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AVIAN RESPONSE TO CP33 HABITAT BUFFERS IN SOUTHERN ILLINOIS

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AVIAN RESPONSE TO CP33 HABITAT BUFFERS IN SOUTHERN ILLINOIS

by

Brady Yeo Neiles

B.S. University of Wyoming – Laramie, 2009

A Thesis

Submitted in Partial Fulfillment of the Requirements for the
Master of Science Degree.

Department of Zoology
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Brady Yeo Neiles

A Thesis Submitted in Partial
Fulfillment of the Requirements

for the Degree of
Master of Science
in the field of Zoology

Approved by:

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AN ABSTRACT OF THE THESIS OF

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Agricultural grasslands have replaced native Midwestern prairies in the form of pasture, idle cropland and conservation fields. The condition of these cover types directly and indirectly influences the distribution, variety and productivity of avian populations within these landscapes. CP33 habitat buffers are an incentive-based conservation practice specifically designed to increase upland bird habitat and productivity. Landowners are encouraged to remove row crops from production and return them to early successional grassland habitat along the margin of agricultural fields. However, buffers exhibit a high perimeter-to-area ratio, which may increase negative edge effects, thereby creating sink populations. During the 2013 and 2014 breeding seasons, I assessed grassland bird response to CP33 habitat buffers in southern Illinois. Focal species included the northern bobwhite (*Colinus virginianus*), dickcissel (*Spiza americana*), eastern meadowlark (*Sturnella magna*), field sparrow (*Spizella pusilla*), indigo bunting (*Passerina cyanea*), and red-winged blackbird (*Agelaius phoeniceus*). I used a hierarchical multiscale framework to examine the influence of habitat variables at multiple scales on avian abundance, species richness, and occupancy. I also used this same framework, and logistic exposure modeling, to examine daily survival rates of nests found within CP33 habitat buffers. Multiscale occupancy and logistic exposure models consistently performed better than single-scale models for focal bird species; however, relative importance of local variables and landscape variables differed considerably among focal species. Nest survival rate was not strongly affected

by edge effects or edge type. Microhabitat variables were much more influential in predicting nest survival. In my study area, CP33 habitat buffers are unlikely to support source populations for most of the focal grassland bird species I studied. To increase nest survival rates within established CP33 habitat buffers, managers should focus on microhabitat vegetation characteristics. To increase bird occupancy of CP33 habitat buffers in southern Illinois, managers should increase the size of CP33 habitat buffers within a landscape having adequate grassland cover. However, managers should not consider CP33 habitat buffers a panacea for most grassland avian species.

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CHAPTER 1

MULTISCALE HABITAT FACTORS INFLUENCING BREEDING BIRD OCCUPANCY IN CP33 HABITAT BUFFERS IN SOUTHERN ILLINOIS

INTRODUCTION

Grassland ecosystems once covered vast expanses of North America's heartland, of which only a small remnant exists today. Agricultural grasslands have replaced these natural systems in the form of pasture, idle cropland and conservation fields. The condition of these lands directly and indirectly influences the function and integrity of natural ecosystems and determines the distribution, variety, and quality of natural goods and services, including wildlife populations (Burger et al. 2006a).

North American bird populations associated with grassland habitats have been declining since the industrialization of agriculture in the early 20th century. Breeding Bird Survey data collected between 1966 and 2011 indicate population declines in 21 of 28 grassland obligate species (Sauer et al. 2013). Although declines in particular grassland bird populations can be attributed to a wide variety of factors, such as habitat fragmentation, nest parasitism, the use of pesticides, and invasion of woody vegetation, an overriding cause of regional declines appears to be agricultural intensification (Bachand 2001).

Agricultural practices that favor excess production tend to decouple cropland from ecological support systems (Robertson and Swinton 2005). Alternatively, policy incentives that reward producers for environmental stewardship, like the Conservation Reserve Program (CRP), generally have the opposite effect. Originally designed to reduce soil erosion, CRP lands have provided an incidental benefit for grassland birds by promoting valuable habitat (Reynolds et al. 1994). The CRP is a voluntary long-term land diversion program where private landowners idle

highly erodible lands for conservation use in exchange for monetary compensation (U.S. Department of Agriculture [USDA] 2012). Popular among landowners and land managers, the CRP has quickly become one of the most valuable habitat conservation initiatives applied to agricultural systems (Best et al. 1997, Reynolds et al. 2001). However, as a voluntary program, CRP enrollment rates are continually under pressure by national agriculture policy and commodity prices (Rashford et al. 2010, Stubbs 2014).

Although the CRP has provided habitat for a wide variety of wildlife species and likely has altered population trends for some, the benefits of the CRP were more ancillary to programmatic goals than intentional (Burger et al. 2006a). In 2004, the USDA-Farm Service Agency (FSA) implemented Conservation Practice (CP) 33 - Habitat Buffers for Upland Birds. Unique in its targeted approach, CP33 is specifically designed to create wildlife habitat for the Northern bobwhite quail (*Colinus virginianus*, hereafter bobwhite). Bobwhite are an ecologically, socially, recreationally, and economically important grassland game bird species distributed throughout the Midwestern, Southern, and Southeastern United States. This formerly abundant species has experienced an average rate of decline of 4.0% annually over the past 5 decades (Sauer et al. 2013). Historically, small farm agriculture created a landscape mosaic of fallow fields, hardwood forest and croplands amenable to bobwhites and their selection of early-successional habitats and edges (Rosene 1969, Brennan 1991). Clean-farming practices, an increase in farm size and intensive agricultural practices have created a broad-scale change in landscape composition, removing these types of habitat (Brennan 1991). The Northern Bobwhite Conservation Initiative (NBCI; Dimmick et al. 2002) was formed to restore range-wide bobwhite populations to an average density equivalent to that which existed in the baseline year of 1980 (Burger et al. 2006a). Habitat buffers and field borders, such as CP33, are identified by the NBCI

as primary practices that can easily be integrated within crop production systems and, when broadly applied, may achieve habitat goals (Dimmick et al. 2002). CP33 habitat buffers are 9 m to 37 m wide, located immediately adjacent to row crop production, and are planted to native warm-season grasses, legumes, and shrubs or re-vegetated through natural succession (USDA 2012). CP33 habitat buffers aim to replicate early-successional habitat creating nesting, brood-rearing, and roosting opportunities for the bobwhite quail (Puckett et al. 2000, Blank 2013).

As conservation buffers are typically located on field margins, they more effectively balance wildlife and agronomic benefits (Barbour et al. 2007) than do large blocks of herbaceous vegetation (Conover et al. 2014). However, buffers exhibit a high perimeter-to-area ratio, which may increase edge effects. Many studies have shown grassland birds negatively respond to the impacts of edge (Helzer and Jelinski 1999, Winter et al. 2000, Besnard and Secondi 2014). Yet the mechanism driving this relationship is poorly defined, as the association may be regionally based (Johnson and Igl 2001, Whittingham et al. 2007) and differs between species groups (Johnson and Igl 2001, Ewers and Didham 2005).

For nearly 2 decades, researchers have been examining the response of bobwhite and other upland birds to conservation buffers and filter strips (e.g. Major et al. 1999, Puckett et al. 2000, Smith and Burger 2009, Conover et al. 2009, Burger et al. 2013, Evans et al. 2013, Bowling et al. 2014). Most of these studies focused on buffered vs. non-buffered fields (Smith et al. 2005, Evans et al. 2013, Evans et al. 2014a, 2014b, Burger et al. 2013), or some variation of this comparison, such as width of buffers (Conover et al. 2007, 2009), nonlinear vs. linear buffers (Riddle et al. 2008) or mowed vs. unmowed buffers (Blank et al. 2011). Still others examined the landscape composition around these buffers (Riddle et al. 2008, Blank 2013, Bowling et al. 2014), or patch context and edge effects immediate to these buffers (Adams et al.

2015). To the best of my knowledge, however, only 1 study (Evans 2012) examined avian response to CP33 habitat buffers at multiple spatial scales. Various studies have demonstrated the importance of microhabitat, patch context and landscape composition on grassland bird response (Söderström et al. 2001, Renfrew and Ribic 2008). For many species, response variables examined were better explained when spatial scales were combined (Cunningham and Johnson 2006, Osborne and Sparling 2013, Thompson et al. 2014). Although combining spatial levels can allow researchers to identify important scales of influence to further refine targeted conservation actions (Holland et al. 2004, Whittingham et al. 2007), such approaches are rare in published literature.

I compared the probability of occupancy, relative abundance, species richness and relative conservation value of bird communities (Carter et al. 2000) between CP33 habitat buffers and larger, low area-to-perimeter ratio “block” grasslands. I developed occupancy models using multiple spatial scales to describe habitat association of 6 grassland-associated bird species: bobwhite, dickcissel (*Spiza americana*), eastern meadowlark (*Sturnella magna*), field sparrow (*Spizella pusilla*), indigo bunting (*Passerina cyanea*), and the red-winged blackbird (*Agelaius phoeniceus*). My objectives were to determine which site characteristics were most influential to the probability of avian site occupancy, and at which scale species responded. I hypothesized that grassland obligate and facultative species would respond negatively to an increased area-to-perimeter ratio and, therefore, CP33 habitat buffers would have a lower relative conservation value than block fields. I hypothesized that composition of native herbaceous cover within CP33 habitat buffers would influence patterns of grassland-associated species, but would be limited by larger effects of surrounding landscape structure. I also hypothesized that focal species would have conflicting responses to microhabitat, patch and landscape scale variables.

METHODS

Study Area

I conducted field work in Franklin, Jackson, Perry, and Randolph counties of southern Illinois, a landscape dominated by corn (*Zea* sp.) and soybean (*Glycine* sp.) agriculture (851,710 ha, 64.1%), forests (215,933 ha, 16.2%), wetlands (138,374 ha, 10.4%), urban areas (59,584 ha, 4.5%) and other cover types (e.g. open water, 63,811 ha, 4.8%) (Figure 1.1, Illinois Department of Natural Resources 2014). I sampled 23 habitat buffers, varying in size from 0.9 ha to 11.5 ha. All buffers were privately owned, immediately adjacent to a wooded edge and were planted with grass and forb species such as little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), switchgrass (*Panicum virgatum*), Indiangrass (*Sorghastrum nutans*), goldenrod (*Solidago* sp.), yellow coneflower (*Ratibida pinnata*) and purple cone flower (*Echinacea purpurea*) (Natural Resources Conservation Service 2011). I also sampled 10 large block fields of reclaimed grassland, ranging in size from 6.1 ha to 31.1 ha. These block fields were located within Burning Star 5 Wildlife Management Area of Jackson and Franklin Counties and Pyramid State Park of Perry County, Illinois. Burning Star 5 was actively surface-mined from 1976 to 2002, then reclaimed for wildlife habitat and agriculture. Reclamation established cover included tall fescue (*Schedonorus arundinaceus*), switchgrass, big bluestem, Indiangrass, redtop (*Agrostis gigantea*), smooth brome (*Bromus inermis*), broom sedge (*Andropogon virginicus*), little bluestem, common milkweed (*Asclepias syriaca*), swamp milkweed (*Asclepias incarnata*), black raspberry (*Rubus occidentalis*), goldenrod, sericea lespedeza (*Lespedeza cuneata*) and red clover (*Trifolium pratense*). Most plants present in Burning Star 5 also were present in Pyramid State Park grasslands. All sites were separated by ≥ 250 m to decrease potential double counts in avian surveys.

Between 2013-2014, mean daily temperature for May to July was 21.81°C with monthly averages ranging from 18.56°C (May 2014) to 23.83°C (June 2014) (Illinois State Water Survey 2014; Carbondale Station). Mean precipitation for May to July in 2013-2014 was 10.64 cm with monthly precipitation ranging from 15.31 (May 2014) to 5.94 cm (July 2014) (Illinois State Water Survey 2014; Carbondale Station).

Avian Surveys

During the breeding seasons (10 May – 15 Jul) of 2013-2014, I surveyed birds on all fields by traversing fixed-width line transects (Buckland et al. 2001). Transects were established in ArcMap (ArcMap for Windows, version 10.0; ESRI, Redlands, California) and overlaid on aerial photos of each field. Transects were 200 m in length (walking speed of 1 km/h for 10 minutes is ~200 m, Diefenbach et al. 2003) and oriented at a known azimuth. In buffers, transects were centrally located running parallel to the dimensions of each buffer while in block fields, transects were oriented randomly. Buffers and block fields were surveyed 3 times per year and surveys were conducted between sunrise and 0900 h when songbirds were most active. I recorded weather conditions at the start of each survey, with surveys only being conducted when wind speed was ≤ 15 km/hr and visibility was not compromised. Birds seen or heard within 100 m of transect lines were counted, and the perpendicular distance to the transect was estimated for each. Observed birds were located in specific distance interval bands from the transect line (0-10 m, 10-20 m, 20-30 m, 30-40 m, 40-100 m, and >100 m). To avoid detections of individuals not using CP33 habitat buffers, I right truncated observations at 40 m.

Modeling Covariates

In most wildlife surveys, species detection probabilities are < 1.0 and the probability is likely to vary among species, areas, time (e.g., sampling occasions), and observers. Ignoring

imperfect detection could result in biased estimations of population attributes and misleading inferences (MacKenzie et al. 2002, Dorazio et al. 2006). I accounted for imperfect detection using occupancy models developed by MacKenzie et al. (2002).

Detection covariates.—To model detection, I used survey-specific covariates for each transect. Year, day of year, survey effort (survey duration/survey area), start time, wind speed, percentage of cloud cover, and temperature were collected during each survey to estimate detection probability.

Occupancy covariates.—I collected habitat variables at 3 spatial scales: microhabitat, patch context, and landscape composition (Table 1.1). Microhabitat covariates were within-field characteristics, collected during July-August at random locations generated with ArcGIS software. The number of sampling locations varied depending on field size with 1 location representing 0.4 ha and a minimum of 5 sampling locations per field. Microhabitat covariates included those defined by Fisher and Davis (2010) as most important in describing habitat use by avian species. A 20- by 50-cm frame was randomly placed at the survey point, and cover characteristics were ocularly estimated at 0-5, 5-25, 25-50, 50-75, 75-95 or 95-100% classes (Daubenmire 1959). Cover characteristics included bare ground, grass, dead vegetation, forbs, and litter. Litter depth was measured to the nearest cm at all 4 corners of the frame. Grass cover refers to all graminoids including grasses, sedges, and rushes (families Graminae, Poaceae, Cyperaceae, and Juncaceae). Litter was all organic debris on the soil surface. Dead vegetation was attached to the soil by its roots, yet standing, and bare ground was defined as any surface not covered by vegetation or litter. Forbs were any flowering plant that is not a graminoid. A Robel pole was used to measure visual obstruction, or density, of vegetation from the 4 cardinal directions (Robel et al. 1970). Heights of live and dead vegetation were recorded with live

vegetation height being determined as the height where approximately 80% of vegetation is below, and dead vegetation being measured at the maximum height of the dead vegetation (Fisher and Davis 2010).

To reduce the total number of microhabitat variables and avoid issues associated with overparameterization and multicollinearity, a principal component analysis (PCA) using a correlation matrix was used. Approximately 56% of the variation within microhabitat observations was explained by the first 3 principal components from PCA (Table 1.2). Based on variable factor loading, PC1 described a gradient of increasing live vegetation height and Robel scores. PC2 described percentage forb cover, species richness and mean litter depth, while PC3 described dead vegetation height, percentage dead vegetation cover and percentage litter cover. As such, a higher PC1, PC2 and PC3 score represented a field with higher vertical structure, a more diverse floristic composition and a larger amount of dead vegetation, respectively. Mean PC1, PC2 and PC3 scores for each field were used as the specific microhabitat covariate. I also included the standard deviation of PC1 (SDPC) for each field as a measure of vegetation complexity (August 1983), and calculated plant species richness for each field as species/site (DIV).

To generate landscape-scale variables, I calculated percentage cover type at 800-m and 1600-m radius circles centered at each field (Table 1.1). These sizes encompass home ranges of most songbirds, and are the landscape sizes associated with avian species in other studies (i.e., Hennings and Edge 2003, Porter et al. 2005, Pennington et al. 2008). I used aerial orthographic images from the National Agriculture Imagery Program (USDA 2014, 1-m pixel resolution) to hand-digitize 5 dominant cover types: grassland (CRP, pasture, and hay fields), agriculture (corn, soy, and winter wheat), woodland, water, and development (urban areas and roads). Cover types

were ground-truthed in the field to ensure accuracy. I also calculated total edge (TE), a sum of all edges of all cover types within the 1600-m radius circle, and edge density (ED), representing a spatial configuration (i.e., degree of fragmentation) of agricultural landscapes (Lee and Carroll 2014). At the patch scale I calculated field area (SIZE), edge index (defined as perimeter/area, INDEX), and percentage of woodland edge surrounding field (WOOD.EDGE). I also included the percentage cover type within a 100-m buffer outlining the field (Table 1.1). I used a correlation matrix on all variables collected to reveal multicollinearity; when pairs of variables had correlations ≥ 0.70 , the variable more correlated with other variables was removed from further analysis (Gries 2010). Landscape- and patch-scale covariates were calculated using ArcGIS software and the Patch Analysis extension (ArcGIS version 10.1, Rempel et al. 2012). I standardized all continuous covariates to a mean of 0 before analyses to improve model stability and convergence (Zuur et al. 2009).

Data Analyses

Avian community.—I estimated relative abundance, species richness and relative avian conservation value (ACV) as species response variables. Relative abundance was calculated as the maximum count of 3 visits per area surveyed (1.6 ha, Davis 2004, Conover et al. 2014). Species richness was the total number of species per site surveyed. I calculated relative avian conservation value of CP33 habitat buffers by multiplying each species' abundance by its Partners in Flight conservation priority rank (Carter et al. 2000, Nettle et al. 2003) for the Central Hardwoods bioregion (Panjabi et al. 2012), and then summed the species-specific ACV scores within a site (Conover et al. 2007, 2009). ACV measures relative conservation value using Partners in Flight bird conservation priority ranks, which are based on regional population trends, global population size, regional area importance value, global breeding and wintering

distributions, regional threats to breeding habitat, and global threats to wintering habitat (Carter et al. 2000, Panjabi et al. 2012). Migratory nonbreeding species and unidentified birds were excluded from ACV calculations.

Multiscale occupancy modeling. — Individual species detections were pooled at each site and across site type (block field or buffer) to produce adequate sample sizes for accurate detection curves. Climate variables and time surveyed were used as covariates to improve detection-probability estimates. Vegetation structure, calculated from vertical obstruction measurements, was also added as a covariate. I modeled detection probability, defined as the probability of detecting ≥ 1 individual of a focal species given it was present, using detection covariates collected during transect surveys. A set of 5 single covariate models were used to assess factors explaining variation in detectability. The top detection model having the lowest ΔAIC_c , including the null [$p(.)$] model, was used in all subsequent modeling for a particular species.

I used single-season occupancy models developed by MacKenzie et al. (2002) with the “unmarked” package within R and using the “occu” function (Fiske and Chandler 2011) to describe responses of grassland birds to habitat covariates. Using similar approaches as Renfrew and Ribic (2008), Fletcher and Koford (2002), and Cunningham and Johnson (2006), I constructed occupancy models following a hierarchical modeling process. Occupancy was assessed at 3 spatial scales separately with a priori habitat covariate combinations. At the microhabitat scale, I included mean field PC1, PC2, PC3, SDPC scores and DIV values and all possible additive model combinations. SDPC was the standard deviation of PC1, and was considered a measure of structural diversity. DIV was the number of species found at a vegetation sample. At the patch and landscape scale, I ran only single covariate models

representing 7 and 10 variables, respectively (Table 1.1). Covariates among the top single variable models were then used in combined-scale models. To avoid multicollinearity, I did not combine 100-m, 800-m and 1600-m variables of the same land cover type in any single model (Graham 2003). Each year was treated as 1 season, as sites were not re-sampled across years. I used model selection based upon Akaike's Information Criterion adjusted for small sample size (AICc); occupancy models $\leq 2 \Delta AIC_c$ were considered competitive (Burnham and Anderson 2002). A final model set including all possible scale combinations (microhabitat + patch + landscape, and alternate combinations) and the best models from each individual scale were created to determine if the combination of scales improved model fit. Beta (β) parameter estimates with standard errors and confidence intervals for detection and initial occupancy were calculated.

RESULTS

I observed 44 species of birds from 150 surveys across 33 fields. Of these 44 species, 6 grassland-obligate and grassland-facultative species had naïve occupancy rates (defined as the number of sites a species was present divided by the number of total sites) suitable for modeling (MacKenzie et al. 2006) and served as focal species for my analyses. These species, with naïve site occupancy noted in both habitat buffers and block fields, respectively, were indigo buntings (100% / 70%), red-winged blackbirds (52% / 100%), field sparrow (91% / 60%), eastern meadowlark (4.3% / 100%), dickcissel (26% / 100%), field sparrow (91% / 60%), and northern bobwhite (56% / 100%). The red-winged blackbird was the most common bird detected in the study ($n = 347$) followed by field sparrow ($n = 340$) and indigo bunting ($n = 260$) (Appendix A). Low naïve site occupancy precluded accurate predictive models for other grassland-associated species detected such as the Henslow's sparrow (0% / 50%), grasshopper sparrow (13%, 10%),

and sedge wren (0%, 30%). CP33 habitat buffers and block fields did not differ in relative abundance (95% CI, $0.12 \leq 0.39 \leq 0.67$, 95% CI, $-0.17 \leq 0.44 \leq 1.07$, respectively), or ACV (95% CI, $60.65 \leq 119.60 \leq 178.54$, 95% CI, $24.58 \leq 57.95 \leq 91.32$, respectively). Also, CP33 habitat buffers and block fields did not differ in overall species richness (95% CI, $9.94 \leq 11.00 \leq 12.06$, 95% CI, $7.86 \leq 9.33 \leq 10.81$, respectively). However, when only considering grassland obligate and facultative species, richness was significantly higher within large blocks (95% CI, $4.33 \leq 5.17 \leq 6.00$) than CP33 habitat buffers (95% CI, $3.28 \leq 3.78 \leq 4.29$).

For all 6 focal species, the null model was competitive with top detection models ($\Delta AIC_c \leq 2$), therefore the null detection model was used in all subsequent analyses. All but 1 focal species included covariates from multiple scales in the final competitive model sets. The relationship between local and landscape variables and species occupancy varied among species, but 3 of the 6 species did respond positively to PC1. Habitat buffers had a negative PC1 score and a positive PC2 score, suggesting habitat buffers had low overall vegetation structure and high vegetative species richness (Figure 1.2). Block fields had a positive PC1 score and a negative PC2 score, suggesting taller vegetation and a relatively low species richness. Habitat buffers and block fields had similar PC3 scores.

Multiscale Occupancy

Northern bobwhite. –Each of the 3 scales was represented in the bobwhite competitive model set. Bobwhite responded negatively to the edge-to-area ratio (INDEX) and positively to PC3 scores. Bobwhite probability of occupancy increased with more grassland present at the landscape level (GRASS.800) and increased significantly with greater field area (SIZE, Table 1.3, Figure 1.3).

Field sparrow. – Three models were competitive in the field sparrow model set, all including a positive response to crop at 1600 m (CROP.1600). At the patch scale, field sparrow probability of occupancy significantly decreased with increasing developed area (DEV.100) and decreased with increasing grassland area (GRASS.100). Probability of occupancy significantly decreased with increasing PC1 (Table 1.3, Figure 1.3).

Indigo bunting. –Only 1 variable was included in the competitive model set of Indigo buntings, thus no model averaging was performed. Indigo bunting probability of occupancy decreased as GRASS.800 increased (Table 1.3).

Eastern meadowlark. –Meadowlark probability of occupancy significantly decreased with increasing total edge within the landscape, and increasing edge index at the patch scale (Table 1.3). Meadowlarks responded positively to increasing PC2. As reference, the null model was 23.90 ΔAIC_c points from the top model (Table 1.3).

Dickcissel. – Two scales were represented in the dickcissel competitive model set. Top models had good support compared to top detection and null models (Table 1.3). Dickcissels responded negatively to increasing percentage woodland area at the 800-m buffer scale (WOOD.800) and it was a significant predictor. Dickcissels also responded positively to increasing PC1 and PC2 scores within the field, while only PC1 was a significant predictor.

Red-winged blackbird. –Only 1 model was included in the competitive model set of red-winged blackbirds; habitat affiliations were represented at 2 scales. Red-winged blackbird occupancy declined significantly with increasing percentage woodland area at the patch scale (WOOD.100), and increased with higher PC1 scores at the microhabitat scale (Table 1.3, Figure 1.3).

DISCUSSION

I found that multiscale habitat occupancy models consistently performed better than single-scale models for focal bird species; in fact, competitive model sets for 5 of 6 species included variables from multiple scales. Also, 5 of the 6 species responded to landscape variables at the 800-m or 1600-m levels. This response was expected, as explanatory power of landscape features becomes greater when that landscape is heavily altered (Miller et al. 2004, Tsharntke et al. 2012). In southern Illinois, CP33 habitat buffer placements are limited by topography, creating small fields (< 12 ha) with high levels of edge. As a landscape historically dominated by hardwood forest, soil quality is low compared to other bird conservation regions where CP33 habitat buffers are in place, such as the tallgrass prairie (Bailey 1995). While considered grassland cover, CP33 habitat buffers are designed to create early successional habitat. However, in general, the narrow shape of most CP33 habitat buffers precludes use by many grassland obligate species, especially those considered area sensitive. My results agree with this generality, as species richness of grassland obligate and facultative species was significantly higher in large block fields than CP33 habitat buffers. However, I found no significant difference between CP33 habitat buffers and block fields concerning relative abundance of all species or ACV. That buffers and blocks did not differ in ACV may be attributed to the low PC2 scores in block fields. In my study, larger block fields were dominated by grasses, with low floristic variation, limiting available perches, nesting cover, nest support and possible invertebrate food sources found in areas with more diverse plant communities (Dechant et al. 2002).

Relative importance of local variables and landscape variables differed considerably among focal species within their respective competitive model sets. The competitive model set for bobwhites included all 3 scales used in analysis. Field area, a patch-scale covariate, was a

stronger predictor of bobwhite occupancy than landscape composition. Small home ranges and limited dispersal capabilities of bobwhite could explain this response (Brennan 1991). Bobwhite also responded negatively to an increase in edge-to-area ratio at the patch scale. This may seem counterintuitive, as bobwhite are widely considered an edge species and edge habitat is necessary for prime bobwhite habitat (Leopold 1933, Williams 2000). However, above a certain density, edge becomes redundant and may have a negative effect by fragmenting the landscape (Guthery and Bingham 1992) and introducing unnaturally high movement patterns of predators (Helzer and Jelinski 1999). This redundancy seems plausible within the study area where edge densities ranged from 3 to 6 times the threshold edge density of 60 m/ha suggested by Roseberry and Sudkamp (1998), below which bobwhite have a positive relationship with edge density.

Surprisingly, the bobwhite competitive model set did not include a response to woodland area or woodland edge. The importance of wooded areas has been well established in bobwhite literature (Guthery 1997, Twedt et al. 2007, Janke and Gates 2012), likely because it would provide escape cover for bobwhite during severe winter weather (Roseberry and Klimstra 1984). This response, however, is better observed during the non-breeding season. A lack of a response to woody edge may be attributed to an increased use of grasslands for nesting and brooding cover during the breeding season. In agreement with this idea, bobwhite did respond positively to a higher percentage of grassland within the surrounding landscape. Roseberry and Sudkamp (1998) also observed this relationship in Illinois, suggesting 20-30% grassland within a landscape was optimal. Veech (2006) indicated landscapes with less pastureland and rangeland harbored bobwhite populations that were in decline. More recently, Duren et al. (2011) found occupancy of bobwhite positively related with grassland, and Janke and Gates (2012) found home ranges of bobwhite were established in areas with more grassland cover, although selection

diminished at larger spatial scales. Grass habitat provides crucial nesting cover for bobwhite (Roseberry and Klimstra 1984, Taylor et al. 1999), yet this cover is suitable only if within a certain distance of woody cover (Guthery and Bingham 1992). Competitive models for the bobwhite suggest woodland area and woodland edge are not restricting bobwhite occupancy in southern Illinois, but a positive response to grassland cover at the landscape level indicates bobwhite may be limited by the amount of existing grassland habitat.

Bobwhite use microhabitats that vary widely in vegetative characteristics based upon specific life cycle needs (Taylor et al. 1999). In my study, bobwhite responded positively to PC3. Component loading within PC3 suggests bobwhite responded positively to an increase in dead vegetation height and percentage dead vegetation, and positively to a decrease in percentage litter within the field. This is consistent with other studies, most attributing this response to greater nest site concealment and higher mobility for broods, respectively (Lusk et al. 2006, Collins et al. 2009, Liberati 2013). A negative relationship between bobwhite occupancy and increased litter cover may indicate fields aging past the disturbance interval needed to maintain quality bobwhite nesting habitat (Osborne et al. 2012, Liberati 2013).

Indigo buntings and field sparrows have similar spatial needs to bobwhites, requiring woodland and grassland habitat in close proximity (Payne 2006, Carey et al. 2008). However, they did not respond to edge or woodland area. This is interesting, as both species are often associated with woodland and shrub land habitat (Best 1977), and have been found to select patches with more edge (Weldon and Haddad 2005). However, indigo buntings were ubiquitous across my study area, and exceptionally common in 2014, possibly compromising occupancy estimates. Also, just as observed with bobwhite, woodland and shrub land habitat may not be limiting distribution of indigo buntings and field sparrows in southern Illinois. Both species

responded negatively to grassland cover, yet at different scales. This is in contrast to Evans et al. (2014b), who found field sparrow density significantly higher in landscapes with CP33 habitat buffers surrounding agriculture fields. In my study, field sparrow occupancy significantly decreased with increasing urban development at the patch scale. Burhans and Thompson (2006) observed a similar relationship in Missouri, where field sparrows were more abundant in rural sites. Field sparrows were also significantly more likely to be found in fields with low PC1 scores. PC1 describes a gradient of vegetation height, suggesting field sparrows were responding negatively to an increase in vertical structure. High PC1 values within block fields may have precluded field sparrow use, further reducing the relative ACV values of block fields.

Probability of occupancy of eastern meadowlark significantly decreased with (1) increasing total edge at the landscape scale and (2) increasing edge index at the patch scale. Most attribute edge avoidance by avian species as a response to increased nest predation risk and brood parasitism risk (Paton 1994, Lima and Valone 1991). In fact, in Illinois Herkert et al. (2003) observed increasing nest-predation rates with decreasing fragment area in eastern meadowlarks. Studies often observe the greatest increase in nest depredation and brood parasitism near wooded edges (Bakker 2003). However, eastern meadowlarks did not respond to woodland area or woodland edge, suggesting they perceived a risk at all cover type edges. This is in contrast to many studies finding percentage forest surrounding CRP fields a good predictor of eastern meadowlark densities (Renfrew and Ribic 2008, Osborne and Sparling 2013). When considering the larger community of grassland birds, however, Renfrew et al. (2005) found grassland songbirds avoided edges, with no difference in nest density between wooded and nonwooded edges. Area of field was also not included in the competitive model set, yet eastern meadowlarks were missing from all but the largest CP33 habitat buffers. My findings may

provide additional support to those who have also suggested this species is area sensitive (Herkert 1994, Vickery 1994, Osborne and Sparling 2013). Eastern meadowlark responded positively to PC2 at the microhabitat scale. Component loading within PC2 suggests meadowlark responded positively to an increase in percentage forb cover. Meadowlarks often nest in dense litter cover with a higher proportion of grass and more structural homogeneity (Granfors et al. 1996). Using fields with greater forb cover, though, could accommodate suitable nesting sites while increasing arthropod food resources (Dechant et al. 2002).

Dickcissels were significantly less likely to be detected in a landscape with a larger amount of woodland area at the 800-m scale. Similarly, Osborne and Sparling (2013) observed a negative relationship with greater percentages of forest surrounding study fields at the 500-m buffer scale. At the 800-ha scale, or region level, Murray et al. (2008) also found a negative relationship to percentage forest cover. In my study, competitive models for the dickcissel did not include any response to edge. Herkert (1994) also did not find a relationship between dickcissel abundance and edge, suggesting dickcissels may be relatively tolerant of habitat fragmentation at broad scales. Winter and Faaborg (1999) also found little evidence of area-sensitivity in dickcissel, though nest survival decreased with decreasing fragment size. However, other studies have shown a negative association between dickcissels and the amount of edge relative to area at the patch scale (Osborne and Sparling 2013, McLaughlin et al. 2014).

At the microhabitat scale, PC1 values had a positive and significant effect on dickcissel probability of occupancy. Dickcissels were also associated positively with PC2 values. This suggests dickcissel prefer fields with higher vertical structure and more complex floral composition. Many studies have observed a similar relationship concerning vegetation height (Winter 1999, Hughes et al. 1999, McLaughlin et al. 2014) and plant species diversity (Dechant

et al. 2002, Osborne and Sparling 2013). Fields with more diverse forb communities are thought to provide better nesting structure, better song perches for singing males, and increased arthropod food resources (Benson et al. 2007, Benson et al. 2013).

Red-winged blackbird probability of occupancy was very similar to that of the dickcissel. Blackbirds responded negatively to an increase in woodland area at the patch scale. At the microhabitat scale, red-winged blackbirds responded positively to an increase in vertical structure. Both of these relationships, again, could be attributed to breeding season habitat selection. For example, in Wisconsin, Clotfelter (1998) found proximity to trees increased risk of brood parasitism by brown-headed cowbirds. Also, Pribil (1998) found red-winged blackbirds preferred nesting in tall patches in plants with thick stems.

MANAGEMENT IMPLICATIONS

To further conservation of bobwhite, sufficient habitat characteristics at the microhabitat and patch scales must be created within the proper landscape context. In southern Illinois, management should focus on increasing the size of CP33 habitat buffers within a landscape having adequate grassland cover. Buffers must be large enough (>2 ha, Edminster 1954) and wide enough (Conover et al. 2009) to provide adequate resources to bobwhite, where many sites within our study fell short of this. Increasing breeding habitat at the landscape scale could prove especially important as large areas of unoccupied habitat between occupied patches may isolate local populations (Fies et al. 2002). Managers should aim to increase heterogeneity within the field, using disturbance to maintain early successional cover types highlighted by abundant standing dead vegetation and bare ground, and scarce litter cover.

Field borders benefit the entire avian community year-round by providing nesting habitat, foraging habitat, roosting sites, movement corridors and escape cover (Smith et al. 2005,

Conover et al. 2009). However, managers should use caution when ascribing broad-scale conservation success from targeted practices to a suite of species. Targeted practices rarely address the multiple resource requirements of multiple species concurrently (Brennan & Kuvlesky 2005). CP33 habitat buffers are limited in their reach, most apparently for grassland-obligate species like the eastern meadowlark and dickcissel. By combining CP33 with other conservation practices, managers may create the landscape complexity needed to meet multispecies recovery objectives and enhance biodiversity and ecosystem services (Batary et al. 2011, Evans et al. 2014a).

CHAPTER 2

INFLUENCE OF MULTISCALE CHARACTERISTICS OF CP33 HABITAT BUFFERS ON NEST SURVIVAL OF AVIAN SPECIES

INTRODUCTION

Bird conservation theory argues for large habitat patches of continuous forest or grassland cover (Herkert et al. 1994, Robinson et al. 1995, Askins et al. 2007). Improving reproductive success is often cited as the justification for these recommendations, as many studies have observed higher rates of nest predation near habitat edges in populations of forest and grassland interior songbirds (e.g., Gates and Gysel 1978, Johnson and Temple 1990, Paton 1994, Winter et al. 2000). These effects are often stronger near wooded edges and specifically at abrupt, agriculture-wooded edges (Jensen and Finck 2004). However, current agricultural production goals, which encourage clean farming methods, make establishment of large habitat patches in many regions unrealistic. For example, most grassland habitat in the agriculture-dominated Midwest occurs in relatively small hay fields, pastures, or Conservation Reserve Program (CRP) grassland (Herkert et al. 1996). In Illinois, 89% of grassland cover is in patches of <10 ha, and the mean CRP contract in the state is 5.6 ha in area (McKinney et al. 1998). These areas, however small, provide crucial habitat for breeding grassland and shrubland bird species and are easily integrated within a working landscape (Lovell and Sullivan 2006).

Conservation Practice 33 (CP33; Habitat Buffers for Upland Birds), a program of the United States Department of Agriculture's CRP, provides a financial incentive for landowners to create small-patch, grassland habitat in agricultural landscapes. CP33 habitat buffers are 9 m to 37 m wide, located immediately adjacent to row crop production, and are planted to native warm-season grasses, legumes, and shrubs or re-vegetated through natural succession (USDA

2012). CP33 habitat buffers aim to replicate early-successional habitat creating nesting, brood-rearing, and roosting opportunities for the northern bobwhite (*Colinus virginianus*; Puckett et al. 2000). Although targeted at bobwhite, agricultural fields with CP33 buffers have also been shown to attract greater abundances of other grassland songbirds, such as the field sparrow (*Spizella pusilla*) and dickcissel (*Spiza americana*; Smith et al. 2005, Evans et al. 2014b). These songbirds are also often found nesting in CP33 fields, but little information exists regarding the importance of patch characteristics on bird productivity in buffers (Conover et al. 2011, Adams et al. 2013). Such an evaluation is particularly important as the linear shape of CP33 habitat buffers may increase negative edge effects. If negative edge effects on nest survival are considerable, CP33 habitat buffers may function as population sinks (Heske et al. 1999).

Edge effects are often difficult to detect, as they can be obscured by factors not accounted for in simplified study designs (i.e., Mayfield 1961). Developments in nest survival modeling allow comparisons of multiple factors on nest survival including variables specific to individual nests (Jones and Guepel 2007). For example, edge effects can be examined directly by including nest-specific distance-to-edge covariates instead of arbitrary distance-to-edge bins (Shake et al. 2011). Temporal variation, differences in survival among stages or random variation among sites can also be accounted for in logistic exposure modeling (Shaffer 2004). This variation may otherwise bias estimates of nest survival (Grant et al. 2005). Other variables that may influence predator abundance or a predator's ability to find nests, such as landscape composition and vegetation characteristics, can be modeled using logistic exposure techniques. Further understanding of how grassland-nesting birds respond to CP33 habitat buffers is crucial to assist land managers in designing farm-wide, conservation management systems that benefit a suite of grassland birds.

I examined daily survival rates of nests found within a network of CP33 habitat buffers surrounded by cropland and woody vegetation in southern Illinois. My objectives were to determine whether nest success varied over a range of grassland patch sizes and if nest success was influenced by proximity to cropland-grassland and wooded grassland edges. Most previous studies of avian production in CP33 habitat buffers have focused on 1 particular scale or question (Conover et al. 2011, Adams et al. 2013). Few have evaluated avian production in a multiscale framework, though various studies have demonstrated the importance of assessing microhabitat, patch context and landscape composition on avian production (Davis et al. 2004, Winter et al. 2006, Thompson et al. 2014). Landscape context is particularly important for some edge-sensitive species using herbaceous buffers. Larger-scale spatial processes can strongly influence nest survival and, in some landscapes, may supersede local-scale effects (Donovan et al. 1997, Thompson 2007). Although cropland-grassland edges have the potential to greatly influence grassland birds that nest in these small patches, the effects of agricultural edges on nest success have been reported infrequently but are generally weak (Jensen and Finck 2004, Renfrew et al. 2005). I used a multiscale hierarchical framework to examine nest success, quantified as daily survival rate (DSR; Shaffer 2004), in CP33 habitat buffers varying in size and shape. I hypothesized that (1) at the microhabitat scale, DSR will positively correlate with vegetative diversity and structural complexity; (2) at the patch scale, DSR will be positively related to larger fields with less edge; (3) and at the landscape scale, DSR will inversely correlate with landscape-level indices of fragmentation and percentages of agricultural and woodland cover.

METHODS

Study Area

I conducted field work in Randolph county of Southern Illinois, a landscape dominated by corn (*Zea* sp.) and soybean (*Glycine* sp.) agriculture (851,710 ha, 64.1%), forests (215,933 ha, 16.2%), wetlands (138,374 ha, 10.4%), urban areas (59,584 ha, 4.5%) and other cover types (e.g. open water, 63,811 ha, 4.8%) (Figure 2.1, Illinois Department of Natural Resources 2014). Approximately 1,100 farms make up about 75% of the land area in the county (Illinois Department of Natural Resources 2014). I sampled 23 CP33 habitat buffers, 15 fields in 2013 and 8 fields in 2014, varying in size from 0.9 ha to 11.5 ha. All buffers were privately owned, immediately adjacent to a wooded edge and were planted with grass and forb species such as little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), switchgrass (*Panicum virgatum*), Indiangrass (*Sorghastrum nutans*), goldenrod (*Solidago* sp.), yellow coneflower (*Ratibida pinnata*) and purple cone flower (*Echinacea purpurea*) (Natural Resources Conservation Service 2011).

Between 2013-2014, mean daily temperature for May to July was 21.81°C with monthly averages ranging from 18.56°C (May 2014) to 23.83°C (June 2014) (Illinois State Water Survey 2014; Carbondale Station). Mean precipitation for May to July in 2013-2014 was 10.64 cm with monthly precipitation ranging from 15.31 (May 2014) to 5.94 cm (July 2014) (Illinois State Water Survey 2014; Carbondale Station).

Nest Monitoring

I searched each habitat buffer once a week during May-August 2013-2014. Nests were located through systematic nest searches, rope dragging and behavioral observation. For systematic searches, observers walked 2-5 m apart through sites using 1.2 m wooden rods to

disturb vegetation and flush incubating females. For rope dragging, I used a 20-m length of rope tied between 2 observers to cover all ground possible. I monitored all nests of passerine species located in CP33 habitat buffers. Nests were marked with survey tape 5 m north of the nest, and the contents were checked twice per week until their fates were determined. Nest data included nest stage (laying, incubation, and nestling), age, clutch or brood size, parental activity, cowbird parasitism, and nest fate. I considered a nest successful if ≥ 1 nestling fledged. When I could not locate fledglings near a nest, and nestlings were near fledgling age, I determined success or failure based on nest evidence (e.g. droppings in the nest, nest condition) and parental behavior (e.g., carrying food, frantic calling). Causes of nest failure were classified as depredation (eggs or nestlings were removed from the nest or destroyed), desertion (I observed no adult activity at or around the nest for >2 weeks), brood parasitism, weather-caused, or human-caused. For each nest, I determined distance (m) to nearest cropland edge (corn, soybeans, wheat) and woodland edge with a 100-m measuring tape.

Modeling Covariates

Nest site characteristics – At the nest, I measured nest height and the vegetation characteristics defined by Fisher and Davis (2010) as being most important in affecting habitat use by avian species (Table 2.1). All vegetation and nest characteristics were collected within 7 days after the success or failure of a nest. I centered a 20- by 50-cm frame at the nest, and estimated cover characteristics at 0-5, 5-25, 25-50, 50-75, 75-95 or 95-100% classes (Daubenmire 1959). Cover characteristics included bare ground, grass, dead vegetation, forbs, and litter. Litter depth was measured to the nearest cm at all 4 corners of the frame. Grass cover referred to all graminoids including grasses, sedges, and rushes (families Graminae, Poaceae, Cyperaceae, and Juncaceae). Litter was all organic debris on the soil surface. Dead vegetation

was attached to the soil by its roots, yet standing, and bare ground is defined as any surface not covered by vegetation or litter. Forbs were any flowering plant that is not a graminoid. A Robel pole was used to measure visual obstruction, or density, of vegetation around the nest from the 4 cardinal directions (Robel et al. 1970). Height of live vegetation and dead vegetation were recorded with live vegetation height being determined as the height where approximately 80% of vegetation is below, and dead vegetation being measured at the maximum height of the dead vegetation (Fisher and Davis 2010).

To reduce the total number of vegetation covariates and avoid issues associated with overparameterization and multicollinearity, I conducted a principal component analysis (PCA) using a correlation matrix. Approximately 62% of the variation within microhabitat observations nesting sites was explained by the first 3 principal components from PCA (Table 2.2). Based on variable factor loading, PC1 described a gradient of live vegetation height and Robel scores. PC2 described percentage litter cover and mean litter depth, while PC3 covered a gradient of dead vegetation height and percentage dead vegetation cover. As such, a higher PC1, PC2 and PC3 score represented a field with higher vertical structure, a smaller amount of litter and little dead vegetation, respectively (reported as Nest.PC1, Nest.PC2, and Nest.PC3).

Habitat characteristics at other scales – To quantify available habitat within CP33 buffers, I also measured vegetation at random points between 15 June and 1 August of both study years collecting the same variables as those at nesting sites. The number of sampling locations varied depending on field size with 1 location sampled per 0.4 ha and a minimum of 5 sampling locations per field. Again, I used PCA to reduce the total number of vegetation covariates. Approximately 56% of the variation of within-field vegetation was explained by the first 3 principal components from PCA (Table 2.3). Based on variable factor loading, PC1

described a gradient of increasing live vegetation height and Robel scores. PC2 described percentage forb cover, species richness and mean litter depth, while PC3 represented dead vegetation height, percentage dead vegetation cover and percentage litter cover. A higher PC1, PC2 and PC3 score represented a field with higher vertical structure, a more diverse floristic composition and a larger amount of dead vegetation, respectively. Mean PC1, PC2 and PC3 scores for each field (Field.PC1, Field.PC2, and Field.PC3) were used as the specific microhabitat covariate. I included the standard deviation of PC1 (SDPC) for each field as a measure of vegetation complexity (August 1983), and calculated plant diversity for each field as number of plant species at the site (DIV).

To generate landscape scale variables, I calculated percentage cover type at 800-m and 1600-m radius circular buffers centered at each field (Table 2.1). These sizes encompassed home ranges of most songbirds, and are the landscape size associated with avian species in other studies (i.e. Hennings and Edge 2003, Porter et al. 2005, Pennington et al. 2008). I used aerial orthographic images from the National Agriculture Imagery Program (USDA 2014, 1-m pixel resolution) to hand-digitize 5 dominant cover types: grassland (CRP, pasture, and hay fields), agriculture (corn, soy, and winter wheat), woodland, water, and development (urban areas and roads). Cover types were ground-truthed in the field to ensure accuracy. I also calculated total edge (TE), a sum of all edges of all cover types within the 1600-m radius circle, and edge density (ED), representing a spatial configuration (i.e., degree of fragmentation) of agricultural landscapes (Lee and Carroll 2014). At the patch scale I calculated field area (SIZE), edge index (defined as area/perimeter, INDEX), and percentage of woodland edge and cropland edge surrounding field (WOOD.EDGE, CROP.EDGE, respectively). I also included the percentage cover type within a 100-m buffer outlining the field (Table 2.1). I used a correlation matrix on all

variables collected to reveal multicollinearity; when pairs of variables had correlations ≥ 0.70 , the variable correlated most with other variables was removed from further analysis (Gries 2010). Landscape- and patch-scale covariates were calculated using ArcGIS software and the Patch Analysis extension (ArcGIS version 10.1, Rempel et al. 2012). I standardized all continuous covariates to a mean of 0 before analyses to improve model stability and convergence (Zuur et al. 2009).

Statistical analyses

All statistical analyses were performed in R version 3.0.3 (R Core Team 2014). To assess model covariates effect on DSR, I constructed generalized linear mixed models using the `glmer` command in the `lme4` package, with a logistic-exposure link function (Shaffer 2004). I followed a hierarchical modeling process to avoid over-fitting the data while still accounting for spatial and temporal variation (Burnham and Anderson 2002). I constructed models using 4 steps that considered (1) temporal variables, such as year, date and stage of the nest; (2) patch scale variables; (3) landscape scale variables; and (4) local vegetation and nest-site characteristics. Julian date provided the best temporal model, and was subsequently used in all other models. At the microhabitat scale, I included Nest.PC1, Nest.PC2, Nest.PC3 as well as nest height and distance to edge variables. Also at the microhabitat scale were the mean Field.PC1, Field.PC2, Field.PC3, and SDPC scores and DIV values. At the patch and landscape scale, I ran only single covariate models representing 7 and 10 variables, respectively (Table 2.1). Covariates among the top single variable models were then used in combined-scale models. To avoid multicollinearity, I did not combine 100 m, 800 m and 1600 m variables of the same land cover type in any 1 single model (Graham 2003). All models included 2 random effects: (1) field, to control for field variation in nest survival; and (2) nest ID as a nested factor within field, to control for multiple

observations at the same nest. Including year within preliminary models did not improve model fit, and was therefore dropped from subsequent analyses. I used model selection based upon Akaike's Information Criterion adjusted for small sample size (AICc). Logistic exposure models with $\Delta\text{AIC}_c \leq 4$ were considered plausible (Burnham and Anderson 2002). To account for model-selection uncertainty, I used model averaging to determine beta (β) parameter estimates with standard errors and confidence intervals for DSR.

For species with ≥ 15 nests and 100 exposure days, I examined species-specific DSR by constructing constant-only logistic-exposure models with no fixed effects and only field and nest ID as random effects (Shaffer and Thompson 2007). I calculated DSR following Shaffer (2004), as $\text{DSR} = \frac{e^{b_0}}{1 + e^{b_0}}$ where b_0 is the intercept parameter. I defined the length of the nesting period for each species from published literature (Ehrlich et al. 1988), and estimated the proportion of nests surviving the entire nesting period by multiplying DSR for each day of the nesting period (i.e., $\text{DSR}^{\text{nesting_period}}$).

RESULTS

I found 197 active nests of 9 species nesting in 20 of the 23 CP33 habitat buffers. Nesting species included field sparrow (85 nests), dickcissel (42 nests), red-winged blackbird (26 nests), indigo bunting (15 nests), common yellowthroat (*Geothlypis trichas*; 10 nests), brown thrasher (*Toxostoma rufum*; 9 nests), yellow breasted chat (*Icteria virens*; 5 nests), northern cardinal (*Cardinalis cardinalis*; 4 nests), and eastern towhee (*Pipilo erythrophthalmus*; 1 nest). Northern bobwhite were not among the species found nesting in CP33 habitat buffers. Of the 197 nests, I located 114 in 2013 and 83 in 2014. Seventy-six percent of all nests were initiated before 30 June, with only 5% initiated after 15 July. Nests were found 0.1–127 m from a cropland edge (median = 11.6 m) and 0.5–94 m from a woodland edge (median = 15.4 m). Frequency of nest

parasitism by brown-headed cowbirds was low; only 2 of 197 nests I located were parasitized (< 1%) and neither failed as a result.

After removing nests that failed due to desertion (5%) and weather (1%), I analyzed 186 nests of all species combined (effective sample size [n] = 1,886 exposure days). Five models were found to be competitive for all nesting species, all of which included date as a fixed effect, and field and nest ID as random effects (Table 2.4). F.PC3, a measure of dead vegetation within the field, had a significantly positive affect on DSR and was included in all competitive models. Interestingly, percentage woodland area at the 100 m level and percentage of woodland edge surrounding the buffer had a significantly positive affect on DSR of nests. Percentage of cropland area at the 1600 m landscape scale had a significantly negative relationship with DSR. N.PC3, a measure of decreasing dead vegetation at the nest site, also had a negative relationship with DSR, suggesting DSR was positively related to increasing dead vegetation at the nest. For the 4 species with ≥ 15 nests monitored, daily nest survival ranged from 0.907 to 0.963, resulting in a probability of 0.14 to 0.45 (mean = 0.275) of surviving the entire nesting period (Table 2.5).

DISCUSSION

Nest survival rate was not strongly affected by edge effects or edge type, which contrasts with many reports of negative effects of nesting near wooded edges (Johnson and Temple 1990, Burger et al. 1994, Jensen and Finck 2004). Furthermore, percentage woodland area within 100 m had a positive effect on nest survival rate. This is interesting, though not surprising, as others have observed the degree of negative edge effects varies depending on regional predator communities (Chalfoun et al. 2002). For instance, Woodward et al. (2001) found field sparrow in Missouri used habitat in proportion to availability in small patches, with no apparent decrease in nest survival rates near wooded edges. Weatherhead et al. (2010) also documented no clear

patterns of increased nest predation in edge habitat in southern Illinois. During my study, I observed 4 direct predation events, 3 being by black rat snakes (*Elaphe obsoleta*) and 1 by a field mouse (*Peromyscus sp.*, B. Y. Neiles, SIU, personal observation). The black rat snake has been identified as an important nest predator in similar regions (Weatherhead et al. 2010, Benson et al. 2010, Cox et al. 2012), and has demonstrated preferences for edge habitat in past studies (Blouin-Demers and Weatherhead 2001; Sperry et al. 2009). In fact, Cox et al. (2012) found black rat snake nest depredation events were positively influenced by forest edge in southern Illinois. However, CP33 habitat buffers are designed to mitigate the abrupt transition of vegetation conditions at forest-cropland edges, and may weaken negative edge effects. Yet, given snake response to edge habitat and their importance as nest predators in different habitat types (Weatherhead and Blouin-Demers 2004; Thompson 2007), further research should assess how snake abundance and activity changes in response to landscape forest cover and habitat characteristics.

Although I surveyed a range of CP33 habitat patch sizes (<12 ha) that are typical of CRP contracts in Illinois (McKinney et al. 1998), I did not find a strong influence of patch size on nest success. Forest-breeding birds often respond to patch size and landscape structure consistently in the midwestern and northeastern United States (e.g., Donovan et al. 1995, Robinson et al. 1995, Driscoll and Donovan 2004). However, a consistent response of grassland birds to patch size and landscape composition is less likely because of interannual and interregional changes in distributions of many grassland species (Igl and Johnson 1999; Winter et al. 2005). High climatic variability causes many populations of grassland birds to fluctuate greatly among regions and years (Igl and Johnson 1997). Although I did not examine this exact question, the lack of a response of grassland species to patch size suggests this is the case in southern Illinois. Others

have found similar relationships. Walk et al. (2010) found small patch size and proximity to cropland edges did not negatively affect nesting success in dickcissel and eastern meadowlark (*Sturnella magna*) in central Illinois. Winter et al. (2006) observed no consistent relationship between patch size and nest success in Minnesota. And, in a recent meta-analysis, Benson et al. (2013) examined 37 studies conducted across the eastern United States and found no impact of edge proximity and patch size on nest survival rates of grassland birds.

Although patch size itself may not be a reliable predictor of nest success, landscape context may play a role in increased predation risk. I observed a significantly negative relationship between percentage cropland area and DSR at the landscape level. Patterns of habitat use by primary nest predators may help explain why I observed this association. Corvids and mesocarnivores are often cited as efficient nest predators of songbird nests (Angelstam 1986, Crooks and Soulé 1999), and the conversion of prairie and forest landscapes in Illinois to intensive row-crop agriculture has allowed these predators to flourish (Pedlar et al. 1997, Heske et al. 1999), in turn creating a hostile landscape for songbirds (Askins 2000). Both American crows and raccoons may be drawn to row crops as an additional food source (Best et al. 1990, Dijak and Thompson 2000). Andrén (1992) also found corvids to be much more abundant in agriculture-dominated landscapes than forested landscapes. My observations are contrary to observations by Shake et al. (2011) in North Carolina, who documented field sparrow nest predation was considerably lower in habitat patches with high percent agricultural cover within 2.5 km. Also, Riddle and Moorman (2010) found higher nest success of indigo buntings and blue grosbeaks in agriculture-dominated landscapes than in forest-dominated landscapes in eastern North Carolina. Again, differences in nest predator communities between Eastern and Midwestern landscapes may explain these differences. Although individual species of nest

predators may respond to features such as patch size, proximity to edges, and landscape structure, it may not be apparent when averaged over a community of predators with different and sometimes contrasting behaviors (Benson et al. 2010).

As there is much more temporal and geographical variation in grassland habitat than other habitats, I expected to see a stronger influence of microhabitat variables on nest site selection. In fact, this is what I observed in southern Illinois. Field.PC3 was included in all competitive models, and was the strongest predictor of DSR, besides Julian date. Field.PC3 described a gradient of increasing dead vegetation structure and decreasing percentage of litter cover within individual CP33 habitat buffers. Also included in the competitive model set was Nest.PC3, a variable described by dead vegetation structure at the nest. Both variables suggest focal species selected fields and specific nest site locations with higher amounts of dead vegetation. Nesting in areas composed of taller, thicker vegetation may reduce predation risk by providing increased concealment for the nest and attending adult (Davis 2005). Others have also observed a response by dickcissel to standing dead vegetation, but suggest this relationship may relate to an increased invertebrate food source (Conover et al. 2011). A decrease in percentage of litter cover may also provide more effective foraging habitats for adult songbirds to search for prey items for nestlings (Osborne and Sparling 2013).

CP33 habitat buffers we surveyed likely are population sinks for dickcissels. Estimated nest success of the dickcissel was 19%. Although this falls within the range several other studies have reported, from 15% to 31% (e.g., Churchwell et al. 2008, Frey et al. 2008, Burhans et al. 2010), McCoy et al. (1999) suggest a nest success of at least 35% in a given habitat for it to be considered a source. The red-winged blackbird nest success of 32% is near those reported in Missouri CRP fields considered sink habitats (27.6%; McCoy et al. 1999). And, although our

observed nesting success of 14% is low, it is not atypical of field sparrows in Illinois or other regions of the U.S. (10%, Best 1978; 15%, Hinnebusch 2008; 15%, Giocomo et al. 2008). Yet, these numbers are still unlikely to support a source population. Nest success of indigo buntings (45%), however, was much higher than reported nest success estimates from other regions of the United States. Weldon (2006) reported indigo bunting nest success probability of 31% in shrubby patches in South Carolina. Riddle and Moorman (2010) observed nest success rates of 39% in agriculture-dominated landscapes of North Carolina. Our estimate is not surprising, though, as early successional habitat, like CP33 habitat buffers, is considered preferred habitat for indigo buntings (Payne 2006).

MANAGEMENT IMPLICATIONS

In my study area, CP33 habitat buffers are unlikely to support source populations for a majority of the focal grassland bird species I studied. If, however, those individuals would not have nested in intensively farmed areas, then CP33 habitat buffers may still provide an important conservation service for these species (McCoy et al. 1999). Despite commonly voiced concerns that conservation buffers may have limited value as nesting habitat because of low survival, nest success during this study was not substantively lower than previously reported for other habitats. Even narrow buffers provide greater benefits than non-buffered field margins and likely represent an important ancillary component to a whole-farm management regime that targets nesting songbirds. To increase nest survival rates within established CP33 habitat buffers, managers should focus on microhabitat vegetation characteristics. Standing vegetation from the previous year provides crucial vegetative cover for nesting activity and, thus, should remain undisturbed except when periodically managing to maintain early succession vegetation.

Table 1.1. Explanatory variables used in occupancy modeling of avian response to block fields (n=10) and CP33 habitat buffers (n=23) in southern Illinois, USA, May-August 2013-2014.

Habitat Covariate	Definition
Microhabitat	Within-field structural and floristic vegetation composition
PC1	Mean PC1 score for a field (vertical structure)
PC2	Mean PC2 score for a field (floristic composition)
PC3	Mean PC3 score for a field (dead vegetation structure)
SDPC	Standard deviation of PC1 and PC2 (structural complexity)
DIV	Plant diversity from coverage (Daubenmire 1959)
Patch	Field context and immediate surrounding area
SIZE	Total area of field
INDEX	Field area to field perimeter ratio
WOOD.EDGE	% woody edge surrounding field
GRASS.100	% grassland (CRP, hay fields, pasture) cover within 100-m Buffer surrounding field
WOOD.100	% woodland cover within 100-m buffer surrounding field
DEV.100	% urban infrastructure within 100-m buffer surrounding field
CROP.100	% crop cover within 100-m buffer surrounding field
Landscape	Landscape composition within 1600-m circular buffers
GRASS.800,1600	% grassland cover within designated buffer

Table 1.1 (continued)

	(CRP, hay fields, pasture)
WOOD.800,1600	% woodland cover within designated buffer
DEV.800,1600	% urban infrastructure within designated buffer
CROP.800,1600	% crop cover within designated buffer
TE	Total amount of edge within 1600-m buffer of the 6 land cover types
ED	Amount of edge relative to area within 1600 m

Table 1.2. Principal component analysis from 482 vegetation sampling locations, where 11 different structural vegetation variables were measured at each location. Vegetation surveys were conducted during July-August 2013-2014 on CP33 habitat buffers (n=23) and block fields (n=10) in southern Illinois, USA. Remaining principal components were excluded because they were not used in subsequent occupancy modeling. Component loading was used to interpret meaning of each principal component.

Microhabitat Variable ^a	PC1 ^b	PC2 ^c	PC3 ^d
Bare ground	-0.118	0.314	0.092
Bead veg. height	0.163	-0.264	0.478
% dead veg.	-0.122	-0.362	0.555
% forb	0.006	0.513	-0.078
% litter	-0.186	-0.281	-0.567
Mean litter depth	0.063	-0.434	-0.329
Mean Robel	0.609	0.181	0.012
Species Richness	-0.318	0.370	0.096
Live veg. height	0.657	0.023	-0.092
Standard deviation	1.391	1.353	1.151
Proportional variance	0.215	0.204	0.147
Cumulative proportion	0.215	0.418	0.566

^a Estimated from a 20 cm by 50 cm randomly placed quadrat.

^b PC1 a gradient of increasing Robel score and live vegetation height (vertical structure).

^c PC2 a gradient of increasing percentage forb cover, species richness and decreasing mean litter depth (floristic composition).

^d PC3 a gradient of dead vegetation height, percentage dead vegetation cover and percentage litter cover (dead vegetation structure).

Table 1.3. Multiscale model sets of breeding season probability of detection (p) and probability of occupancy (ψ) of grassland associated birds in CP33 habitat buffers (n=23) and block fields (n=10) during May-July 2013-2014 in southern Illinois, USA. Detection (p) was modeled with observational covariates (DATE, TIME, EFFORT, WIND, CC and TEMP) as occupancy (ψ) was estimated at the microhabitat, patch, and landscape scales; variables are defined in Table 1.1. The full null model [$p(\cdot)\psi(\cdot)$] was included as reference. Competitive models ($\Delta AIC_c \leq 2$) are displayed for each species along with direction (+, -) of parameter relationship to covariate. ΔAIC_c = current model AIC_c score minus top model AIC_c , K = number of parameters, ω_i = relative weight (likelihood) of model, CN = condition number (degree of multicollinearity and model stability; models with CN > 100 not used).

Model	ΔAIC_c	K	ω_i	CN
Northern Bobwhite				
$p^a\psi(-\text{INDEX} + \text{GRASS.800} + \text{PC3})$	0.00	5	0.47	88
$p^a\psi(+\text{SIZE}^b)$	1.02	3	0.28	54
$p^a\psi(-\text{INDEX} + \text{PC3})$	1.23	4	0.25	96
$p(\cdot)\psi(\cdot)$	12.34	2	<0.01	1
Dickcissel				
$p^a\psi(-\text{WOOD.800}^b + \text{PC1}^b)$	0.00	4	0.71	6.6
$p^a\psi(-\text{WOOD.800}^b + \text{PC1}^b + \text{PC2})$	1.88	5	0.28	6.2
$p(\cdot)\psi(\cdot)$	22.74	2	<0.01	1.6
Eastern Meadowlark				
$p^a\psi(-\text{TOTAL EDGE}^b - \text{INDEX}^b)$	0.00	4	0.68	9.6
$p^a\psi(-\text{TOTAL EDGE}^b - \text{INDEX}^b + \text{PC2})$	1.47	5	0.32	32.1
$p(\cdot)\psi(\cdot)$	23.90	2	<0.01	1.3

Table 1.3 (continued)

Field Sparrow

$p^a\psi(+\text{CROP.1600} - \text{PC1}^b)$	0.00	4	0.52	69
$p^a\psi(+\text{CROP.1600} - \text{DEV.100}^b)$	1.51	4	0.24	34
$p^a\psi(+\text{CROP.1600} - \text{GRASS.100} - \text{PC1}^b)$	1.59	5	0.23	71
$p(\cdot)\psi(\cdot)$	11.90	2	<0.01	2

Indigo Bunting

$p^a\psi(-\text{GRASS.800})$	0.00	3	0.98	75
$p(\cdot)\psi(\cdot)$	7.88	2	0.02	4

Red-winged Blackbird

$p^a\psi(-\text{WOOD.100}^b + \text{PC1})$	0.00	4	0.99	42
$p(\cdot)\psi(\cdot)$	20.24	2	<0.01	2

^a The null detection model was competitive with all detection covariates.

^b Significant predictor of given parameter (ψ) based on model averaged unconditional 95% confidence intervals that do not overlap 0.

Table 2.1. Explanatory variables used in occupancy modeling of avian response to block fields (n=10) and CP33 habitat buffers (n=23) in southern Illinois, USA, May-August 2013-2014.

Habitat Covariate	Definition
Microhabitat	Within-field structural and floristic vegetation composition
NEST.HEIGHT	height of the nest from the ground to the nest rim (cm)
DIST.CROP	Distance to nearest cropland edge (m)
DIST.WOOD	Distance to nearest woodland edge (m)
Nest.PC1	PC1 score at the nest
Nest.PC2	PC2 score at the nest
Nest.PC3	PC3 score at the nest
Field.PC1	mean PC1 score for a field
Field.PC2	mean PC2 score for a field
Field.PC3	mean PC3 score for a field
SDPC	standard deviation of PC1 (structural complexity within field)
DIV	plant diversity from coverage (Daubenmire 1959)
Patch	field context and immediate surrounding area
SIZE	total area of field (ha)
INDEX	field area to field perimeter ratio
WOOD.EDGE	% woody edge surrounding field
CROP.EDGE	% crop edge surrounding field

Table 2.1 (continued)

GRASS.100	% grassland (CRP, hay fields, pasture) cover within 100-m buffer surrounding field
WOOD.100	% woodland cover within 100-m buffer surrounding field
DEV.100	% urban infrastructure within 100-m buffer surrounding field
CROP.100	% crop cover within 100-m buffer surrounding field
Landscape	Landscape composition within 1600-m circular buffers
GRASS.800,1600	% grassland cover within designated buffer (CRP, hay fields, pasture)
WOOD.800,1600	% woodland cover within designated buffer
DEV.800,1600	% urban infrastructure within designated buffer
CROP.800,1600	% crop cover within designated buffer
TE	total amount of edge within 1600 m buffer of the 6 land cover types
ED	amount of edge relative to area within 1600 m

Table 2.2. Nest site principal component analysis from nest site vegetation sampling (n=197), where 9 different structural vegetation variables were measured at each location. Vegetation surveys were conducted within 7 days after the nest was found inactive during July-August 2013-2014 on CP33 habitat buffers (n=23) in southern Illinois, USA. Remaining principal components were excluded because they were not used in subsequent logistic exposure analysis. Component loading was used to interpret meaning of each principal component.

Microhabitat Variable ^a	Nest.PC1 ^b	Nest.PC2 ^c	Nest.PC3 ^d
bare ground	0.080	0.463	0.403
dead veg. height	-0.139	0.208	-0.682
% dead veg.	-0.365	0.015	-0.435
% grass	-0.350	-0.05	-0.040
% litter	0.138	-0.521	0.131
mean litter depth	0.083	-0.671	-0.113
mean Robel	0.479	0.109	-0.246
live veg. height	0.488	0.065	-0.122
standard deviation	1.670	1.195	1.164
proportional variance	0.31	0.159	0.151
cumulative proportion	0.31	0.469	0.619

^a Estimated from a 20 cm by 50 cm quadrat and Robel pole centered at the nest.

^b Nest.PC1 a gradient of increasing Robel score and live vegetation height (vertical structure).

^c Nest.PC2 a gradient of percentage litter cover and mean litter depth (litter).

^d Nest.PC3 a gradient of dead vegetation height and percentage dead vegetation cover (dead vegetation structure).

Table 2.3. Field principal component analysis from 482 vegetation sampling locations, where 9 different structural vegetation variables were measured at each location. Vegetation surveys were conducted during July-August 2013-2014 on CP33 habitat buffers (n=23) in southern Illinois, USA. Remaining principal components were excluded because they were not used in subsequent occupancy modeling. Component loading was used to interpret meaning of each principal component.

Microhabitat Variable ^a	Field.PC1 ^b	Field.PC2 ^c	Field.PC3 ^d
bare ground	-0.118	0.314	0.092
dead veg. height	0.163	-0.264	0.478
% dead veg.	-0.122	-0.362	0.555
% forb	0.006	0.513	-0.078
% litter	-0.186	-0.281	-0.567
mean litter depth	0.063	-0.434	-0.329
mean Robel	0.609	0.181	0.012
species Richness	-0.318	0.370	0.096
live veg. height	0.657	0.023	-0.092
standard deviation	1.391	1.353	1.151
proportional variance	0.215	0.204	0.147
cumulative proportion	0.215	0.418	0.566

^a Estimated from a 20 cm by 50 cm randomly placed quadrat.

^b Field.PC1 a gradient of increasing Robel score and live vegetation height (vertical structure).

^c Field.PC2 a gradient of increasing percentage forb cover, species richness and decreasing mean litter depth (floristic composition).

^d Field.PC3 a gradient of dead vegetation height, percentage dead vegetation cover and percentage litter cover (dead vegetation structure).

Table 2.4. Top models considered for predicting daily nest survival of all nests found in CP33 habitat buffers (n=20) during May-July 2013-2014 in southern Illinois, USA. -2 log-likelihood ($-2\log L$), number of parameters included (K), ΔAIC_c values, and Akaike weights (w_i) for model selection. Models $\Delta AIC_c > 4$ are not listed. DSR was estimated at the microhabitat, patch, and landscape scales; variables are defined in Table 2.1. The null model and Julian date temporal model were included as reference. Analyses were based on 489 days of nest monitoring at 186 nests in CP33 habitat buffers. F.PC3 = mean PC3 score for a field. N.PC3 = PC3 score at the nest.

Model	$-2\log L$	ΔAIC_c	K	w_i
DATE ^a + Field.PC3 ^a + WOOD.100 ^a	542.44	0.00	6	0.35
DATE ^a + Field.PC3 ^a – CROP.1600 ^a	542.62	0.19	6	0.32
DATE ^a + Field.PC3 ^a + WOOD EDGE	544.28	1.84	6	0.14
DATE ^a + Field.PC3 ^a	547.06	2.56	5	0.10
DATE ^a + Field.PC3 ^a – Nest.PC3	545.36	2.93	6	0.08
DATE ^a (best temporal model)	553.14	6.60	4	0.01
Null	559.92	11.35	3	0.00

^a Significant predictor of given parameter (ψ) based on model averaged unconditional 95% confidence intervals that do not overlap 0.

Table 2.5. Estimated nest survival, using intercept-only models, for 4 species (with 15 or more nests monitored) nesting in CP33 habitat buffers (n=20) during the 2013-2014 breeding season in Southern Illinois, USA. DSR = estimated daily survival rate.

Species	<i>N</i> nests	<i>N</i> observations	<i>N</i> exposure days	DSR (95% CI)	Nesting period (days)	Probability of nest success
Dickcissel	42	93	389	0.924 (0.875-0.954)	21	0.19
Field sparrow	85	207	742	0.907 (0.879-0.929)	20	0.14
Indigo bunting	15	48	181	0.963 (0.903-0.986)	21	0.45
Red-winged blackbird	26	74	286	0.947 (0.913-0.969)	21	0.32

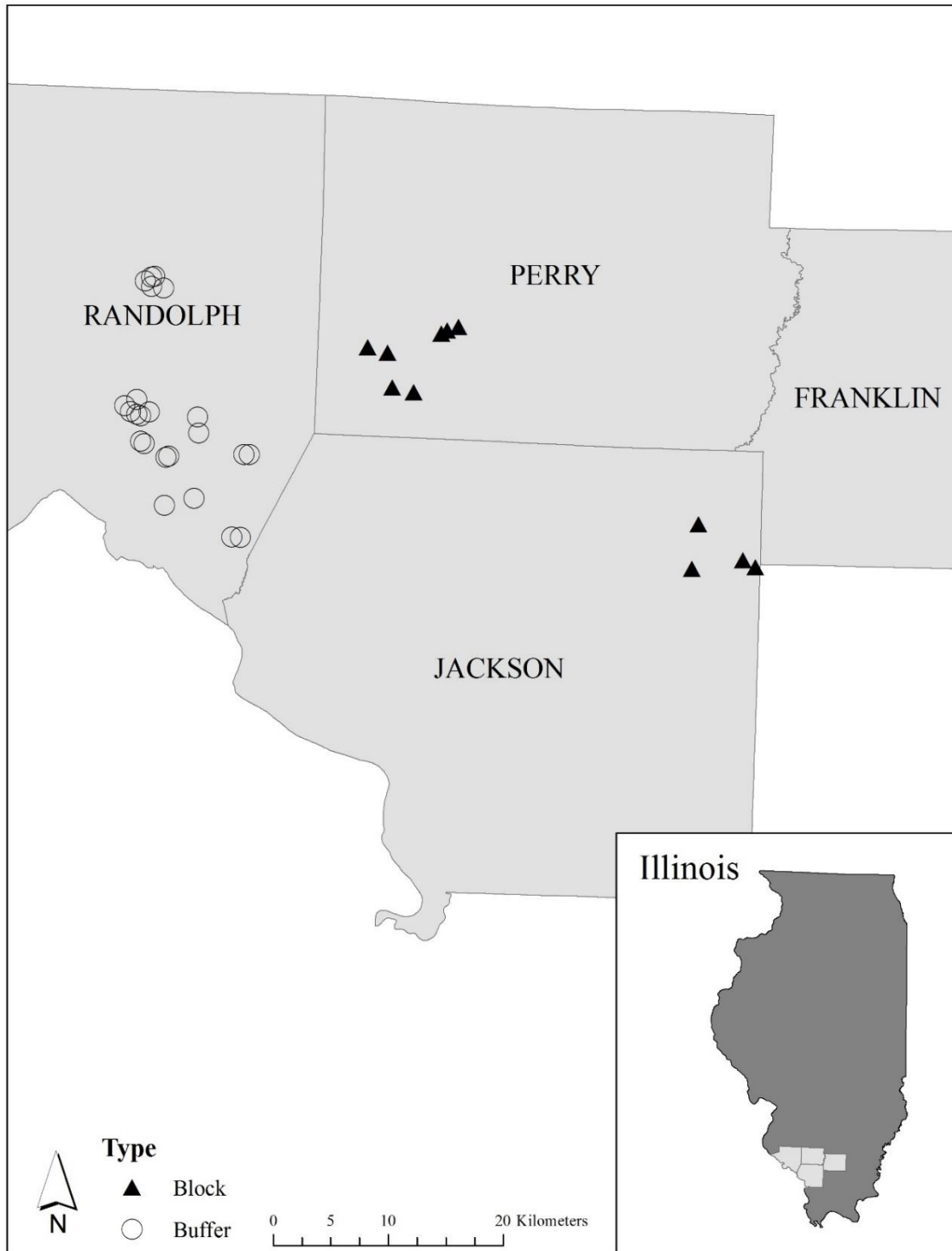


Figure 1.1. Locations of CP33 habitat buffers (n=23) and block fields (n=10) where avian surveys were conducted during May-July 2013-2014 in southern Illinois, USA.

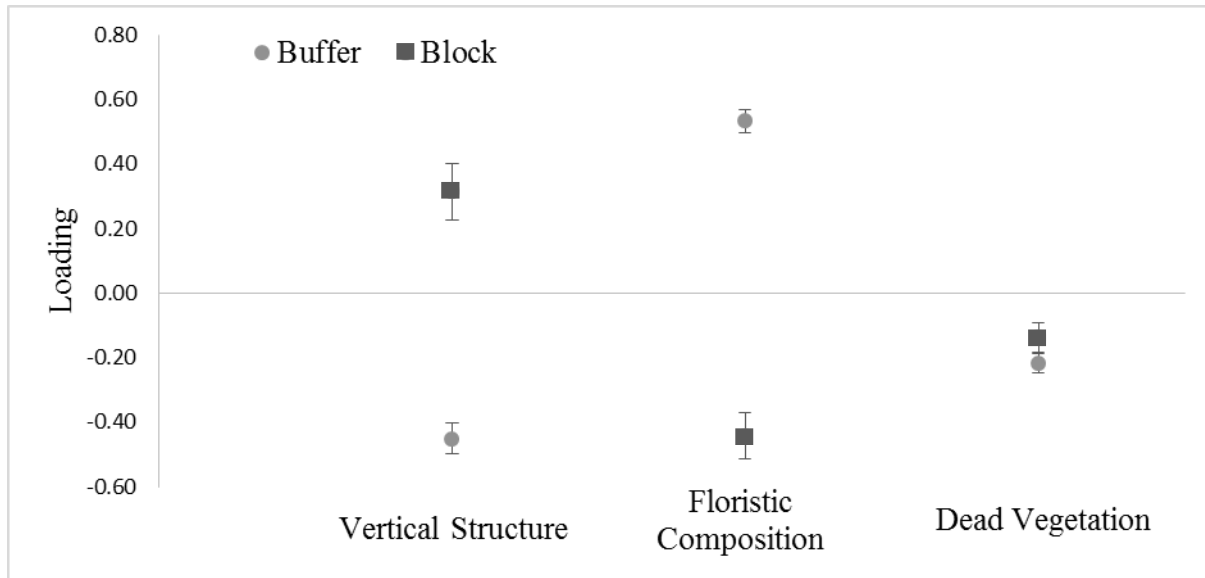


Figure 1.2. Mean site PC1, PC2 and PC3 scores with standard error from cumulative principal component analysis from vegetation surveys conducted during July-August 2013-2014 in CP33 habitat buffers (n = 23) and larger block fields (n = 10) in southern Illinois, USA. PC1 was described by gradient of increasing Robel score and live vegetation height (vertical structure). PC2 was described by a gradient of increasing percentage forb cover, species richness and decreasing mean litter depth (floristic composition). PC3 was described by a gradient of dead vegetation height, percentage dead vegetation cover and percentage litter cover (dead vegetation structure).

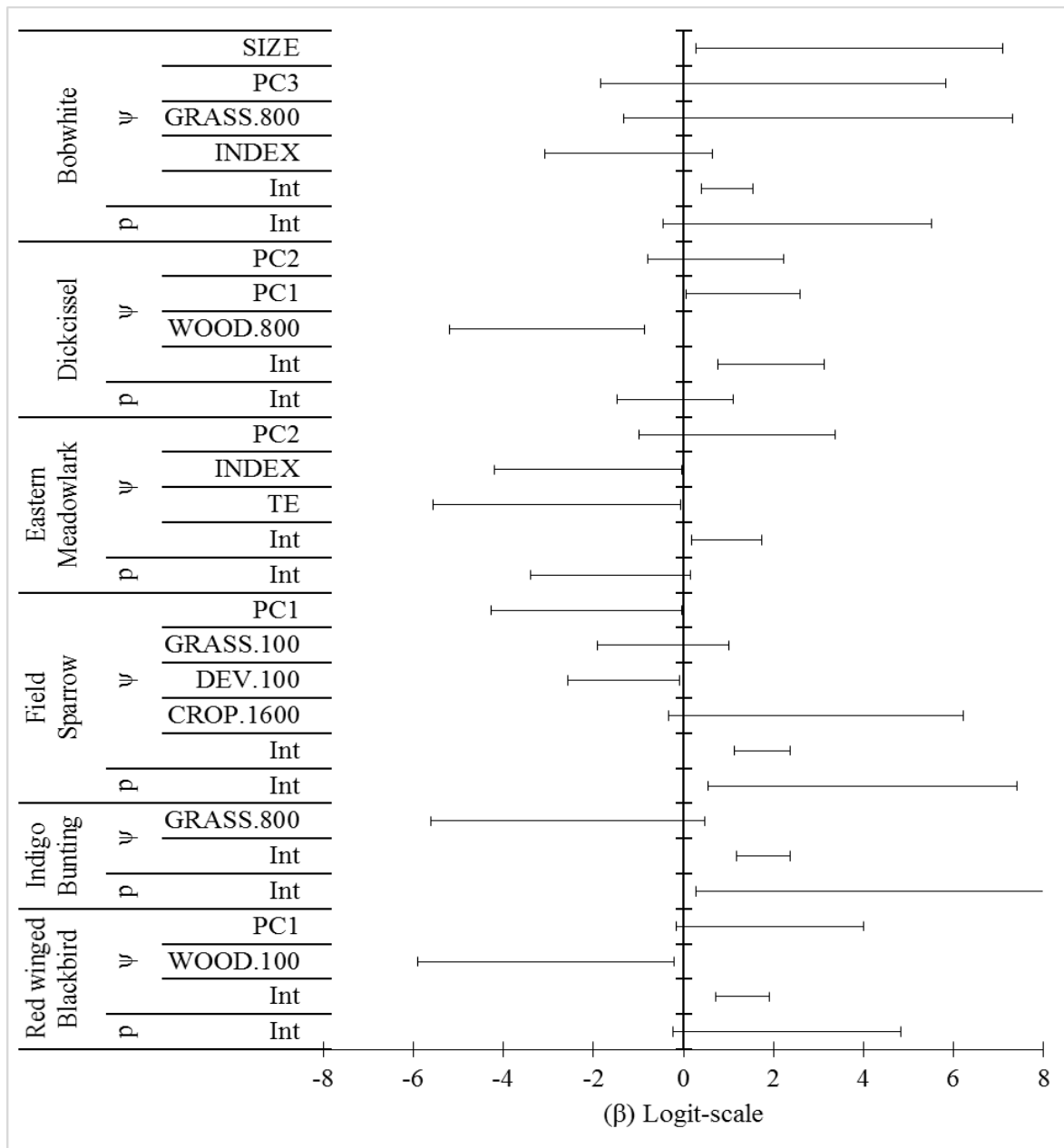


Figure 1.3. 95% confidence interval of slope estimates (β coefficients) for detection (p) and occupancy (ψ) from top multiscale occupancy models of breeding grassland associated species in southern Illinois, USA, 2013-2014. Intercepts (Int) represent logit-scale p or ψ while holding covariates constant at a standardized mean of 0 (see Table 1.1 for covariate definitions). Confidence intervals not overlapping 0 are considered significant predictors of the given parameter.

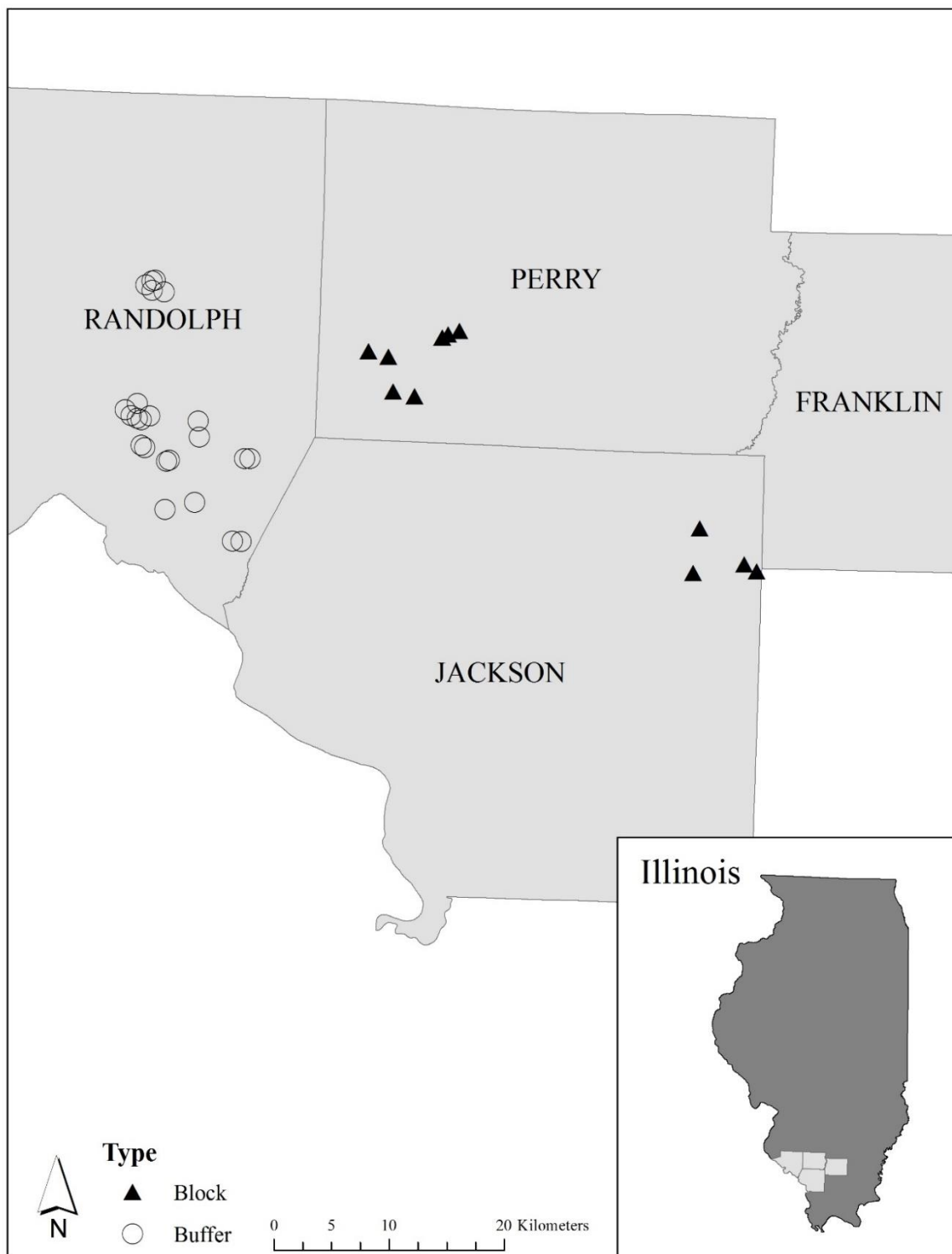


Figure 2.1. Locations of CP33 habitat buffers (n=23) and block fields (n=10) where avian surveys were conducted during May-July 2013-2014 in southern Illinois, USA.

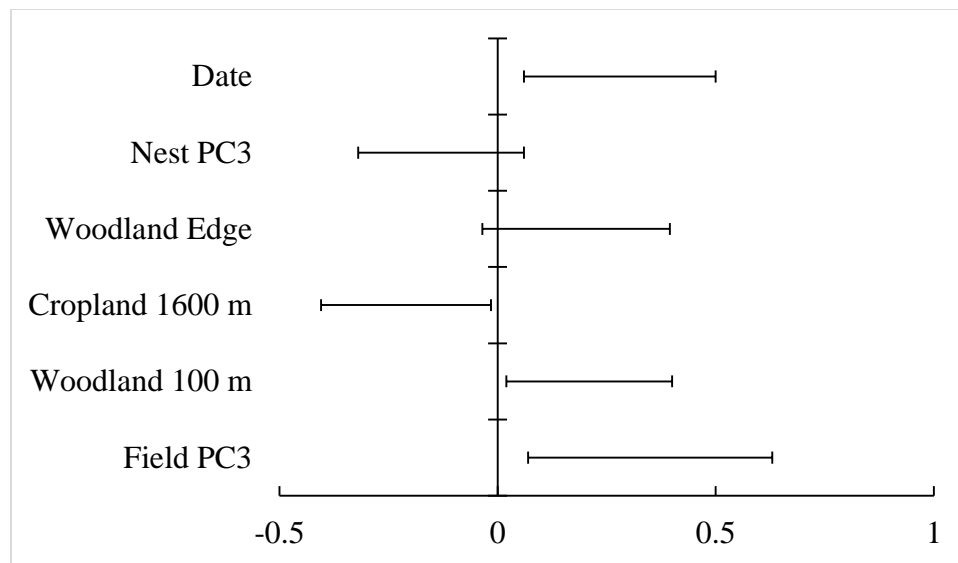


Figure 2.2. Model-averaged parameter estimates (β and 95% confidence intervals) for factors influencing daily nest survival (logit scale) of all nests found in CP33 habitat buffers (n=23) during May-July 2013-2014 in southern Illinois, USA. Models included field and nest ID as random effects. Confidence intervals not overlapping 0 are considered significant predictors of the given parameter.

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APPENDICES

APPENDIX A

Bird observations (number of detections) in block fields (n=10) and CP33 habitat buffers (n=23) in southern Illinois, May-August 2013-2014. DICK = dickcissel, EAME = eastern meadowlark, FISP = field sparrow, INBU = Indigo Bunting, NOBO = northern bobwhite, RWBL = red-winged blackbird.

		Species																	
Field		DICK			EAME			FISP			INBU			NOBO			RWBL		
		1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
CP33 Habitat Buffer	1							10	7	8	2	9	3					1	1
	2			1						2	1	2	2				6	6	7
	3	13	5	12	1		1	3	3	4	2	2	1		1	3	19	28	55
	4			4				5	4		6		2				2	3	2
	5	13	11	10				3	2	2	3		3	1	1		12	10	6
	6							1		1	7	6	4			1	1		
	7										4	5	2				10	5	13
	8							5	5	4	3	6	5		3				
	9							3	1	2	1	3	4	2					
	10			1				4		1	4	7	6						1
	11										2	4	3					1	
	12								1	4	3	2	1		1				
	13							2	4	3	1	3	2				2	1	
	14							3	3	2	1	2	2				1		
	15							1	4	1	3	1	1						
	16							1		4	4	3	2						
	17							1	8	4	1	2							

Appendix A (continued)

	18							3	2	3	4	3	4						
	19	2	2	1				5	8	6	6	6	6				1	2	
	20							20	16	11	8	9	7						
	21							9	8	9	2	4	4						
	22							3	1	3	2	2	3						
	23							2		1	1	4	4						
Large Block	24	3	3	9	2	3	2	9	10	7	2	3	3	4	1	2			1
	25	8	7	5						1		1		1	1		3		1
	26	6	5	7		3	2	4	3	2	1	1	1	1	1		2	10	2
	27	12	20	14		3	1	5	7	8		2				2	7	8	12
	28	1	1	1	1	1	2										5	5	5
	29	5	4	4			1	1	1							2	4	4	1
	30	6	5	1	3	2	1									1	3	3	8
	31	9	9	4	2	2	2						1				5	5	1
	32	7	3	11	2	2	5				1						10	14	16
	33	5	6	6		2	1	1		4	1			1		1	6	8	2

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