fields, unbalanced sample sizes reflect loss of non-buffered fields to subsequent enrollment of CP33, loss of access permissions, or other logistical constraints.

As described in Chapter I, survey points were located in 10 Bird Conservation Regions [BCR] (i.e., ecological regions exhibiting similar habitat structure and land use [North American Bird Conservation Initiative 2000]) (Fig. 4.1). However, because spatial locations of survey points depend on spatial locations of CP33 contracts, survey points in 5 BCRs were located on peripheral margins of the region and not representative entirely of the respective BCR. Prior to analysis, I sub-grouped survey points based on natural groupings within or adjacent to a BCR (Fig. 4.1). Most points were categorized by boundaries of a single BCR (e.g., Eastern Tallgrass Prairie) or a subdivision of a BCR (e.g., Eastern Southeastern Coastal Plain, Western Southeastern Coastal Plain). Points in Texas were classified as Central Texas grouping because they represent a contiguous portion of the Central Mixed-grass Prairie and Oaks and Prairies regions (Fig. 4.1).

Methods

Autumn covey surveys

Because the NBCI plan frames bobwhite recovery goals in terms of autumn coveys added to the population (Dimmick et al. 2002), a primary objective of the National CP33 Monitoring Program was to estimate autumn bobwhite covey densities across the core range (Burger et al. 2006*b*). I coordinated state-level point transect surveys for coveys annually (once per autumn per point minimally) from the last week of September to the second week of November, 2006-2008 (Burger et al. 2006*b*). The sampling period was determined based on bi-weekly peak covey calling rates observed in Wellendorf et al. (2004). Paired buffered and non-buffered points were surveyed simultaneously to reduce weather-related variation. Covey surveys were only conducted during favorable conditions (i.e., winds <6.5 km/hr, <75% cloud cover, no precipitation, and <0.05 in/Hg change in barometric pressure (1 am – 7 am) (Burger et al. 2006*b*). Uniquely identifiable coveys and time of covey calling were recorded once at their initial estimated location during the daily peak calling period (45 min before sunrise – 5 min before sunrise) (Hansen and Guthery 2001) by marking a point onto aerial imagery provided by the National Agricultural Imagery Program (U. S. Department of Agriculture 2007). I recorded covey locations into ArcGIS (ESRI 2009) and measured radial distances from survey points to estimated covey locations. Prior to analysis, I excluded all sites from Arkansas and Ohio because of minimal sample size and large variability of detection probability estimates. I also excluded all sites that were not surveyed at least once each year (2006-2008) and points that were not paired spatially (non-buffered and buffered). After removing samples above, 369 paired sites remained from 11 states.

Two stage analytical approach

Evidence suggests variable ability to detect calling bobwhite coveys within survey plots (Rusk et al. 2009), and thus the NBCI recommends survey and analytical methods account for detection probability (Evans et al. 2011). For point transects, it is assumed that detectability decreases as a function of distance between the observer and object of interest (Buckland et al. 2001). Assuming points are distributed randomly relative to covey distribution, distances are measured accurately, coveys do not exhibit responsive movement, and probability of detecting a covey at the survey point is 100% (Buckland et al. 2001), distance sampling can be used to model covey detection probability to increase reliability of autumn covey density estimates (Wellendorf and Palmer 2005).

Covariate models within distance sampling adjust the detection function to account for variables affecting detectability, but make no statement regarding the degree to which covariates influence observed density across plots. One cannot evaluate effects of potential covariates on observed densities without further application of robust analytical methodology (e.g., generalized linear models). When working in an experimental context, robust statistical methods should be used to evaluate covariate models while also accounting for detection probability (Buckland et al. 2009). The 2-stage analytic approach incorporates estimates of effective area (i.e., probability of detection multiplied by survey area) derived from distance sampling into a linear modeling framework (Buckland et al. 2004, 2009). In the first stage, a probability density function (*pdf*) is modeled using likelihood methods for distance data and effective area is estimated from the *pdf*. In the second stage, effective area is used as an offset in a linear model, providing a means to assess covariate effects (e.g., treatment type) on measures of density (Buckland et al. 2009).

Stage one: assessing detection probability

In the first stage, I pooled covey data at each point across years (2006-2008) and adjusted effort accordingly. I visually inspected probability density function plots within DISTANCE 6.0 (Thomas et al. 2010) and right truncated to radial distance (*w*) where detection probability falls below 0.1 for all candidate models (Buckland et al. 2001). I assessed possible heterogeneity in detection probability (Buckland et al. 2004) within the Multiple Covariate Distance Sampling [MCDS] engine of Distance by evaluating fit of half-normal [HN] and hazard rate [HR] key function models with necessary series adjustments (cosine [HN, HR], hermite polynomial [HN]) (Thomas et al. 2010). I evaluated model fit with and without covariates, and with and without post-stratification by state, physiographic region, and field type (buffered, non-buffered; Buckland et al. 2001; Table 4.1). Post-stratification accounts for heterogeneous detection probabilities by fitting separate detection functions to each specified strata (Buckland et al. 2001). Covariate models in the MCDS engine are more parsimonious, where the scale parameter of the detection function is modeled as a function of given covariates (Buckland et al. 2004).

MCDS covariate models included factor-level covariates of state, region, field type, year, state + year, and state + field type, and continuous covariates of Julian day, cloud cover (%), 6 hr change in barometric pressure (in/Hg; 1 am-7am), wind speed (km/hr), and number of adjacent calling coveys (Table 1). The latter 4 variables can influence covey calling rate (Wellendorf et al. 2004). I used covariates of field type, region, and year in stage one MCDS models and stage 2 count models to assess presumed influence on measures of detectability and density. I presumed the remaining MCDS covariates only influenced measures of detectability and not observed density. I used

Akaike's Information Criterion ([AIC]; Akaike 1973), visual inspection of quantile-quantile plots, and Kolmogorov-Smirnov [KS] and Cramer-von Mises [CM] goodness of fit tests to determine best fitted model of the detection function (Buckland et al. 2001, 2004). For post-stratified analysis, I summed AIC values across strata for comparison to other models (Buckland et al. 2001).

Using the best approximating model in program R, I fit a *pdf* to the observed distance data ($f(r)$ for non-covariate models, or $f(r \mid z)$ where the detection function scale parameter was modeled as a function of z covariates [Buckland et al. 2004], and where r represents the radial distance between the survey point and estimated covey location [Buckland et al. 2001]). I then used $f(r)$ or $f(r \mid z)$ to estimate effective area v, the area beyond which as many coveys are presumed to have been observed as were missed within the area (Buckland et al. 2001). For non-covariate models $v = \pi w^2 \times P_a$, where P_a (probability of detection of a covey in area a) equals $\frac{2}{w^2}\int_0^w rg(r)dr$, where dr is the incremental width at distance r from the survey point, $g(r)$ is the probability of detection at distance r, and w is the radial truncation distance (500 m) (Buckland et al. 2001). Effective area is probability of detection times the circular area out to truncation distance w. For covariate models, effective area $v = \pi w^2 \times P_a(z)$, where: $P_a(z) = \frac{2}{w^2}\int_0^w rg(r,z)dr$ where z represents covariates used in modeling the detection function (Buckland et al. 2004). In the covariate model, effective area as a function of z covariates is probability of detection as a function of z covariates times the circular area out to truncation distance w.

Under the best approximating covariate model, I then implemented a non-parametric bootstrap ($B = 999$) using a call to the MCDS engine of DISTANCE 6.0 from R to account for uncertainty in parameter estimation and better estimate precision of the detection function parameters using bootstrap replicates (Buckland et al. 2009). The bootstrap is a simulation mechanism that allows for B random resamples of the original data set with replacement (Efron 1979). Sample variance from B total resamples is then used as an estimated variance around parameter estimates and bootstrap standard error [BSE]. Thus with each bootstrap resample, all detection function parameter estimates are re-estimated, and effective area offset is re-calculated (Buckland et al. 2009).

Stage two: Poisson regression incorporating effective area offset

If I assume detection probability is constant across the survey plot, then I could model counts of coveys at each point visit using a Poisson-distributed generalized linear mixed model (*glmm*), with spatial structure of paired sites as a random effect (Buckland et al. 2004). With a log-link function I would consider expected count λ at visit l to point k of paired site j, a Poisson random variable, such that:

$$\lambda_{jkl} = \exp\left(\beta_0 + b_j + \sum_{i=1}^{I} x_{ijkl} \ \beta_i\right) \qquad \text{(Equation 4.1)}$$

where: β_0 is the fixed effect intercept, b_j is the random effect for paired buffered and non-buffered site j with $b_j \sim N(0, \sigma_b^2)$, x_i is the i^{th} fixed effect, x_{ijkl} are measured fixed effect values, and β_i associated coefficients for each fixed effect. However, if analysis in stage one suggests differences in effective area (i.e., probability of detection multiplied by survey area), I must then account for differences in log of effective area in the count model as an offset such that λ_{jkl} / v_{jkl} becomes fitted density at visit l to point k of paired site j:

$$\lambda_{jkl} = \exp\left(\beta_0 + b_j + \sum_{i=1}^{I} x_{ijkl}\ \beta_i + \ln(v_{jkl})\right) \quad \text{(Equation 4.2)}$$

I fit 31 Poisson *glmm* models (log-link function) with a log effective area offset in the *glmer* function of the lme4 package in R (Bates 2010; Table 4.2). Potential fixed effects included field type (buffered vs. non-buffered), state-recommended contract cover (i.e., state-specific practice standards related to establishing cover in CP33 buffers), region, year, and weekly period. My treatment of interest was effect of field type on bobwhite density. I anticipated among-state variation in bobwhite densities, but only due to differences in state-level step-down plans that specified suitable contract cover. Therefore, rather than evaluate densities across geopolitical boundaries of state, I evaluated biological effects of recommended contract cover (native warm-season grass [NWSG] only, natural regeneration [NR] only, NWSG/NR choice). Anecdotal vegetation surveys at buffered fields suggest compliance with state contract cover recommendations upon buffer establishment, with limited non-compliance related to mismanagement (e.g., mowing) and incidental misuse (e.g., herbicide drift, crop encroachment, roads, turn-rows and equipment storage) within buffers.

Because of the broad geographic range of survey points, I anticipated interactions among region × field type, region × year, region × weekly period, field type × year, and contract cover × year. Because of expected peaks in calling activity during the survey period (Seiler et al. 2002, Wellendorf et al. 2004), I modeled linear and quadratic effects of weekly period. I modeled paired buffered and non-buffered sites as random effect b_j, which were assumed distributed normally. I modeled log of effective area v_{jkl} as an offset in each model, which was assumed a constant (Buckland et al. 2009). I manually set number of quadrature points [nAGQ] for the Gauss-Hermite approximation to 10 for all candidate models (Lesaffre and Spiessens 2001). I evaluated the global model for evidence of overdispersion prior to implementing the remaining candidate model set.

Provided data lacked overdispersion, I used an automated selection routine in R to compare AIC values of candidate models and selected the best approximating model based on minimum AIC (Buckland et al. 1997, Burnham and Anderson 1998). If AIC values indicated no model uncertainty, I used a non-parametric bootstrap (B=999) in R to estimate precision of model parameters of the best count model using paired site (non-buffered vs. buffered) as the resampling unit (Buckland et al. 2009). Because measures of precision from Poisson count model parameters do not account for uncertainty in the offset, I used bootstrap to ensure that all model variation was accounted for adequately (Buckland et al. 2009). I determined significance of model parameters using 95% confidence intervals generated from the bootstrap in combination with z-tests from analytical point estimates (Buckland et al. 2009).

Estimating density

Because survey design and access constraints on private lands precluded flushing detected coveys, I was limited to estimating covey densities only. I estimated covey density based on fitted values from the best count model by dividing observed count λ_{ijk} at each point visit by effective area v. Adapted from Buckland et al. (2001), for point transect sampling covey density D is estimated by $D = n/(a \times Pa)$, where n is observed number of detected coveys, circular area $a = \pi w^2$, and P_a is probability of detection in area a. Assuming a single visit per point, given effective area $v = \pi w^2 \times P_a$, then density is estimated as $D = n / v$.

I estimated density at the field type level and by field type within region level by subsetting densities from overall fitted values. Analytical variances and standard errors [ASE] were estimated by field type within region each year. However, analytical variances do not incorporate variance in effective area and are thus non-representative of full variability of density estimates. Variance estimates must account for uncertainty in fitted counts *n*, derived from the model, and effective area *v* (Buckland et al. 2004). I used combined bootstrap variances of fitted counts and effective area (above) (Buckland et al. 2004) to incorporate multiple variance components into density estimates. This assumes independence among variance components (Buckland et al. 2004).

Results

Stage one: detection probability

The MCDS hazard rate model with no adjustment terms and state and year as covariates was the best approximating model (Table 4.1), with KS fit of 0.016 (P = 0.597), CM uniform weighted fit of 0.079 (0.600 < P < 0.700), and CM cosine weighted fit of 0.044 (0.700 < P < 0.800). Mean probability of detection to w (500 m) was 0.327, effective detection radius was 285.79 m, and effective area was 25.660 ha. This model contained 14 parameters (2 for HR, 2 for year covariate [n = 3], 10 for state covariate [n = 11]). The covariate of interest, field type, did not affect covey detectability, but was an important linear predictor as an interaction with region effect of the count model (below). The intercept parameter estimate from the HR global MCDS model with state and year covariates was 161.54 (BSE = 16.70), and the shape parameter was fixed at 3.23 (BSE = 0.288). Scale parameter estimates ranged from 141.52 (BSE = 23.74) for the SC-2007 covariate to 328.13 (BSE = 20.86) for the MO-2006 covariate (Table 4.3). Effective area, effective detection radii, and probability of detection within a 500 m radii from the point ranged from 12.52 ha (BSE = 3.44), 199.60 m (BSE = 26.91), and 0.159 (BSE = 0.044) for SC-2007 samples to 47.26 ha (BSE = 3.58), 387.86 m (BSE = 14.73), and 0.602 (BSE = 0.046) for MO-2006 samples, respectively (Table 4.3).

Stage two: regression model

The global Poisson count model failed to indicate evidence of overdispersion ($\chi2 = 1.00$, P = 0.550), therefore quasi-Poisson methods were not necessary. The best Poisson model included fixed main effects of year, type, and region plus a type × region interaction effect (Table 4.2). This suggests observed covey densities are determined by year of survey in combination with an effect of treatment type (buffered vs. non-buffered) which varies by ecological region. The best approximating model exhibited excellent fit ($\chi2 = 1.00$, P = 0.540). I did not account for model uncertainty because AIC values for the second best and all remaining models were distant sufficiently (≥ 3.95 ΔAIC) from the best approximating model (Burnham and Anderson 1998, Buckland et al. 2009). Thus, point estimates and subsequent analytical and bootstrapped precision estimates are conditioned on the best approximating model. Because I incorporated effective area into the offset (i.e., probability of detection multiplied by area), the glmm approach used here models density λ_{jkl}.

Effects of CP33 on covey density

Based on *z*-tests and 95% bootstrap confidence intervals, covey densities were greater on buffered fields in the Eastern Southeastern Coastal Plain ([ESCP]; $P \leq 0.001$), Mississippi Alluvial Valley ([MAV]; $P \leq 0.001$), and Western Southeastern Coastal Plain ([WSCP]; $P = 0.010$) regions (Table 4). The remaining regions (Central Hardwoods

[CH], Central Texas [CTX], Eastern Tallgrass Prairie [ETP]) did not exhibit density differences across field types. Because density is modeled as a log-link function, a measure of proportional change relative to the intercept was obtained by transforming coefficients for fixed effects. Because an interaction of type × region was evident, I log-transformed the coefficient for each interaction level to determine the proportional effect of CP33 buffers within each region relative to the intercept. Transformation of coefficients from these significant interactions in the best model suggest covey densities were 123.43%, 241.34%, and 59.56% greater on buffered than non-buffered fields in the ESCP, MAV, and WSCP, respectfully, over all years.

Fitted densities from the best count model suggested covey densities on non-buffered and buffered fields were greater substantially in the CTX region compared to other regions (Fig. 4.2). Covey densities on non-buffered fields over all years ranged from 0.008 coveys/ha (ASE = 0.001; BSE = 0.003) in the MAV region to 0.168 coveys/ha (ASE = 0.006; BSE = 0.036) in the CTX region (Fig. 4.2). Densities on buffered fields over all years ranged from 0.029 coveys/ha in the MAV (ASE = 0.004; BSE = 0.010) and WSCP (ASE = 0.002; BSE = 0.005) regions to 0.204 coveys/ha (ASE = 0.007; BSE = 0.044) in the CTX region (Fig. 4.2). Based on the best count model, I estimated covey density across all survey points to be 0.031 (ASE = 0.001; BSE = 0.006) and 0.047 (ASE = 0.002; BSE = 0.008) coveys/ha on non-buffered and buffered fields, respectively (Fig. 4.2), suggesting an effect size of 0.016 coveys/ha (52%) greater density on buffered fields compared to non-buffered fields (95% CI = 0.011-0.020 coveys/ha). Note that because a single detection function model was fitted across field types (with state and year as covariates) type-specific density estimates lack independence (Buckland et al. 2009).

Discussion

Bobwhite coveys exhibited a disproportionate response to CP33 buffers, where a 5% change in primary land use resulted in 50% greater densities on buffered vs. non-buffered fields across the study area. However, substantial regional variation in effect of CP33 buffers was evident, such that approaching bobwhite conservation within a regional context as specified in the NBCI is warranted (National Bobwhite Technical Committee 2011). This conclusion is based on the assumption that observed responses represent population increases and not an artifact of population redistribution from the surrounding landscape, which was not addressed directly in this study.

The greatest effect of CP33 buffers on autumn bobwhite densities occurs in the MAV, ESCP and WSCP regions. The region with the greatest effect (MAV) also exhibited the least covey densities compared to other regions, greatest amount of row-crop (76%) and least amount of grass (3%) in the immediate landscape surrounding survey points (500 m radii). On average, covey densities in the MAV increased from 1 covey/132 ha on non-buffered row-crop fields to 1 covey/34 ha on buffered row-crop fields. This suggests lesser-density populations in intensively cropped landscapes with little alternative grass cover might benefit from habitat provided by buffers. The ESCP region exhibited the least amount of row-crop (39%), 10% grass cover, and greatest amount of woody cover (42%), suggesting bobwhite may respond positively to buffers in landscapes where woody cover composes a substantial portion of the immediate landscape. The WSCP region exhibited slightly greater amounts of row-crop and grass (45%, 17%, respectively), and lesser amounts of woody cover (29%) than the ESCP, but still exhibited substantial response to buffers. Substantial density increases on buffered compared to non-buffered fields in these 3 regions suggests coveys responded to increased availability of native herbaceous habitat provided by buffers regardless of composition of other landscape features in each region. I presume increases in grassland habitat amount (and hence usable space), though incremental at most, may be driving observed responses in these different landscapes. However, given response was greater in the intensively cropped MAV region, these results support the conclusion of Riddle et al. (2008) that bobwhite will respond more positively to buffers in agriculture-dominated landscapes than in forest-dominated landscapes.

In contrast, I observed small response (~10% increase) by autumn coveys in the Eastern Tallgrass Prairie [ETP], though bobwhite exhibited strong response to CP33 buffers during breeding season in this region (see Chapter II). One would expect a similar autumn response in the ETP as was observed in the MAV because both are intensive row-crop dominated landscapes (64% row-crop around survey points in the ETP). One possibility may be related to latitudinal differences in rate of succession among northern and southern regions in this study. Evaluation of covey densities 1-3 years after establishment in the ETP may not have allowed enough time for buffers to develop structure necessary to provide adequate autumn cover. Another possibility is bobwhite may require greater composition of woody cover (currently 15% around survey points) to meet thermoregulatory requirements and maximize predator avoidance strategies in the northern portion of their range (i.e., in the ETP) compared to the MAV. Bobwhite in Kansas and Ohio exhibit preferential selection for woody and herbaceous CRP cover during non-breeding season (Flock 2006, Janke 2011), and selection for woody cover in row-crop landscapes has been shown to decrease predation risk (Williams et al. 2000, Janke 2011) and provide foraging and thermoregulatory opportunities for autumn bobwhite coveys during snow events (Roseberry and Klimstra

1984). Also, a lack of response in the ETP region could plausibly demonstrate combined effects of alternative grassland habitats and preferential selection of woody cover not available in buffers.

Buffers elicited the least response in the CTX region (representing loosely the Central Mixed-grass Prairie [BCR 19]). Covey densities in the CTX were on average an order of magnitude greater on non-buffered and buffered fields than in other regions, though response to CP33 buffers was small (~5%). Texas exhibits typically substantially greater bobwhite densities than other parts of the range (Brennan 1999). However, abundant Texas bobwhite populations showed little response to buffered habitats in the breeding season (see Chapter I) and autumn, suggesting the surrounding landscape matrix is providing sufficient habitat to sustain viable bobwhite populations. Perhaps available rangeland and other grassland habitats in the surrounding landscape (21% and 4%, respectively) present sufficient usable space such that addition of buffer habitats produces a relatively small proportional change in total usable space.

Though regional variation in autumn bobwhite abundances is expected, prior to this study there was no comprehensive evaluation of autumn bobwhite response to management across most of the natural range such that potential regional differences could be accounted for. Previous research on autumn bobwhite response to buffer habitats is also limited, with most studies insufficient in scale to address regional variability and draw comprehensive conclusions regarding range-wide efficacy of buffers. Three previous studies demonstrated autumn covey abundances on CP33 and other buffered fields were 62-119% greater than on non-buffered fields in Kansas, Oklahoma, and North Carolina (Palmer et al. 2005, Moorman and Riddle 2009, Pitman and Sams 2010), whereas one study showed no significant response to narrow buffers in Mississippi (Smith and Burger 2009).

Compounding evidence that native herbaceous buffers elicit increases in autumn covey densities suggests coveys may be seeking out these linear patches of grassland habitat for cover and food resources. Further, my results suggest state-specified contract cover (natural regeneration vs. planting native warm-season grass mixes) may not influence covey response to buffers during autumn. However, more detailed research on covey and breeding season response to vegetative structure in planted vs. regenerated buffers is warranted prior to drawing inference regarding necessity of planting. Plowed row-crop fields in autumn may provide necessary bare ground, but insufficient cover and decreased seed availability compared to buffers. Buffers offer abundant seed resources (Vickery et al. 2002) and adequate escape cover in autumn agricultural landscapes (Clark and Reeder 2007). Hence, increases in habitat amount provided by buffers may be increasing suitability of the landscape for autumn populations (Smith and Burger 2009), particularly in regions with extensive row-crop systems and little alternative grass cover such as the MAV.

Though preferential selection for grassland habitats by bobwhite coveys has not been shown to impact survival (Lohr et al. 2011), selection for linear patches of grassland cover may beget implicit survival costs (Best 2000, Oakley et al. 2002, Holt et al. 2009). Condensed food resources provided by linear herbaceous cover (Vickery et al. 2002) may be sought out at the expense of increased mortality (Oakley et al. 2002, Bro et al. 2004, Holt et al. 2009). Inferences regarding quality of buffer habitat based on density alone should be drawn with caution, as increased covey densities in buffered habitats may give managers a false sense of security regarding habitat quality (Van Horne 1983, Vickery et al. 2002).

Some measures to avoid increased risk of mortality include maximizing buffer width (Clark and Reeder 2005, Conover et al. 2007, Conover et al. 2009) and integration of systems that combine targeted whole-field and buffer practices at the landscape scale (Williams et al. 2004). Maximizing buffer width will decrease linearity of buffer configuration, such that edge-to-area ratios are minimized (Clark and Reeder 2007). Further, bobwhite densities increased linearly with increases in buffer composition in immediate landscapes (McConnell 2011). Where applicable, integrating targeted whole-field and buffer practices under a conservation management system [CMS] will be considerably more effective in achieving NBCI recovery goals. One study demonstrates 116-238% greater bobwhite density under an integrated CMS compared to surrounding conventionally cropped landscapes in the MAV (Dinsmore et al. 2009). The key point is that increasing amount of habitat (i.e., decreasing diffuse application of single buffers) will likely elicit greater positive population effects. Given these results, managers are advocating for avoiding spatially diffuse "piecemeal conservation" at farm-scales in exchange for strategic use of conservation practices targeted intentionally for greatest wildlife and ecosystem benefits across the landscape (Sotherton 1998, Williams et al. 2004, Clark and Reeder 2007). "Scaling up" these conservation strategies beyond single-farm systems is therefore critical for comprehensive bobwhite recovery (Peterjohn 2003, Williams et al. 2004).

Given all factors that influence potentially bobwhite response to conservation, and assuming overall covey effect size represents an average estimate over all regions and years, and coveys are being added to extant populations instead of redistributed from the surrounding landscape, I estimated number of coveys added to the population because of the CP33 buffer practice. Through digitizing land cover, I estimated average amount of CP33 at 5.41% and 0.27% in the 78.54 ha (500 m radial) landscape surrounding survey points for buffered and non-buffered fields, an increase of 5.14% on buffered compared to non-buffered fields. On average, 5.14% of 78.54 ha is 4.04 ha of buffer in the survey radius. Overall effect size (0.016 coveys/ha) observed across the study region suggests 1.26 greater coveys in the 78.54 ha survey region around buffered fields than non-buffered fields. Given observed effect size, an average of 4.04 ha CP33 buffer, and July 2011 CP33 enrollment of 96,375 ha (U.S. Department of Agriculture 2011), this would translate into 30,000 coveys added to the fall population. If mean autumn covey size was assumed to be 12 birds/covey, this would translate into 360,000 individual bobwhites added to the fall population. If enrollment in CP33 was maximized to the current acreage cap (141,640 ha; U.S. Department of Agriculture 2010), 44,090 coveys (529,084 individual bobwhites) would be added to the fall population. Given observed effect size, 7.71 million ha of CP33 would be necessary to meet the target population recovery goal of 2.4 million added coveys described in the NBCI (National Bobwhite Technical Committee 2011). Similar to NBCI predictions, this would constitute a 5% change in land use practices on the current ~145 million ha of cropland in the contiguous U.S. (U. S. Department of Agriculture 2009). This exercise is purely for illustrative purposes and extends the range of inference from this study to the range of established CP33 acres without accounting for expected regional differences. But it does reaffirm the NBCI prediction that minimal change in primary land use at large spatial scales has potential to restore bobwhite to sustainable levels.

Addition of 7.71 million ha of CP33 seems like an unrealistic objective, given the acreage cap is set currently at 141,640 ha (U. S. Department of Agriculture 2010). To meet the NBCI recovery goals based on CP33 habitat buffers alone would require a transformative shift in the current agricultural management paradigm. Yet a 5% change in land use is plausible. Targeting agro-ecological conservation systems within working agricultural landscapes holds tremendous potential to establish wildlife habitat and increase permeability across the landscape (Kostyack et al. 2011), while providing landowners opportunities that promote broad-scale resource stewardship and also offsetting opportunity costs of conservation (Burger et al. 2006*a*).

Fine-scale management practices like upland habitat buffers are by no means a "panacea" for bobwhite management (Williams et al. 2004), but they can be an important tool for targeted and adaptive conservation management systems aimed to increase bobwhite densities at larger spatial scales. Evidence of increased covey densities on buffered fields warrant further investigation into strategies that maximize effect of buffers in the landscape, including evaluation of effects of surrounding landscape composition on bobwhite response (e.g., Riddle et al. 2008), evaluating effects of successional management to maintain habitat quality throughout the contract period (Best 2000, Gray and Teels 2006, Harper 2007), discerning variable regional needs for efficacious buffer implementation, evaluating changes in population demographics because of buffer implementation, and development of strategies that encompass other declining bird species that make use of similar habitat structure and composition (Giocomo et al. 2009). Though buffers like CP33 have potential to improve overall ecosystem health in the landscape (Lovell and Sullivan 2006), detailed examination of seed mixes in targeted buffers is warranted to guarantee maximization of ecosystem services offered by buffers (Thomas and Marshall 1999, Pywell et al. 2005, Olson and Wackers 2007). Finally, ensuring that scientific evidence plays a key role in adaptive management of buffer practices such that policy is effective and constituents are informed appropriately will help ensure long-term success of targeted wildlife-friendly conservation practices (Wossink et al. 1999, Williams et al. 2004, Gray and Teels 2006).

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Table 4.1 ΔAIC scores and number of parameters [K] for candidate models of the detection function for northern bobwhite covey data truncated at 500 m on CP33 buffered and non-buffered fields [type] in 11 U.S. states (7 regions; 2006-2008). Continuous covariates Julian day [day], wind speed ([wind]; km/hr), cloud cover ([cloud]; %), 6-hr change in barometric pressure ([bp]; in/Hg; 1 am-7 am), and number of adjacent coveys [adj] have been shown to influence calling rate of bobwhite coveys (Wellendorf et al. 2004). Covariates were not evaluated in post-stratified models to minimize the candidate model set.

Key function	Post-stratified	Covariates	K	ΔAIC
HR[a]		state[c] + year[c]	14	0.00
HR[b]		state[c] + type[c]	13	9.91
HR	state		22	21.43
HR		state[c]	12	22.40
HN		state[c] + year[c]	13	24.51
HN		state[c] + type[c]	12	48.35
HN		state[c]	11	56.66
HN	state		11	57.56
HR		region[c]	8	75.12
HR	region		14	76.35
HN		region[c]	7	107.13
HN	region		7	108.03
HR		day	3	158.56
HR		wind	3	180.23
HR		year[c]	4	185.51
HR	type		4	185.69
HR		cover	4	195.11
HR			2	196.12
HR		type[c]	3	197.51
HN		wind	2	199.51
HR		cloud	3	200.83
HN		day	2	201.42
HR		adj	3	202.48
HR		bp	3	203.43
HN		cover	3	210.79
HN		year[c]	3	211.05
HN		type[c]	2	212.48
HN	type		2	213.36
HN		cloud	2	224.03
HN			1	227.85
HN		adj	2	228.69
HN		bp	2	228.97

[a] Half-normal

[b] Hazard-rate

[c] Factor-level covariate

Table 4.2 AIC, change in AIC relative to the best approximating model [ΔAIC], and model degrees of freedom [df] for the candidate set of Poisson count models evaluating categorical fixed effects year, type (non-buffered, buffered), region, state-planned contract cover and continuous effect of survey week on northern bobwhite covey densities in 11 states, 2006-2008.

Model	AIC	ΔAIC	df
year + type + region + type × region	3,351.279	0	15
region + type + region × type	3,355.224	3.945	13
type + region + contcov + year + week	3,365.334	14.055	13
type + region + week + region × week	3,368.681	17.402	14
type + region + year + week	3,379.3	28.021	11
type + region + week	3,387.245	35.966	9
type + contcov + region	3,389.832	38.553	10
region + type + year + type × year	3,396.633	45.354	12
year + type + region	3,400.018	48.739	10
region + type	3,403.959	52.68	8
type + region + year + region × year	3,408.449	57.17	20
region + week + region × week	3,462.236	110.957	13
contcov + year + type + year × type	3,481.233	129.954	9
region + week	3,481.425	130.146	8
contcov + region	3,484.579	133.3	9
type + contcov + year	3,484.628	133.349	7
type + contcov	3,488.473	137.194	5
year + region	3,494.745	143.466	9
type + week	3,497.015	145.736	4
region	3,498.685	147.406	7
year + region + year × region	3,503.112	151.833	19
year + type + year × type	3,504.357	153.078	7
year + type	3,507.741	156.462	5
type	3,511.604	160.325	3
year + contcov	3,579.377	228.098	6
contcov	3,583.221	231.942	4
year + week	3,583.725	232.446	5
week	3,591.199	239.92	3
week + week × week	3,593.199	241.92	4
year	3,602.464	251.185	4
intercept only	3,606.325	255.046	2

Table 4.3 Point estimates of scale parameter [σ], effective area [v] in ha, effective detection radius [ρ] in m, and probability of detection [p] out to a 500 m radius for the detection function parameters for each state-year combination in evaluating northern bobwhite covey densities on buffered and non-buffered fields in 11 states, 2006-2008. Standard error estimates from 999 bootstrap resamples are in parentheses for each parameter.

		2006	2007	2008
Georgia	σ	241.82 (45.08)	194.77 (38.60)	216.97 (43.31)
	v	30.79 (8.18)	21.77 (6.88)	25.97 (7.84)
	ρ	313.08 (40.00)	263.21 (39.17)	287.52 (40.83)
	p	0.392 (0.104)	0.277 (0.088)	0.331 (0.100)
Iowa	σ	183.00 (34.99)	147.40 (27.18)	164.20 (30.06)
	v	19.60 (6.10)	13.46 (4.39)	16.27 (5.10)
	ρ	249.79 (35.80)	206.97 (30.09)	227.58 (32.08)
	p	0.250 (0.078)	0.171 (0.056)	0.207 (0.065)
Illinois	σ	310.11 (42.78)	249.77 (35.58)	278.25 (36.96)
	v	43.96 (7.29)	32.35 (6.54)	37.90 (6.62)
	ρ	374.08 (30.84)	320.89 (31.82)	347.34 (29.68)
	p	0.560 (0.093)	0.412 (0.083)	0.483 (0.084)
Indiana	σ	309.61 (44.95)	249.37 (35.51)	277.79 (39.57)
	v	43.87 (7.79)	32.27 (6.53)	37.81 (7.20)
	ρ	373.68 (33.20)	320.50 (32.46)	346.93 (32.89)
	p	0.559 (0.099)	0.411 (0.083)	0.482 (0.092)
Kentucky	σ	308.18 (33.97)	248.22 (28.74)	276.51 (30.13)
	v	43.60 (5.99)	32.04 (5.32)	37.57 (5.54)
	ρ	372.54 (25.23)	319.38 (26.23)	345.79 (24.99)
	p	0.555 (0.076)	0.408 (0.068)	0.478 (0.071)
Missouri	σ	328.13 (20.86)	264.29 (17.14)	294.42 (18.73)
	v	47.26 (3.58)	35.19 (2.94)	41.01 (3.28)
	ρ	387.86 (14.73)	334.67 (14.01)	361.29 (14.36)
	p	0.602 (0.046)	0.448 (0.037)	0.522 (0.042)

Table 4.3 (Continued)

Mississippi	σ	301.89 (23.53)	243.16 (20.77)	270.87 (20.91)
	v	42.42 (4.24)	31.06 (3.74)	36.47 (3.80)
	ρ	367.47 (18.39)	314.41 (19.04)	340.72 (17.69)
	p	0.540 (0.054)	0.395 (0.048)	0.464 (0.048)
North Carolina	σ	327.30 (33.19)	263.62 (27.00)	293.67 (30.27)
	v	47.11 (5.79)	35.06 (4.93)	40.87 (5.50)
	ρ	387.25 (24.14)	334.05 (23.79)	360.66 (24.46)
	p	0.600 (0.074)	0.446 (0.063)	0.520 (0.070)
South Carolina	σ	175.70 (29.03)	141.52 (23.74)	157.65 (26.87)
	v	18.29 (4.85)	12.52 (3.44)	15.16 (4.25)
	ρ	241.28 (31.35)	199.60 (26.91)	219.63 (29.86)
	p	0.233 (0.062)	0.159 (0.044)	0.193 (0.054)
Tennessee	σ	261.95 (37.40)	210.98 (32.74)	235.03 (35.12)
	v	34.73 (6.84)	24.82 (5.90)	29.47 (6.45)
	ρ	332.49 (32.34)	281.09 (32.54)	306.27 (32.83)
	p	0.442 (0.087)	0.316 (0.075)	0.375 (0.082)
Texas	σ	180.03 (18.55)	145.01 (15.52)	161.54 (16.70)
	v	19.06 (2.81)	13.07 (1.95)	15.81 (2.33)
	ρ	246.34 (17.75)	203.99 (14.84)	224.36 (15.88)
	p	0.243 (0.036)	0.166 (0.025)	0.201 (0.030)

Table 4.4 Parameter estimates from the best approximating generalized linear mixed model with analytic [ASE] and bootstrap [BSE] standard error estimates and 95% bootstrap confidence interval for northern bobwhite covey data collected in 11 states, 2006-2008. The best approximating model included fixed main effects of year, treatment type (non-buffered, buffered), region, and a type × region interaction.

				BS Percentile CI		
	Estimate	ASE	BSE	2.50%	97.50%	
Intercept	-13.29	0.162	0.184112	-13.74	-13.00	***
2007	0.144	0.052	0.122218	-0.079	0.400	
2008	0.050	0.050	0.108213	-0.167	0.245	
Type[a]	0.141	0.109	0.137221	-0.114	0.410	
CTX[b]	2.150	0.245	0.218921	1.773	2.62	***
ESCP[c]	-0.576	0.208	0.233293	-1.053	-0.147	**
ETP[d]	-0.127	0.196	0.207859	-0.559	0.255	
MAV[e]	-1.223	0.400	0.517821	-2.491	-0.439	**
WSCP[f]	-0.439	0.229	0.226293	-0.883	0.050	
Type*CTX	0.055	0.141	0.159604	-0.263	0.351	
Type*ESCP	0.804	0.153	0.200464	0.418	1.18	***
Type*ETP	0.096	0.135	0.177587	-0.271	0.435	
Type*MAV	1.228	0.322	0.554695	0.290	2.48	***
Type*WSCP	0.467	0.166	0.213381	0.046	0.884	**

**Significant at $P = 0.010$ (analytical *z*-test), and 95% bootstrap confidence interval does not include 0.

***Significant at $P < 0.001$ (analytical z-test), and 95% bootstrap confidence interval does not include 0.

[a] CP33 buffered, non-buffered

[b] Central Texas region

[c] Eastern Southeastern Coastal Plain region

[d] Eastern Tallgrass Prairie region

[e] Mississippi Alluvial Valley region

[f] Western Southeastern Coastal Plain region

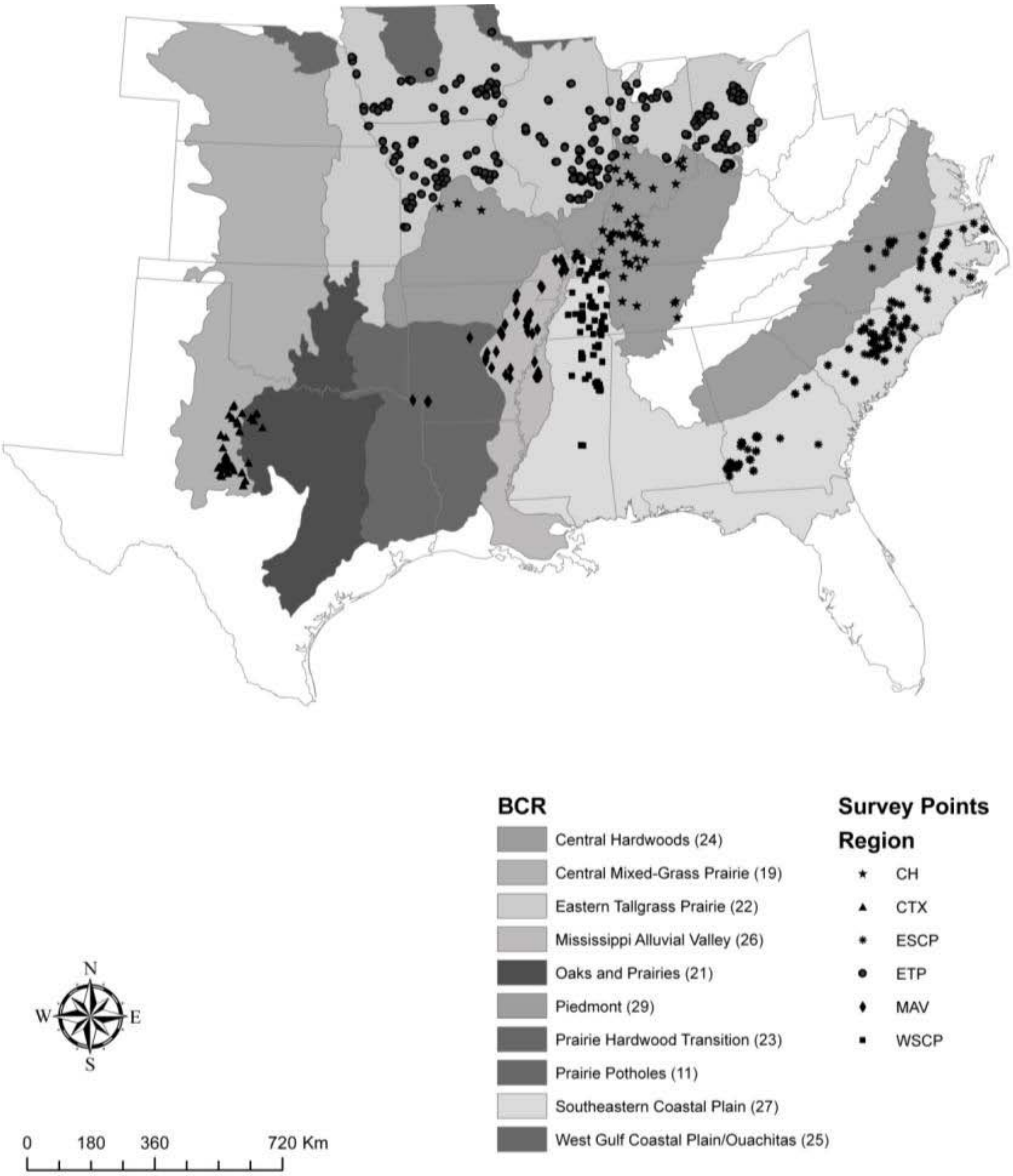

Figure 4.1 Point transect survey locations on non-buffered and CP33 buffered row-crop fields, categorized by spatial location of point clusters within ecological region (Central Hardwoods [CH], Central Texas [CTX], Eastern Southeastern Coastal Plain [ESCP], Eastern Tallgrass Prairie [ETP], Mississippi Alluvial Valley [MAV], Western Southeastern Coastal Plain [WSCP]) in 13 states on which autumn northern bobwhite covey surveys were conducted, 2006-2008.

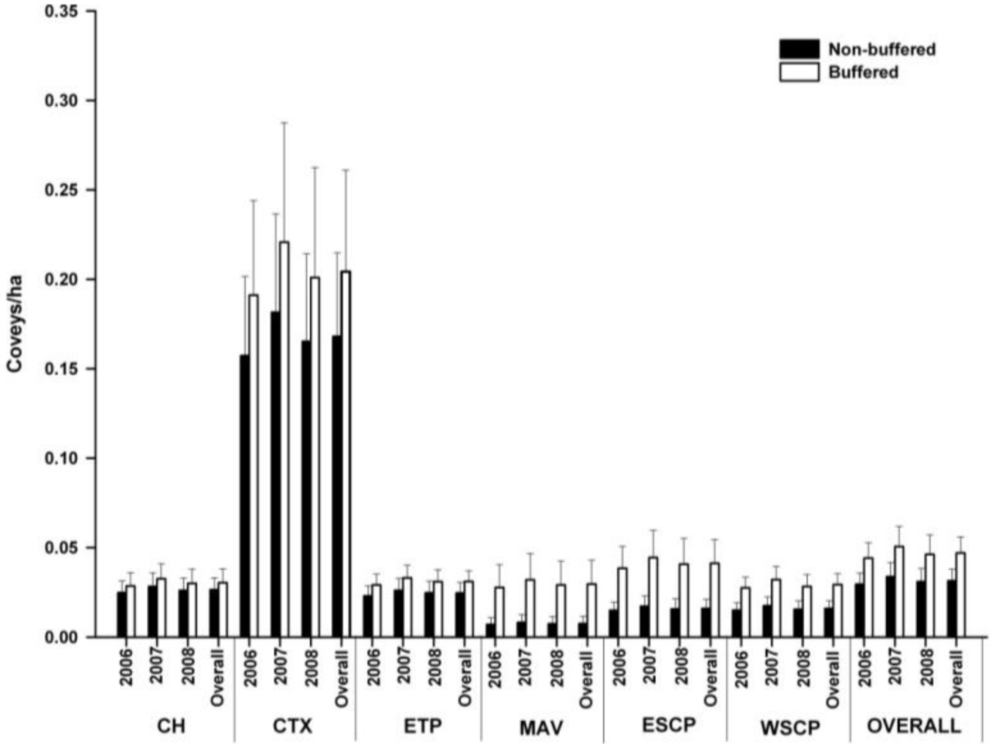

Figure 4.2 Regional and overall fitted northern bobwhite covey densities (coveys/ha ± 95% bootstrap CIs) derived from the best Poisson count model (year + region + type + region × type) on non-buffered and CP33 buffered row-crop fields in 13 states, 2006-2008. Regions were categorized based on spatial clustering of survey points within Bird Conservation Regions [BCR] (Central Hardwoods [CH], Central Texas [CTX], Eastern Southeastern Coastal Plain [ESCP], Eastern Tallgrass Prairie [ETP], Mississippi Alluvial Valley [MAV], Western Southeastern Coastal Plain [WSCP]).

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CHAPTER V

RESPONSE OF OVERWINTERING SONGBIRD COMMUNITIES TO TARGETED CONSERVATION BUFFERS

Intensification of agriculture to maximize production has caused a loss of ecological heterogeneity and subsequent decline in abundance and diversity of early-succession birds in North America and Europe (Benton et al. 2003, Murphy 2003, Newton 2004, Vickery et al. 2004). In the eastern U.S., 43% of grassland and 36% of successional-scrub bird species have experienced significant population declines in the last half-century (Sauer et al. 2011). Many of these species have been relegated to habitat remnants within agricultural landscapes to carry out all or part of their life history. However, reduced availability and diversity of food and cover resources in increasingly monotypic landscapes has contributed to declines of early-succession bird populations (Atkinson et al. 2002). Unfavorable weather conditions and limited food resources in agricultural landscapes during winter may limit survival and exacerbate declines of early-succession bird species (Peach et al. 1999). Practices that promote heterogeneous habitat structure and abundant food resources in winter agricultural landscapes may be key factors in offsetting declines in some species (Atkinson et al. 2002, Bradbury et al. 2004). However, there is unfortunately an alarming gap in knowledge regarding abundance, diversity, and habitat relationships among overwintering early-succession birds occupying agricultural landscapes (Peterjohn 2003).

In the U.S., federally subsidized conservation programs (similar to agri-environmental schemes [AES] in Europe) are authorized under a series of legislation referred to commonly as Farm Bills and administered by the U.S. Department of Agriculture. Standing winter herbaceous cover provided by these conservation programs, such as the Conservation Reserve Program [CRP], have potential to provide food and cover resources for declining resident and short-distance migratory early-succession bird species on their winter range (Best et al. 1998, Bradbury and Allen 2003). The continuous signup CRP offers a suite of practices intended for implementation in production systems and offers several conservation buffer practices (i.e., linear strips of uncultivated vegetation established along crop field margins) to help meet water and soil quality and wildlife habitat objectives in row-crop production landscapes. Conservation buffer practices have been shown to increase breeding densities of early-succession birds in the U.S. (Smith et al. 2005a, Riddle et al. 2008, Conover et al. 2009) and Europe (Peach et al. 2001, Ewald et al. 2010, Perkins et al. 2011). However, greater wildlife gains will be realized if habitat established through buffer practices provides food and cover resources during winter.

No studies currently demonstrate effects of buffers on overwintering avian populations at large spatial scales (i.e., across multiple landscapes) in the U.S. (Smith et al. 2005b, Conover et al. 2007, Blank et al., 2011), or response to grassland buffer practices targeted specifically to provide wildlife habitat. There is considerable need for greater understanding of ecology of overwintering birds in agricultural landscapes (Atkinson et al. 2002) and their response to linear grassland patches provided by conservation buffers (Best 2000, Clark and Reeder 2005), particularly using large-scale replicated studies with controlled experimental designs (Donovan et al. 2002).

My objectives were to evaluate large-scale effects of a targeted grassland buffer practice on overwintering avian communities in agricultural landscapes. Conservation Practice 33, Habitat Buffers for Upland Birds (CP33; U. S. Department of Agriculture 2004) targets recovery objectives of the Northern Bobwhite Conservation Initiative (Dimmick et al. 2002), a habitat and population recovery directive with the primary objective of restoring populations of northern bobwhite (*Colinus virginianus*) and other early-succession species across their native range. To determine if upland habitat buffers provide year-round habitat for a suite of overwintering bird species, I evaluated differences in overwintering bird communities and densities on buffered and non-buffered fields in 3 states in the southeastern U.S. For species exhibiting strong responses to buffers, I also evaluated effects of buffer width on observed bird densities.

Study Area

The study area for overwintering songbird monitoring included 3 of 14 states participating in the coordinated National CP33 Monitoring Program described in detail in Chapter I (Table 1.1, Fig. 5.1). CP33 contracts and survey locations were selected randomly according to a modified multi-stage sampling design described in Chapter I. Winter survey transects were located on the same fields as those surveyed during breeding season and autumn in the 3 state study area.

I coordinated winter bird monitoring on 219 paired transects selected randomly on CP33-buffered and non-buffered row-crop fields in Arkansas, Kentucky, and Mississippi from 2007-2008 (Fig. 5.1). I located randomly a single 200 m line transect on each survey field parallel to the buffer-non-crop edge for buffered fields (n=109) and the crop-non-crop edge for control fields (n=110). I placed transects along the buffer-non-crop edge for buffered fields, rather than through the buffer center, to ensure comparability between buffered and non-buffered sampling locations (Fig. 5.2).

Methods

Winter songbird surveys

Non-breeding birds are difficult to detect (Peterjohn 2003, Diefenbach et al. 2003). I accounted for detectability by implementing line transect distance sampling (Buckland et al. 2001). Line transect surveys were conducted from January-March on 201 fields (100 buffered; 101 non-buffered) in Arkansas, Kentucky and Mississippi in 2007 and on 145 fields (72 buffered; 73 non-buffered) in Kentucky and Mississippi in 2008. Transects in Arkansas were not sampled in 2008. Unbalanced allocation of survey effort on buffered and non-buffered fields was due to loss of CP33 buffers after initial set-up or inaccessibility of survey fields due to landowner restrictions or weather events. Surveys were conducted simultaneously on each buffered and non-buffered field between sunrise and 1100 hrs on days with no precipitation and winds <6 km/hr. All observations were recorded into one of 7 distance intervals as perpendicular observations from the transect centerline (0–10, 10–20, 20–30, 30–40, 40–50, 50–100, >100 m). I assumed all birds on the transect centerline were detected, were recorded at their initial location, and were recorded accurately into appropriate distance intervals (Buckland et al. 2001). Potential covariates of date, time, observer, weather characteristics (% cloud cover, temperature [◦F], wind speed [km/hr]) and side of transect centerline (agricultural [buffer, row-crop], non-agricultural [woody, herbaceous]) were collected during each survey (Marques et al. 2007, Rexstad 2007).

Data analysis

Winter bird community

I evaluated year and stratum-specific (buffered, non-buffered) winter bird community metrics of species richness and total avian conservation value [TACV]. TACV is a weighted index to assess relative conservation value using species-specific Partners in Flight [PIF] conservation priority scores which incorporate rankings of relative abundance, population trend, breeding and non-breeding distribution, and population threats to North American (Carter et al. 2000, Nuttle et al. 2003). I calculated stratum-specific TACV at 3 levels: over all winter bird species, a grassland bird guild and a woodland bird guild. Classification of grassland and woodland guilds were defined from expert opinion, and classifications provided by species accounts from the American Ornithologists' Union (Vickery et al. 1999, Poole 2005; Table 5.1). For each community, I summed conservation value scores across species to calculate a TACV score for each transect. I evaluated species richness and TACV by year in SAS PROC MIXED (Littell et al. 2006) with field type (buffered, non-buffered) as a fixed effect and paired buffered and non-buffered transects as random effects.

I also evaluated species richness and TACV differences on buffered fields in relation to buffer width (<23 m, >23 m). Buffer widths were measured annually on each CP33 buffered field at 10 points placed systematically along buffers during growing season from 2007-2008. Width measurements were not taken at paired non-buffered fields because buffers did not exist and, thus, had zero width. Because 23 m represents the midpoint of allowable contract range for CP33 buffers (9-37 m; U. S. Department of Agriculture 2004), I used that as criteria to define wide (>23m) vs. narrow (<23 m) buffers. Although some outlier buffer widths <9 m and >37 m were recorded, these were considered non-compliant buffer widths and do not reflect the allowable range of buffer widths in the CP33 practice. I evaluated differences in richness and TACV by year in SAS PROC MIXED (Littell et al. 2006), with buffer width (<23 m, >23 m) as a fixed effect and buffered transect as a random effect.

Winter bird density

For species exhibiting sufficient sample size for analysis (>40 observations), I evaluated overwintering densities on buffered and non-buffered fields pooled over all states using Conventional Distance Sampling [CDS] and Multiple Covariate Distance Sampling [MCDS] engines in program DISTANCE 6.0 version 2 (Thomas et al. 2010). I also included 3 species groups (wood warblers (*Setophaga* spp.), raptors, and other sparrows) that were composed of species with insufficient sample size for individual analysis, but that shared similar life history strategies. Although winter birds occur in clusters occasionally, bird observations ranged from single individuals to loosely aggregated groups of individuals. Because of general lack of discrete aggregations, I analyzed each observation independently. To avoid density estimates biased from outlier detections, I right-truncated observations for each species/group at distances (m) where probability of detection $g(w) < 0.1$. In CDS and MCDS analyses, I evaluated fit of 2-3 models of the detection function: uniform (CDS only), half-normal (CDS, MCDS), and hazard rate (CDS, MCDS), with and without series expansion adjustments (cosine, simple polynomial, hermite polynomial; Buckland et al., 2001). I used Akaike's Information Criteria ([AIC]; Akaike 1973), goodness of fit tests of the model and probability density function plots of each candidate model to determine appropriate models of the detection function for analysis (Buckland et al. 2001, Marques and

Buckland 2003, Pacifica et al. 2008). When sample size allowed, I used AIC to determine if the detection function was better estimated over buffered and non-buffered sites combined (i.e., global; assumes equal detectability across treatments) or separately on each treatment type (i.e., stratified; calculates unique detection function for buffered and non-buffered fields) for each species (Buckland et al. 2001). If AICs were competing (ΔAIC < 2.0) between global and stratified models and both models had adequate fit, I selected the model with the least AIC (Buckland et al. 2001). For species with limited sample size (<40 observations), I calculated only a global detection function and evaluated type (buffered, non-buffered) as a factor-level (i.e., categorical) covariate in MCDS analysis. For MCDS analysis, I evaluated factor-level covariates state, date, year, observer and side of transect centerline (agricultural, non-agricultural), and continuous weather covariates % cloud cover, temperature (^{o}F), and wind speed (km/hr) for each species/group.

Under the appropriate global or stratified CDS or MCDS model of the detection function, I calculated stratum-specific density (*D*; birds/ha) over all states and years for each species or group. I used density differences on buffered and non-buffered fields to calculate simple ($D_{\text{buffered}} - D_{\text{non-buffered}}$) and relative effect size ($[D_{\text{buffered}}-D_{\text{non-buffered}}]/D_{\text{non-buffered}}$), and I used 95% confidence intervals to determine significance (Gardner and Altman 1989, Sim and Reid 1999).

I also evaluated density differences in relation to buffer width for species/species groups exhibiting $\geq$100% relative effect size on buffered compared to non-buffered fields. To maintain consistency across analyses, I used the same stratification, detection function and covariate analysis scheme as above for each species, but calculated densities on buffered fields categorized by buffer width (<23 m; >23 m). Density differences on fields containing < 23 m and > 23 m buffers were used to calculate simple ($D_{>23m} - D_{<23m}$) and relative effect size ($[D_{>23m} - D_{<23m}] / D_{<23m}$) and 95% confidence intervals were used to determine significance in relation to buffer width (Gardner and Altman 1989, Sim and Reid 1999).

Results

Winter bird community

I recorded 75 and 69 species on non-buffered and buffered transects, respectively from 2007-2008. Mean species richness did not differ on non-buffered and buffered fields in 2007, but was 29% greater on buffered fields in 2008 ($P = 0.010$; Table 5.2). TACV, grassland bird TACV, and woodland bird TACV did not differ between non-buffered and buffered fields in either year ($0.070 < P > 0.900$; Table 5.2). Species richness, overall TACV, grassland bird TACV, and woodland bird TACV did not differ between fields containing buffers >23 m and <23 m in width ($0.130 < P > 0.830$).

Winter bird density

I recorded 16,259 individuals over 70,200 m of transects in 3 states from 2007-2008. The covariate state was included in top models for 65% of species/groups. Other covariates relating to year and side of transect were included in top models for 35% and 30% of species/groups, respectively (Table 5.1). Weather covariates such as temperature, cloud cover, and wind speed were included in top models for ≤15% of species/groups (Table 5.1).

Of 20 grassland and woodland species/species groups I evaluated, I observed substantially greater densities (100-2,707%) of field sparrows (*Spizella pusilla*), song sparrows (*Melospiza melodia*), swamp sparrows (*M. georgiana*), and red-bellied woodpeckers (*Melanerpes carolinus*) on buffered transects, whereas I observed substantially greater densities of Carolina chickadees (*Poecile carolinensis*) on non-buffered transects (Fig. 5.3, Table 5.1). No species exhibited responses in density to buffer width (buffers <23 m vs. >23 m wide), though effect sizes varied by species (Fig. 5.4).

Discussion

Overwinter survival may be a limiting factor in some farmland bird populations (Peach et al. 1999). Landscapes that promote heterogeneity in habitat structure increase substantially abundances of overwintering farmland birds (Atkinson et al. 2002, Bradbury et al. 2004) and may be a key factor in offsetting declines in some species. Habitat provided by CRP and AES benefit overwintering avian communities by providing critical food and cover resources (Best et al. 1998, Bradbury and Allen 2003). For example, 83% of declining granivorous farmland bird species increased in abundance on areas with AES set-aside compared to conventional arable landscapes, suggesting set-aside is important for winter farmland bird populations (Buckingham et al. 1999). These benefits are increased greatly when practices are targeted for wildlife benefits (Brickle 1997, Bradbury and Allen 2003, Hinsley et al. 2010).

In my study, habitat provided by targeted upland habitat buffers doubled minimally density of 4 overwintering bird species and was beneficial particularly to grassland associated species (e.g., Emberizid sparrows). Response by these species (100-2,707% density increase) was disproportionate to amount of buffer habitat added to the immediate and surrounding landscape (7.3% at 500 m, 2.1% at 1,500 m). Increased use of buffered habitats were also observed in other species, including eastern meadowlark

(*Sturnella magna*), savannah sparrow (*Passerculus sandwichensis*), slate-colored junco (*Junco hyemalis*), American goldfinch and the wood warbler group, which exhibited 123-685% greater densities on buffered than non-buffered fields. However, confidence intervals for these large effects included 0.0 because of variability in encounter rates across transects. Increased densities and diversity observed in this study may result from increased availability of forage, particularly seeds, in buffered habitats (Robinson and Sutherland 1999) combined with thermoregulatory and security benefits of greater cover availability.

Density of red-bellied woodpeckers and warblers doubled on buffered fields, though percent coverage of woody habitat in the immediate and surrounding landscape was only greater slightly on buffered compared to non-buffered sites (6.2% greater at 500 m, 2% at 1,500 m). These increases may be an artifact of greater wooded cover in buffered landscapes, or buffers may provide either additional foraging opportunities or a soft edge that offers greater vegetative diversity for these species (Peak and Thompson 2006). An increase in density of >100% on buffered sites suggests these woodland species may be responding disproportionately to presence of herbaceous buffers in the landscape, warranting further investigation into effects of targeted agricultural conservation practices on non-target species in adjacent or nearby wooded habitat.

Though density differences between buffers <23 and >23 m wide were not substantiated due to large encounter rate variability, some species appeared to be more abundant in wider buffers (e.g., savannah and swamp sparrows, eastern meadowlark) during winter. Positive relations with habitat area have been documented widely during breeding season for savannah sparrows and eastern meadowlarks, though some studies of savannah sparrow suggest variable or negative response (see summary in Ribic et al.

2009). Swamp sparrows are not typically considered area sensitive during breeding season (Ribic et al. 2009), but they are influenced substantially by vegetation structure, insofar as to be denoted a “vegetation-restricted species” (Herkert 1994, Benoit and Askins 2002). However, no studies demonstrate area sensitivity among overwintering populations of these species (Brennan and Kuvlesky 2005). Sensitivity to patch area may be driven by different causal mechanisms related to food resources and thermoregulatory and escape cover than reproductive success. My data suggest overwintering populations of swamp sparrows may be sensitive to width (a form of area) in linear patches. Negative edge effects related to overwinter survival may be more pronounced in linear patches compared to square patches like fields, remnant grasslands and wetlands in which area relationships of swamp sparrows have been studied previously during breeding season (e.g., Riffell et al. 2001). Other species that appeared to respond favorably to presence of buffers, but negatively to buffer width during winter included song sparrow and American goldfinch, which have been shown previously to be influenced negatively by patch area during breeding season (Herkert 1994). These truly “edge” species may avoid buffer habitats with greater patch area because they perceive reduced availability of edge habitat.

This study represents the first in the U.S. to examine winter bird response to targeted native herbaceous buffer habitats across a large spatial extent. However, my results are consistent with those observed in previous studies conducted at smaller, farm-level extents. Native herbaceous buffers similar to those provided by targeted CP33 buffers increased total avian abundance and sparrow abundances (Marcus et al. 2000, Smith et al. 2005*b*, Conover et al. 2007, Blank et al. 2011) compared to conventionally cropped non-buffered fields. However, in these studies, response to buffered habitats was influenced by buffer width (Conover et al. 2007, Blank et al. 2011) and adjacent habitat type (Smith et al. 2005*a*, *b*). Similar to my study, woodland and edge species such as northern cardinal (*Cardinalis cardinalis*), eastern towhee (*Pipilo erythrophthalmus*) and white-throated sparrow (*Zonotrichia albicollis*) did not respond to buffers at the farm scale (Smith et al. 2005*a*, *b*, Conover et al. 2007). Other farm-scale studies are contrasting, with one suggesting species richness, diversity, and TACV are not influenced by buffered habitats (Smith et al. 2005*a*,*b*) and others suggesting these metrics are influenced greatly by buffered habitats (Conover et al. 2007, Blank et al. 2011). These differences demonstrate importance of evaluation of avian response to buffered habitats beyond the farm scale. Value of buffers as overwintering bird habitat may be actually a function of landscape context rather than farm or field-level management, or a combination of both (Best 2000, Bradbury et al. 2004, Moreira et al. 2005).

Gains in biodiversity from conservation programs may be maximized if program practices are targeted toward specific conservation objectives (Bradbury and Allen 2003) and promote ecological heterogeneity in agricultural landscapes (Benton et al. 2003). This study exemplifies how management targeted for restoration of northern bobwhite can have tremendous positive impacts on other farmland bird species sharing similar habitat requirements (Brennan and Kuvlesky 2005). Substantive responses by some overwintering bird species suggests policy makers should remain cognizant of these potential secondary outcomes when conservation practices are targeted toward specific taxa. Benefits of targeted practices will be further maximized if practices are delivered strategically across the landscape with intentional and optimal placement to support biodiversity gains (Bignal and McCracken 1996).

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Table 5.1 Level of stratification of the detection function [Dfn], covariates used in best selected model [Cov], density [D] in birds/ha and standard error [SE] on buffered and non-buffered fields, and relative effect size [RES] = ([D_{buffered}-$D_{\text{non-buffered}}$]/$D_{\text{non-buffered}}$ × 100) for 20 winter bird species/species groups in Arkansas, Kentucky, and Mississippi, 2007-2008.

			Non-buffered		Buffered		
	Dfn[a]	Cov[b]	D	SE	D	SE	RES (%)
Raptors[f]	G[d]	Te	0.039	0.012	0.050	0.013	25.94
Red-bellied woodpecker[c] (*Melanerpes carolinus*)	S	C, W	0.115	0.024	0.291	0.072	152.43
Downy woodpecker (*Picoides pubescens*)	G[d]	St, Si, Te	0.073	0.027	0.065	0.019	-10.99
Blue jay (*Cyanocitta cristata*)	G	St	0.216	0.038	0.219	0.038	1.73
Carolina chickadee[c] (*Poecile carolinensis*)	S	St, Y	0.529	0.119	0.204	0.057	-61.48
Carolina wren (*Thryothorus ludovicianus*)	G[d]	Y	0.179	0.043	0.188	0.041	4.63
Eastern bluebird (*Sialia sialis*)	S	St, Si	0.255	0.085	0.179	0.044	-29.86
American robin (*Turdus migratorius*)	S	St	2.812	1.108	0.936	0.421	-66.71
Warblers[g]	G[d]	St, Ty	0.138	0.041	0.309	0.152	123.80
Eastern towhee (*Pipilo erythrophthalmus*)	G	Si	0.302	0.066	0.308	0.075	1.72
Field sparrow[c] (*Spizella puswella*)	G	St, Si	0.390	0.185	1.235	0.346	216.73
Savannah sparrow (*Passerculus sandwichensis*)	G	St, Y	0.841	0.403	2.111	1.174	150.92

Table 5.1 (Continued)

Song sparrow[c] (*Melospiza melodia*)	S	C, Si, Y	3.562	0.668	7.139	0.816	100.43
Swamp sparrow[c] (*Melospiza georgiana*)	G[d]	St, Y, Ty, Si	0.169	0.055	4.733	0.770	2707.69
White-throated sparrow (*Zonotrichia albicollis*)	S	St, Y	2.906	0.725	2.186	0.490	-24.77
Other sparrow	G	C, Te	0.806	0.251	2.018	0.814	150.24
Slate-colored junco (*Junco hyemalis*)	G[d]	St, Si	0.205	0.082	0.715	0.271	248.77
Northern cardinal (*Cardinalis cardinalis*)	S	St, Y	2.038	0.716	1.071	0.209	-47.45
Eastern meadowlark (*Sturnella magna*)	S	St	0.132	0.038	0.327	0.110	147.26
American goldfinch (*Spinus tristis*)	G		0.042	0.020	0.329	0.148	684.71

[a] Abbreviations: stratified by treatment type (S); global over treatment types (G)

[b] Abbreviations: percentage cloud cover (C), side of transect (Si), state (St), temperature (Te), treatment type (Ty), wind (W), year (Y)

[c] Significant based on 95% CI on ES not including zero (Fig. 5.1)

[d] Insufficient data to evaluate stratified df - global only

[e] Includes American tree sparrow (*Spizella arborea*), chipping sparrow (*Spizella passerina*), fox sparrow (*Passerella iliaca*), house sparrow (*Passer domesticus*), Le Conte's sparrow (*Ammodramus leconteii*), white-crowned sparrow (*Zonotrichia leucophrys*) and all other unknown sparrows.

[f] Includes American kestrel (*Falco sparverius*), Cooper's hawk (*Accipiter cooperii*),northern harrier (*Circus cyaneus*), red-shouldered hawk (*Buteo lineatus*), red-tailed hawk (*Buteo jamaicensis*) and short-eared owl (*Asio flammeus*).

[g] Includes myrtle warbler/yellow-rumped warbler (*Setophaga coronata*), palm warbler (*Setophaga palmarum*), pine warbler (*Setophaga pinus*) and yellow warbler (*Setophaga petechia*).

Table 5.2 Mean [$\bar{x}$] ± standard error [SE] winter bird species richness [Rich], total avian conservation value [TACV], relative effect size ([buffered-non-buffered]/non-buffered × 100, *F* statistic, and *P*-value on non-buffered and CP33 buffered fields in Arkansas, Kentucky and Mississippi, 2007-2008.

		Non-buffered		Buffered				
Year	Metric[a]	$\bar{x}$	SE	$\bar{x}$	SE	RES (%)	F	*P*-value
2007	Rich	5.571	0.346	5.687	0.34	2.08	0.08	0.778
	TACV-O	27.365	3.877	28.016	3.782	2.38	0.02	0.898
	TACV-G	14.764	3.965	23.772	3.7	61.01	2.85	0.094
	TACV-W	13.24	1.66	9.817	1.697	-25.85	2.65	0.107
2008	Rich	4.142	0.397	5.338	0.397	28.87	6.9	0.011[b]
	TACV-O	29.369	13.561	64.879	13.461	120.91	3.49	0.066
	TACV-G	20.947	14.684	56.309	13.444	168.82	3.15	0.078
	TACV-W	9.422	1.862	11.686	1.749	24.03	0.79	0.378

[a] Abbreviations: overall total avian conservation value (TACV-O), grassland bird total avian conservation value (TACV-G), woodland bird total avian conservation value (TACV-W).

[b] Significant at $P < 0.050$.

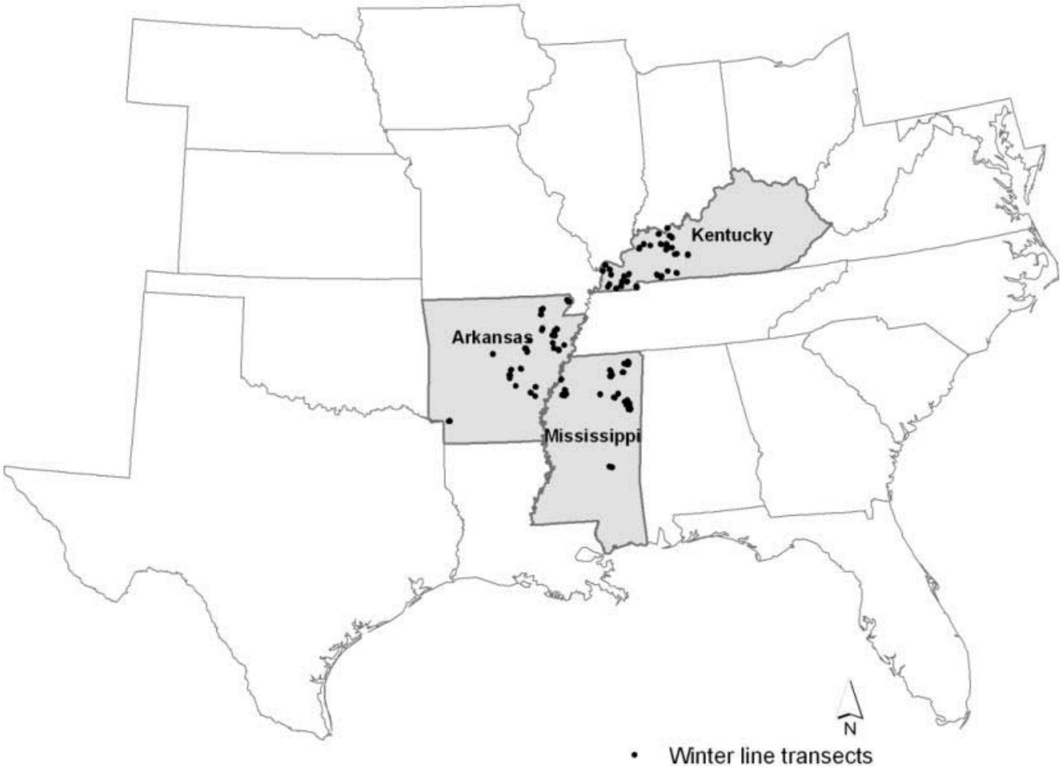

Figure 5.1 Geographic locations of winter line transects on CP33 buffered and non-buffered row-crop fields in Arkansas, Kentucky, and Mississippi, 2007-2008.

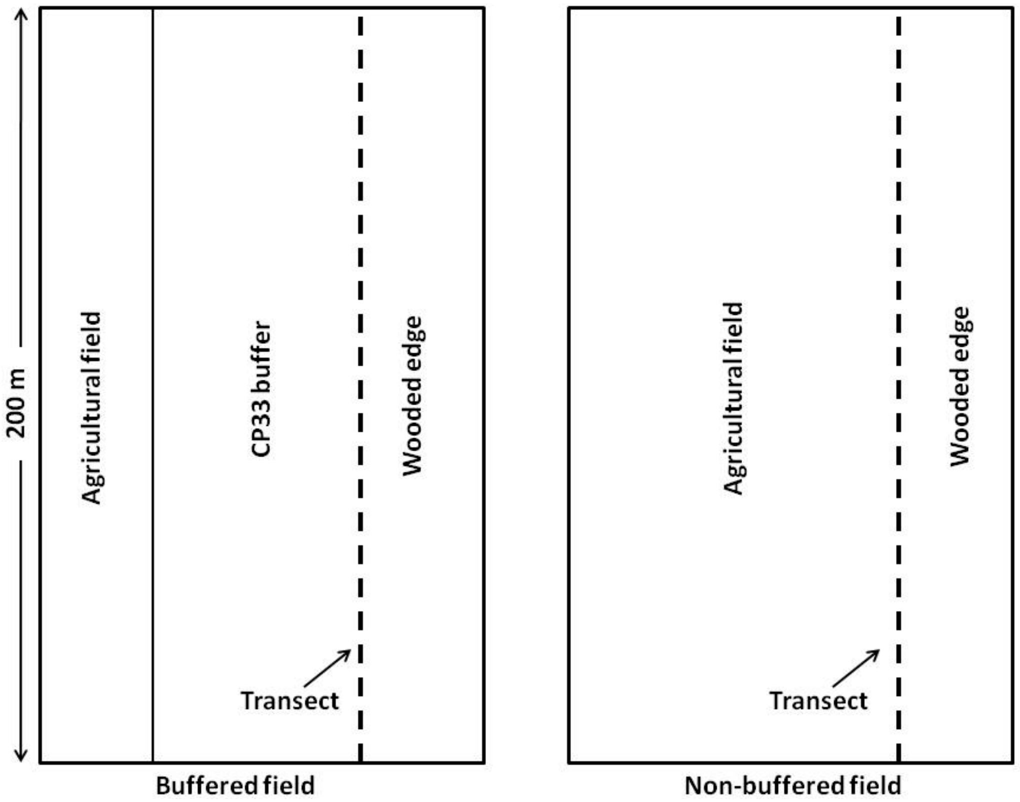

Figure 5.2 An example of layout design for winter line transect bird surveys in 3 states (2007-2008) situated parallel to buffer-non-crop edges for buffered survey fields and crop-non-crop edges for non-buffered survey fields. Winter line transects were 200 m in length and edges may or may not have been wooded.

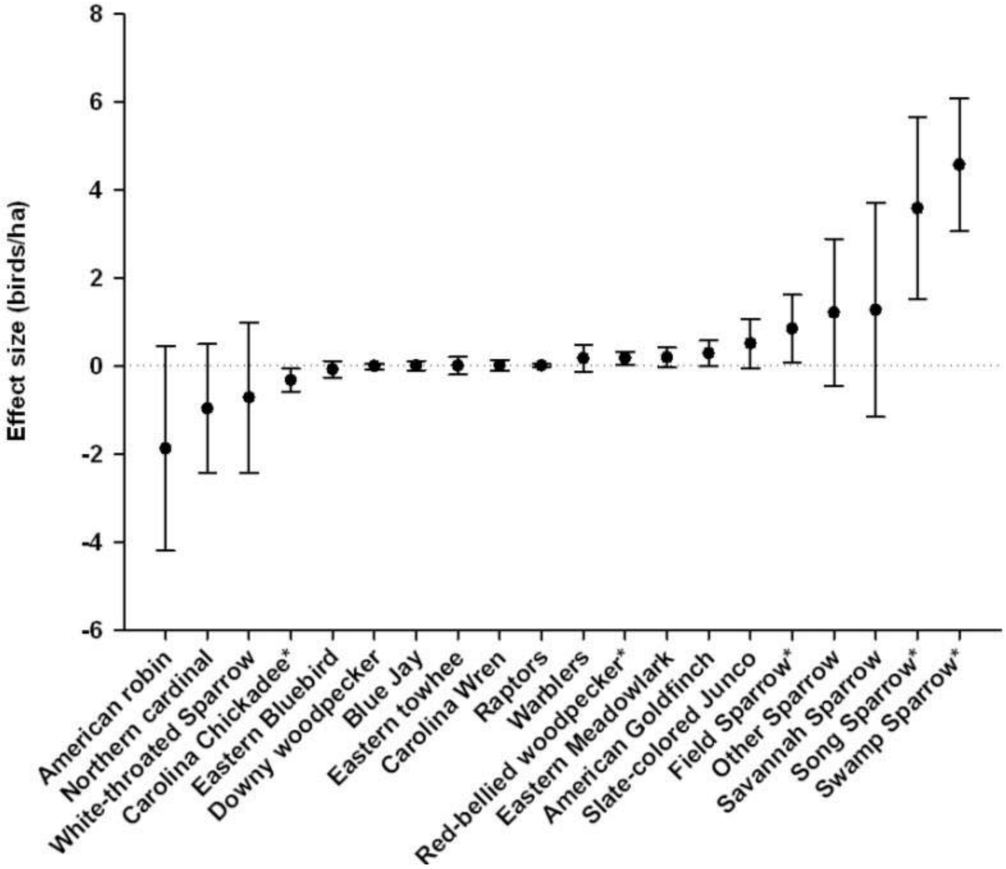

Figure 5.3 Effect size ($D_{buffered}$-$D_{non\text{-}buffered}$) ±95% CI (birds/ha) for winter bird species in Arkansas, Kentucky, and Mississippi, 2007-2008. *significant difference based on 95% CI on effect size.

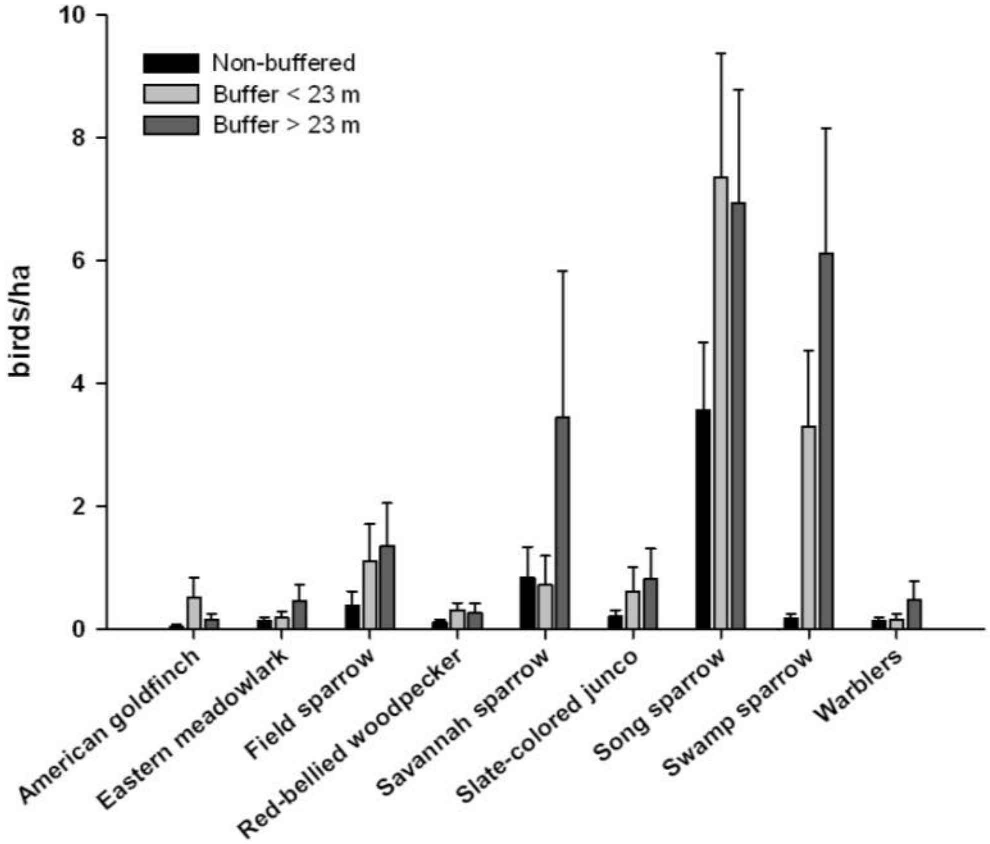

Figure 5.4 Density ±95% CI (birds/ha) on non-buffered, and buffered fields <23 m and >23 m in width for overwintering bird species/species groups that responded positively to buffers in Arkansas, Kentucky and Mississippi, 2007-2008.

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CHAPTER VI

CONCLUSIONS

Conservation practices targeted to deliver specific wildlife objectives have been shown here to produce measurable benefits for some species across multiple seasons. Establishment of native herbaceous cover along row-crop field margins resulted in greater breeding and overwintering densities of several bird species compared to similar non-buffered row-crop fields across broad geographic regions. Overall and persistent response by northern bobwhite during breeding season and autumn suggests targeted CP33 buffers may provide food and cover resources to meet multi-seasonal life history requirements and increase usable space disproportionate to actual change in primary land use. Further, buffers designed for bobwhite conservation may elicit secondary conservation benefits for other resident and migrant early-succession bird species. This includes providing favorable breeding habitat for grassland and scrub-successional species like dickcissel and field sparrow and overwintering habitat for several Emberizid sparrow species. These results support previous evidence of similar responses by breeding and overwintering species to linear buffer habitats demonstrated at lesser spatial scales (e.g., Smith et al. 2005*a*,*b*; Conover et al. 2007, 2009). However, managers should cautiously avoid generalizations regarding overall benefits from practices targeted for bobwhite conservation, as this study demonstrated equally imperiled grassland bird species (e.g., eastern meadowlark, grasshopper sparrow, eastern kingbird) exhibited limited response to buffered habitats.

Bobwhite managers operate typically under the paradigm that establishing and managing appropriate bobwhite habitat will guarantee colonization and establishment of local populations – an “if you build it, they will come” approach. However, managers are increasingly frustrated by absence of colonization in what appears to be quality bobwhite habitat. The reality is - if you build it, they may come - but their arrival and persistence may depend on composition and configuration of the surrounding landscape (e.g., Twedt et al. 2007, Riddle et al. 2008) and even larger-scale effects of ecological region. This study demonstrates that though bobwhites and other upland bird species may exhibit disproportionate increased abundances on fields containing targeted buffers, response to buffers exists within the confines of land-use, climate, and baseline population densities characteristic of the inherent ecological region. Though few studies have capacity to evaluate effects of conservation across ecological regions, results of this study support the general consensus that biodiversity response to agro-ecological conservation will vary regionally (e.g., Davey et al. 2010). Thus, a regional approach to agro-ecological conservation is intuitive, and should be incorporated in conservation practice development and delivery.

Further complexity is added by variability in response to buffers within a given region across the breeding and non-breeding seasons. For example, bobwhites in the Eastern Tallgrass Prairie region exhibited substantive breeding season, but limited fall response to CP33 buffers. However, bobwhites in the Central Mixed-grass Prairie region exhibited a direct contrast, with little to no breeding season, but substantive fall response to CP33 buffers. These differences likely reflect variable resource needs depending on region as a surrogate for latitudinal and land-use variation. Targeted buffers in the Eastern Tallgrass Prairie region offer valuable cover resources during breeding season in an intensively cropped agricultural landscape, but may provide inadequate thermal and protective cover for fall coveys. Conversely, buffers may provide minimum added benefit to already abundant breeding populations in rangelands, pasture-lands, and grassy cover in the Central Mixed-grass Prairie region, but substantial benefit to fall bobwhite populations. Thus assessment of conservation benefits across the annual cycle must always consider regional variation, and assessment of regional conservation benefits must always consider seasonal variation in response. Practices should therefore be tailored to maximize benefits in the landscapes most amenable to population response within a region and across the annual cycle. For example, if a lack of thermal cover is driving limited response to targeted buffers by fall coveys in the Eastern Tallgrass Prairie region, then practice standards in this region should be adapted to increase availability of winter roost sites. Thus, observed regional variation should inform the adaptive management loop by assessing efficacy of conservation practices, and adapting conservation practice delivery to maximize population and societal gains (Lovell and Sullivan 2006).

Landscape structure within regions will also affect local distribution and abundance and response to targeted buffer habitats. In this study breeding season bobwhite abundances were driven by different features of landscape composition and configuration at different spatial scales in each region. Amount of native herbaceous habitat provided by CP33 buffers was present in top models for several regions, but never exhibited strong influence over other landscape parameters. Thus, though bobwhites may respond favorably to targeted buffer habitats, that response is dominated typically by other features within the local and surrounding landscape. Heterogeneity of cover types, represented by features of patch richness and patch density influenced bobwhite abundances in most regions, though scales and direction of influence (i.e., positive, negative) varied. The only landscape feature to consistently rank in top models across nearly all regions was negative effect of urbanization (i.e., development). The negative observed response appeared disproportionate to composition of developed land in the surrounding 1,500 m landscape (only 5-6%). Though somewhat intuitive, this is the first study to demonstrate tangible evidence of negative and disproportionate effects of urbanization across the bobwhite range. However, given the broad-ranging variability of landscape predictors across regions, little inference can be drawn regarding influence of other landscape composition and configuration features across the entire bobwhite range. This outcome is similar to that of Peterson et al. (2002), and lends further support to the argument that bobwhite conservation must be approached from a regional context.

This study demonstrates bobwhite and upland bird distribution and abundance across the landscape is complex and hierarchical, depends on features of the immediate and surrounding landscape, and characteristics of the broader ecoregion (i.e., representative of variation in climate and land use). These features subsequently affect the response to targeted conservation in complex and hierarchical ways. Disproportionately greater breeding season, fall, and winter densities on buffered fields in most regions and overall suggests conservation buffers offer perceived habitat advantages over conventionally cropped fields for several species. However, conclusions regarding conservation benefits of targeted buffers require the assumption that greater bird densities on buffered fields represent net population gains and not redistribution of individuals into buffered areas from the surrounding landscape. If individuals are simply redistributed, conservation benefits of targeted buffers will be diminished substantially.

Relationship to Regional Management Plans

The National Bobwhite Conservation Initiative [NBCI] suggests recovery of range-wide bobwhite populations to huntable levels will require a strategic and multi-faceted regional approach to conservation (National Bobwhite Technical Committee 2011). Targeted conservation buffer practices are one of many available conservation options available to aid in recovery of bobwhite populations in agricultural landscapes. The NBCI suggests in-field and field-margin management for bobwhite should be prioritized in row-crop agricultural landscapes (National Bobwhite Technical Committee 2011). Field margin habitats like targeted CP33 buffers offer an economically advantageous conservation alternative when whole-field enrollments are not an option in a production system (Barbour et al. 2007, McConnell 2011). However, fine-scale management practices like upland habitat buffers are by no means a "panacea" for bobwhite management (Williams et al. 2004). To meet NBCI recovery goals based on CP33 habitat buffers alone would require a transformative shift in the current agricultural management paradigm. Ideally, targeting agro-ecological conservation systems in working production systems should prioritize a mix of whole-field and buffer practices to maximize conservation benefits and economic benefits to producers. Further, strategically tailoring conservation design at the farm and landscape scale may provide substantially greater conservation benefits compared to spatially diffuse conservation scattered across the landscape. Conservation practices targeted and implemented strategically to meet specific resource objectives will provide landowners improved opportunities to promote broad-scale resource stewardship while also offsetting opportunity costs of conservation (Burger et al. 2006).

A Broader Agro-ecological Perspective

Much of Earth's biodiversity exists currently on lands impacted by agricultural land use (Krebs et al. 1999), and agriculture has been suggested as the single greatest threat to imperiled bird species in developed and developing countries (Green et al. 2005). The global human population is expected to reach 8-9 billion by 2050, resulting in doubling of production demands to sustain global food security (Green et al. 2005, Godfray 2011). Yet, agricultural production systems must be managed carefully and sustainably to maintain natural ecosystem function (Butler et al. 2007). The need for "sound ecological science" regarding sustainability of ecosystems in agricultural landscapes is resounding (Robertson and Swinton 2005). This science should be used to adaptively inform conservation design in agricultural landscapes, such that biodiversity and ecosystem benefits are maximized. Targeted agricultural conservation, applied strategically and at landscape scales will provide a major step forward for biodiversity conservation in agricultural landscapes. Conservation applied in an integrated manner with functional production systems will increase heterogeneity and permeability of landscapes, will likely facilitate dispersal among subpopulations, and may impede global population declines.

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APPENDIX A

COMPETING REGIONAL BOBWHITE-LANDSCAPE MODELS

Table A.1 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the second ranked model in the Central Mixed-grass Prairie region (BCR 19; ΔDIC = 0.93), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	-8.027	5.849	0.323	-16.860	6.390	-8.760
% CP33^{1,500}	beta1	0.120	0.035	0.000	0.052	0.190	0.120
Contagion^{1,500}	beta2	-0.097	0.045	0.000	-0.186	-0.009	-0.096
% Urban/ developed^{1,500}	beta3	-0.147	0.047	0.000	-0.240	-0.054	-0.147

Table A.2 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the third ranked model in the Central Mixed-grass Prairie region (BCR 19; ΔDIC = 1.04), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	-3.950	2.792	0.154	-4.056	-8.658	1.893
% CP33^{1,500}	beta1	0.118	0.036	0.000	0.118	0.049	0.189
Contagion^{1,500}	beta2	-0.095	0.046	0.000	-0.094	-0.183	-0.007
% Urban/ developed^{1,500}	beta3	-0.148	0.047	0.000	-0.148	-0.242	-0.057
% Rangeland^{1,500}	beta4	0.011	0.018	0.000	0.011	-0.024	0.046

Table A.3 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the fourth ranked model in the Central Mixed-grass Prairie region (BCR 19; ΔDIC = 1.56), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	-12.120	5.795	0.320	-11.550	-24.480	-3.922
% Grass^{500}	beta1	-0.117	0.052	0.000	-0.116	-0.222	-0.017
Patch richness^{1,500}	beta2	0.087	0.046	0.000	0.086	0.000	0.181
Contagion^{1,500}	beta3	-0.134	0.049	0.000	-0.133	-0.231	-0.040
% Urban/ developed^{1,500}	beta4	-0.169	0.050	0.000	-0.169	-0.266	-0.072

Table A.4 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the second ranked model in the Eastern Tallgrass Prairie region (BCR 22;ΔDIC = 1.38), 2006 - 2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Patch density^{1,500}	beta1	0.641	0.150	0.001	0.348	0.937	0.640
Patch richness^{1,500}	beta2	0.308	0.128	0.001	0.060	0.562	0.307
% Urban/developed^{1,500}	beta3	-0.611	0.115	0.001	-0.841	-0.391	-0.609

Table A.5 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the third ranked model in the Eastern Tallgrass Prairie region (BCR 22; ΔDIC = 1.71), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	1.996	6.335	0.349	-9.864	12.510	2.928
% Urban/ developed^{1,500}	beta1	-0.651	0.116	0.001	-0.883	-0.430	-0.650
Woody edge density^{1,500}	beta2	1.955	0.511	0.014	0.979	2.978	1.944
(Woody edge density^{1,500})^2	beta3	-1.723	0.539	0.015	-2.803	-0.693	-1.711
Patch richness^{1,500}	beta4	0.244	0.134	0.002	-0.018	0.510	0.243

Table A.6 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the second ranked model in the Central Hardwoods region (BCR 24; ΔDIC = 0.07), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	-4.372	8.993	0.495	-19.260	14.140	-3.529
Patch richness^{1,500}	beta1	0.313	0.176	0.001	-0.027	0.669	0.311
% Woody cover^{1,500}	beta2	-0.356	0.139	0.001	-0.629	-0.087	-0.356
Patch density^{500}	beta3	-0.324	0.153	0.001	-0.631	-0.028	-0.323
% Grass^{500}	beta4	0.166	0.129	0.001	-0.084	0.422	0.165
% CP33^{500}	beta5	0.258	0.109	0.001	0.048	0.476	0.257

Table A.7 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the third ranked model in the Central Hardwoods region (BCR 24; ΔDIC = 0.38), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	-5.609	14.400	0.793	-51.910	13.060	-2.508
Patch richness^{1,500}	beta1	0.308	0.179	0.001	-0.039	0.665	0.306
% Woody cover^{1,500}	beta2	-0.375	0.145	0.001	-0.661	-0.091	-0.373
Patch density^{500}	beta3	-0.309	0.158	0.001	-0.622	-0.003	-0.307
% Grass^{500}	beta4	0.163	0.129	0.001	-0.087	0.419	0.163
% CP33^{500}	beta5	0.254	0.110	0.001	0.040	0.471	0.253
% Urban/ developed^{1,500}	beta6	-0.057	0.147	0.001	-0.344	0.234	-0.058

Table A.8 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the fourth ranked model in the Central Hardwoods region (BCR 24; ΔDIC = 0. 51), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	0.119	7.208	0.396	-11.100	17.890	-1.045
Woody edge density^{500}	beta1	-0.452	0.114	0.001	-0.677	-0.230	-0.451
% Grass^{500}	beta2	0.115	0.118	0.001	-0.115	0.355	0.113
% CP33^{500}	beta3	0.207	0.102	0.001	0.008	0.412	0.207
Patch richness^{1,500}	beta4	0.308	0.174	0.001	-0.034	0.650	0.307

Table A.9 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the fifth ranked model in the Central Hardwoods region (BCR 24; ΔDIC = 0. 72), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	-16.100	10.710	0.590	-42.020	-2.308	-12.740
Woody edge density^{500}	beta1	-0.456	0.115	0.001	-0.686	-0.234	-0.455
% Urban/ developed^{1,500}	beta2	-0.058	0.135	0.001	-0.322	0.206	-0.058
% Grass^{500}	beta3	0.114	0.119	0.001	-0.119	0.351	0.113
% CP33^{500}	beta4	0.206	0.104	0.001	0.006	0.412	0.207
Patch richness^{1,500}	beta5	0.306	0.175	0.001	-0.037	0.653	0.306

Table A.10 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the sixth ranked model in the Central Hardwoods region (BCR 24; ΔDIC = 1.09), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	2.630	12.270	0.677	-20.070	27.370	2.659
Woody edge density^{500}	beta1	-0.414	0.110	0.001	-0.630	-0.199	-0.413
Patch richness^{1,500}	beta2	0.411	0.167	0.001	0.089	0.745	0.410

Table A.11 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the seventh ranked model in the Central Hardwoods region (BCR 24; ΔDIC = 1.23), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	-7.888	11.140	0.614	-29.950	12.860	-6.753
Woody edge density^{500}	beta1	-0.419	0.109	0.001	-0.636	-0.209	-0.418
% CP33^{500}	beta2	0.187	0.099	0.001	-0.009	0.382	0.187
Patch richness^{1,500}	beta3	0.320	0.172	0.001	-0.018	0.658	0.319

Table A.12 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the eighth ranked model in the Central Hardwoods region (BCR 24; ΔDIC = 1.30), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	1.484	8.348	0.459	1.426	-16.240	18.340
Patch richness^{1,500}	beta1	0.437	0.172	0.001	0.434	0.104	0.784
% Woody cover^{1,500}	beta2	-0.342	0.138	0.001	-0.342	-0.613	-0.074
Patch density^{500}	beta3	-0.197	0.141	0.001	-0.196	-0.476	0.078

Table A.13 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the ninth ranked model in the Central Hardwoods region (BCR 24; ΔDIC = 1.38), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	1.681	18.820	1.039	3.394	-29.160	35.310
Patch richness^{1,500}	beta1	0.330	0.175	0.001	0.328	-0.010	0.677
% Woody cover^{1,500}	beta2	-0.329	0.135	0.001	-0.330	-0.597	-0.063
Patchdensity^{500}	beta3	-0.253	0.141	0.001	-0.252	-0.533	0.022
% CP33^{500}	beta4	0.217	0.103	0.001	0.217	0.014	0.423

Table A.14 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the tenth ranked model in the Central Hardwoods region (BCR 24; ΔDIC = 1.56), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	1.801	13.820	0.762	-22.640	26.630	-0.404
Patch density^{500}	beta1	-0.330	0.152	0.001	-0.631	-0.032	-0.328
% Woody cover^{1,500}	beta2	-0.391	0.137	0.001	-0.664	-0.123	-0.390
% Grass^{500}	beta3	0.183	0.128	0.001	-0.068	0.437	0.182
% CP33^{500}	beta4	0.313	0.105	0.001	0.112	0.522	0.313

Table A.15 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the eleventh ranked model in the Central Hardwoods region (BCR 24; ΔDIC = 1.86), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	-8.915	14.400	0.794	-32.230	19.450	-9.616
Patch richness^{1,500}	beta1	0.421	0.172	0.001	0.090	0.767	0.419
% Woody cover^{1,500}	beta2	-0.394	0.133	0.001	-0.658	-0.135	-0.392

Table A.16 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the twelfth ranked model in the Central Hardwoods region (BCR 24; ΔDIC = 1.95), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	-3.920	15.750	0.869	-35.520	21.740	-1.974
Patch density^{500}	beta1	-0.312	0.160	0.001	-0.632	-0.006	-0.310
% Woody cover^{1,500}	beta2	-0.411	0.145	0.001	-0.699	-0.129	-0.410
% Urban/ developed^{1,500}	beta3	-0.072	0.147	0.001	-0.360	0.218	-0.072
% Grass^{500}	beta4	0.179	0.130	0.001	-0.074	0.438	0.178
% CP33^{500}	beta5	0.308	0.107	0.001	0.100	0.522	0.308

Table A.17 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the second ranked model in the Mississippi Alluvial Valley region (BCR 26; ΔDIC = 1.91), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	-2.851	22.070	1.216	1.803	-45.370	33.750
Woody edge density^{1,500}	beta1	0.344	0.177	0.001	0.343	0.001	0.693
Patch richness^{1,500}	beta2	-0.260	0.137	0.001	-0.259	-0.536	0.005

Table A.18 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the third ranked model in the Mississippi Alluvial Valley region (BCR 26; ΔDIC = 1.96), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	-9.826	26.590	1.467	-4.162	-69.550	30.520
Woody edge density^{1,500}	beta1	0.342	0.180	0.001	0.341	-0.008	0.701
Patch richness^{1,500}	beta2	-0.266	0.141	0.001	-0.264	-0.548	0.005
% CP33^{500}	beta3	0.031	0.164	0.001	0.031	-0.293	0.352

Table A.19 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the fourth ranked model in the Mississippi Alluvial Valley region (BCR 26; ΔDIC = 1.97), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Woody edge density^{1,500}	beta1	0.2324	0.1655	0.0009	-0.0914	0.5619	0.2328

Table A.20 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the second ranked model in the Southeastern Coastal Plain region (BCR 27; ΔDIC = 0.40), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	-9.232	5.223	0.287	-22.170	-0.539	-8.879
% CP33^{1,500}	beta1	0.103	0.060	0.000	-0.013	0.220	0.103
% Urban/ developed^{1,500}	beta2	-0.170	0.071	0.000	-0.310	-0.030	-0.169
% Row-crop^{500}	beta3	0.174	0.089	0.001	0.001	0.349	0.173
Woody edge density^{1,500}	beta4	-0.358	0.108	0.001	-0.572	-0.147	-0.359
Patch density^{500}	beta5	0.055	0.063	0.000	-0.068	0.180	0.054
% Grass^{500}	beta6	0.286	0.076	0.000	0.137	0.436	0.285
Patch richness^{500}	beta7	0.170	0.093	0.001	-0.014	0.352	0.170

Table A.21 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the third ranked model in the Southeastern Coastal Plain region (BCR 27; ΔDIC = 0.59), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	-3.548	5.313	0.292	-14.990	6.338	-3.438
% CP33^{1,500}	beta1	0.097	0.059	0.000	-0.019	0.213	0.097
% Urban/ developed^{1,500}	beta2	-0.182	0.071	0.000	-0.321	-0.046	-0.182
% Woody cover^{500}	beta3	-0.172	0.073	0.000	-0.316	-0.031	-0.172
Woody edge density^{1,500}	beta4	-0.316	0.109	0.001	-0.529	-0.102	-0.316
Patch density^{500}	beta5	0.068	0.064	0.000	-0.056	0.193	0.068
Patch richness^{500}	beta6	0.214	0.089	0.001	0.039	0.388	0.215

Table A.22 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the fourth ranked model in the Southeastern Coastal Plain region (BCR 27; ΔDIC = 1.00), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	-5.588	8.004	0.441	-18.780	11.640	-6.759
% CP33^{1,500}	beta1	0.081	0.059	0.000	-0.034	0.195	0.081
% Urban/ developed^{1,500}	beta2	-0.195	0.071	0.000	-0.335	-0.058	-0.194
% Woody cover^{500}	beta3	-0.116	0.075	0.000	-0.262	0.029	-0.116
Woody edge density^{1,500}	beta4	-0.354	0.108	0.001	-0.568	-0.140	-0.353
Patch density^{500}	beta5	0.058	0.064	0.000	-0.067	0.183	0.058
% Grass^{500}	beta6	0.206	0.074	0.000	0.061	0.350	0.206
Patch richness^{500}	beta7	0.147	0.092	0.001	-0.033	0.327	0.148

Table A.23 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the fifth ranked model in the Southeastern Coastal Plain region (BCR 27; ΔDIC = 1.09), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	4.487	9.755	0.538	-9.120	20.^{500}	5.451
% CP33^{1,500}	beta1	0.100	0.060	0.000	-0.017	0.217	0.099
% Urban/developed^{1,500}	beta2	-0.162	0.071	0.000	-0.301	-0.025	-0.162
% Row-crop^{500}	beta3	0.185	0.088	0.001	0.013	0.359	0.184
Woody edge density^{1,500}	beta4	-0.348	0.107	0.001	-0.558	-0.141	-0.348
% Grass^{500}	beta5	0.294	0.074	0.000	0.149	0.440	0.294
Patch richness^{500}	beta6	0.196	0.087	0.001	0.026	0.369	0.196

Table A.24 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the sixth ranked model in the Southeastern Coastal Plain region (BCR 27; ΔDIC = 1.95), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	-8.610	14.970	0.826	-34.260	16.600	-9.075
% Urban/ developed^{1,500}	beta1	-0.186	0.070	0.000	-0.322	-0.049	-0.185
% Row-crop^{500}	beta2	0.154	0.086	0.001	-0.014	0.325	0.154
Woody edge density^{1,500}	beta3	-0.365	0.105	0.001	-0.573	-0.161	-0.364
% Grass^{500}	beta4	0.295	0.075	0.000	0.149	0.443	0.295
Patch richness^{500}	beta5	0.199	0.087	0.001	0.029	0.371	0.199

Table A.25 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the seventh ranked model in the Southeastern Coastal Plain region (BCR 27; ΔDIC = 1.98), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	-0.845	8.976	0.436	-13.660	16.410	-3.188
% CP33^{1,500}	beta1	0.091	0.059	0.000	-0.024	0.207	0.092
% Urban/ developed^{1,500}	beta2	-0.175	0.071	0.000	-0.313	-0.038	-0.175
% Woody cover^{500}	beta3	-0.182	0.072	0.000	-0.323	-0.042	-0.182
Woody edge density^{1,500}	beta4	-0.299	0.108	0.001	-0.510	-0.088	-0.299
Patch richness^{1,500}	beta5	0.247	0.084	0.001	0.084	0.414	0.247

Table A.26 Mean posterior probability estimates, standard deviation [SD], Monte Carlo error [MCE], 95% percentiles, and median parameter estimates for variables assessing northern bobwhite-landscape associations for the eighth ranked model in the Southeastern Coastal Plain region (BCR 27; ΔDIC = 2.00), 2006-2008.

Variable	Node	Estimate	SD	MCE	2.50%	97.50%	Median
Intercept	beta0	-5.960	5.370	0.295	-19.^{500}	2.357	-4.878
% Urban/developed^{1,500}	beta1	-0.192	0.070	0.000	-0.329	-0.057	-0.192
% Woody cover^{500}	beta2	-0.183	0.072	0.000	-0.324	-0.043	-0.182
Woody edge density^{1,500}	beta3	-0.310	0.108	0.001	-0.522	-0.099	-0.310
Patch richness^{1,500}	beta4	0.258	0.083	0.001	0.095	0.422	0.258