NORTHERN BOBWHITE AND BIRD COMMUNITY RESPONSE TO HABITAT RESTORATION IN OKLAHOMA

By

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NORTHERN BOBWHITE AND BIRD COMMUNITY RESPONSE TO HABITAT RESTORATION IN OKLAHOMA

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CHAPTER I

EVALUATION OF THE QUAIL HABITAT RESTORATION INITIATIVE IN OKLAHOMA

ABSTRACT The northern bobwhite (*Colinus virginianus*, hereafter bobwhite) has experienced range-wide declines over much of the last century that are concurrent with widespread loss of the early-successional habitat on which this species relies. This has prompted habitat restoration programs such as the Quail Habitat Restoration Initiative (QHRI) in Oklahoma, which seeks to restore bobwhite habitat on private properties. My objectives were to evaluate the success of this program in increasing bobwhite occupancy rates within restoration areas and determine local- and landscape-level habitat factors that best predict bobwhite occupancy. I used data collected during the breeding season in 2009–2011 to develop single-level and hierarchical linear models of the effect of restoration treatments and habitat variables on bobwhite occupancy. I found no significant effect of treatment ($P = 0.521$), and models suggested that the probability of bobwhite occupancy increases substantially when overstory canopy cover falls below a threshold level of 60% and the amount of suitable bobwhite habitat within 1 km of the sample unit is >150 ha. My best-fit linear model explained 59% of the variability in bobwhite occupancy. Hierarchical models showed no effect of the property on which sampling occurred beyond that explained by habitat and landscape variables. My results suggest that the majority of habitat restoration was done within the appropriate landscape context, but that sufficient local habitat conditions were not created to significantly increase bobwhite occupancy. This information can help guide land managers in both the choice of areas for restoration and the appropriate conditions under which bobwhites would be expected to recolonize a restoration area.

INTRODUCTION

The northern bobwhite (hereafter bobwhite) is a socially and economically important game bird species that has seen range-wide declines throughout most of the twentieth century (Stoddard 1931, Brennan 1991, Sauer et al. 2011). This decline is concurrent with a decrease in the brushy prairie and open woodland habitats used by bobwhites and other early-successional bird species (Burger 2002). The decrease in habitat is due mainly to changes in land use such as intensified farming practices, secession of frequent burning, urban expansion, and reforestation (Brennan 1991, Roseberry and Sudkamp 1998, Peterson et al. 2002). Similar to most areas of the country, bobwhites have declined in eastern Oklahoma (Sauer et al. 2011), where gap closures and increases in stand density, primarily by oak (*Quercus* spp.) and pine (*Pinus* spp.), and encroachment of eastern redcedar (*Juniperus virginiana*) has resulted in substantial loss and fragmentation of bobwhite habitat (Bidwell et al. 2002, Sams 2006). It is this reduction in available habitat that is thought to be the driving factor behind the bobwhite decline (Williams et al. 2004). In contrast, bobwhite populations in much of western Oklahoma have remained stable or increased because of an abundance of suitable habitat in that area of the state (Sauer et al. 2011).

Among species with high variability in year-to-year populations and limited dispersal capabilities, such as bobwhites, habitat loss and fragmentation can often result in high risk of extinction within patches and low rates of recolonization from other patches (Hanski and Gilpin 1991, Terhune et al. 2010). Early-successional habitats are by nature ephemeral and reliant on regular disturbances, and increased rates of fragmentation can force individuals to use lower-quality habitats and inhibit dispersal to new patches (Fies et al. 2002, Terhune et al. 2010). Inhibited dispersal caused by fragmentation can affect maintenance of optimal covey sizes in winter and breeding season dispersal in spring, thus increasing the probability of mortality and vulnerability to local extinctions due to an Alee effect (Fies et al. 2002, Williams et al. 2003, Williams et al. 2004).

Historically, management actions for bobwhites have focused on improving habitat at the local level (Williams et al. 2004), and although it is possible to increase the productivity of individual habitat patches, recent theory suggests that habitat management must be addressed at much broader spatial scales than historically conducted if the bobwhite decline is to be reversed (Guthery 1997, Guthery et al. 2001, Williams et al. 2004, Veech 2006). For example, population viability analysis has shown that greater amounts of contiguous usable space can decrease extinction risk among bobwhites (Guthery et al. 2000), and research suggests that the total amount of usable space for bobwhites is the overriding factor determining bobwhite densities in a given area (Guthery et al. 2001, Cram et al. 2002). If restoration creates only small, isolated patches the probability of bobwhites dispersing into those patches is low and the probability of mortality increases. Furthermore, Seckinger et al. (2008) found that changing the composition of the landscape, in the form of lower amounts of closed-canopy forest and increased amounts of usable space, contributes positively to winter survival of bobwhites through decreasing vulnerability to predation. Thus, the amount of habitat and isolation of that habitat from existing bobwhite populations are likely the main factors determining whether bobwhites will recolonize a restoration site and persist if they do recolonize the site.

In response to the population decline of bobwhites in Oklahoma, the Oklahoma Department of Wildlife Conservation (ODWC), in cooperation with the U.S. Department of Agriculture's Natural Resource Conservation Service (NRCS), undertook a 5-year initiative, beginning in 2008, under the federal Environmental Quality Incentive Program (EQIP) to provide cost share and incentive payments for landowners to restore habitat for bobwhites. This program is known as the Quail Habitat Restoration Initiative (QHRI), and its objective is to address habitat at the landscape level, reflecting the current management recommendations for restoring bobwhite populations (Sams 2002, Williams et al. 2004). Five focal areas were identified throughout the state by the ODWC as having the best potential for growth and range expansion of local bobwhite populations (Fig. 1.1). These focal areas were designated according to the Bird Conservation Regions in which they occur, as defined by the North American Bird Conservation Initiative (Fitzpatrick 2002) and a landscape modeling analysis based on bobwhite habitat (Sams 2006). Landowners in 4 of these focal areas, the Central Hardwoods (CH), West Gulf Coastal Plains and Ouachitas (WG), Oaks and Prairies (OP), and Mixed-grass Prairie

(MG) (there was insufficient landowner interest in the Tallgrass Prairie focal area) were enrolled in the program and restoration activities such as mechanical thinning of trees and shrubs, herbicide spraying, prescribed fire, and planting of native grass seed mixtures were prescribed. The ODWC ranked applicants based on the size of the area being offered for restoration, its proximity to existing habitat, and the type of restoration activities being considered. In the eastern focal areas, where bobwhite populations are declining most dramatically, the purpose of this program was to increase the amount of usable space on the landscape for bobwhites. In the western focal area, the purpose was to maintain suitable habitat by controlling eastern redcedar through the use of prescribed fire and mechanical thinning.

My study was initiated to monitor restoration areas to determine if the QHRI program was successful in increasing bobwhite populations and what factors were related to success or failure of restoration efforts. My objectives were to determine the occupancy status of areas designated for restoration and investigate the local- and landscape-level factors associated with bobwhite occupancy. I investigated bobwhite occupancy at 3 different spatial scales representing local habitat characteristics, composition of the surrounding landscape, and a hierarchically structured effect of the property on which restoration occurred. I limited this analysis to the 3 eastern focal areas (CH, WG, and OP; Fig. 1.1), where bobwhite populations were low and habitat restoration, rather than maintenance, was taking place. I hypothesized that, although habitat characteristics at the local level are critical in determining whether bobwhites will inhabit a specific area, the amount of bobwhite habitat in the surrounding landscape also plays a major role in determining bobwhite occupancy. For example, increasing amounts of brushy prairie and grassland habitat in the immediate vicinity of a restoration area would increase the likelihood of the restoration area becoming occupied, given that local habitat conditions were adequate to support bobwhites. As such, success or failure of restoration would depend on the habitat characteristics created at the local level and the land-cover surrounding the restoration area. This information can be useful to land managers in deciding where to invest money in habitat restoration and how much area should be restored.

STUDY AREA

The focal areas I studied in this analysis were the CH (Cherokee and Adair counties), WG (Coal and Hughes counties), and OP (Pontotoc and Johnston counties). These areas were located in northeastern and south-central Oklahoma, respectively (Fig. 1.1). The CH area has rolling topography and is dominated by oak and hickory (*Carya* spp.) forests interspersed with areas of both native and introduced pasture and hayfield and row crops. Encroachment by eastern redcedar is not a significant issue in this area. The WG and OP areas are characterized by a mosaic of tallgrass prairie and cross-timbers forest. Dominant tree species here are post oak (*Q.stellata*), blackjack oak (*Q. marilandica*) and hickories, and the most prominent grasses include big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), and indiangrass (*Sorghastrum nutans*). The main land uses in all 3 focal areas are ranching and row-crop agriculture (Natural Resource Conservation Service 2012). Bobwhite populations in these 3 areas decreased at a rate >1.5% per year between 1966 and 2003 (Sauer et al. 2007).

Among the properties enrolled within the 3 eastern focal areas, there were 92 management units designated for restoration totaling 827 ha and ranging in size from <1 ha to 192 ha, with 75% being <5 ha. Fifty-five of these management units actually received restoration treatments during my study, including 38 management units totaling 135 ha in the CH focal area, 16 management units totaling 325 ha in the WG focal area, and 1 management unit totaling 57 ha in the OP focal area. Treatments included various amounts of overstory tree removal, prescribed fire, and re-seeding with native warm-season grasses.

METHODS

Study Design and Site Selection

Because of the necessity to specifically sample habitat restoration areas, study site selection was not random. I located sample units in portions of the enrolled properties where restoration was prescribed to occur and in control areas where no active restoration would take place. Control areas were either in closed canopy forest with some small areas of prairie, or in areas of early-successional habitat where bobwhites were known to occur, ensuring that our sample units covered the full range of natural upland habitat types available. This design enabled me to examine habitat variables of interest in a continuous distribution rather than a standard control/treatment design. This was necessary because treatments were not uniformly applied spatially, temporally, or methodologically. I did not include agricultural fields or human development within the sample units. In 2009, I was able to establish 31 sample units, 10 of which contained management units that had already received restoration treatments, 14 that had not yet received restoration treatments, and 7 that were designated as controls. Three additional sample units had received treatments by the 2010 breeding season, and 2 more were treated by 2011. Each sample unit consisted of a 400-m-radius circle covering ~50 ha and was large enough to sample one or more management units designated for restoration (Fig. 1.2). I chose this size because the radius of audibility for bobwhites is considered to be ~400 m (Stoddard 1931), and therefore it would be sufficient to sample bobwhites within the restoration areas.

Bobwhite and Habitat Surveys

To survey for bobwhites, I conducted call-count surveys (Hansen and Guthery 2001) at the center point of each sample unit 3 times during the breeding season (mid-May–late July) at intervals of 2–3 weeks in 2009–2011. I grouped sample units based on geographic proximity and surveyed one group per day, alternating the order in which both sample units and groups were surveyed to avoid detection bias due to time of day or time during the breeding season. Each survey consisted of a 5-min call count, done between 0.5 hr before sunrise and 4.5 hr after sunrise, where all bobwhites heard within 400 m were recorded. I did not survey when it was raining or when wind speeds exceeded 20 km per hr (Ralph et al. 1995).

To measure habitat characteristics and ensure that all portions of sample unit were equally represented, I systematically located 16 vegetation sampling points within each sample unit in a design modified from Wilson et al. (1995) and Smith et al. (2008). I did this by using a Global Positioning System (GPS) unit to establish a group of 4 vegetation points, with the initial point at the center of the sample unit and 3 additional points 63 m away from the initial point at angles of 90°, 210°, and 330°. Three additional groups of 4 points were established with their initial points located 250 m away from the sample unit center at angles of 90°, 210°, and 330° (Fig. 1.2).

I measured percent overstory canopy cover at each point beginning in June of 2009 using a hemispheric camera and WinSCANOPY canopy analysis software (Regents Instruments Inc., Canada). Canopy was re-measured in subsequent years (2010–2011) only if coverage had changed due to fire or other restoration activities. To avoid including ground-level vegetation in the photograph, I placed the camera on a tripod and took photographs from a height of 1 m above the ground. From each vegetation point, I extended a 20-m transect in a random direction. At 5, 10, 15, and 20 m along the transect I estimated percent cover of grass, standing dead vegetation, litter, and bare ground using a 1-m^2 quadrat (Daubenmire 1959). I defined standing dead vegetation as any non-living vegetation at an angle >45° from the ground and litter as any non-living vegetation at an angle <45° from the ground. Along the same transect, I also measured visual obstruction at 10 and 20 m using a profile board (Guthery et al. 1981). My metric of visual obstruction was the average of the visual obstruction values from each stratum of the profile board, and it was used as an index of vegetation height (Harrell and Fuhlendorf 2002). I measured percentages of shrub cover and eastern redcedar along the entire transect using the line-intercept method (Canfield 1941) as modified by Harrell and Fuhlendorf (2002). These measurements were taken during the breeding season each year (2009–2011).

Landscape Analysis

I used land-cover data derived from the 2006 National Land Cover Database (NLCD), which uses 30-m resolution LANDSAT data to determine land cover throughout the United States (Homer et al. 2007). For my analysis, I was only concerned with land-cover classes that could be considered as potential bobwhite habitat. These classes were Shrub/Scrub, Grassland/Herbaceous, and Pasture/Hay. I computed the total area in ha of these 3 classes combined within 1 km of the outer edge of each sampling unit. I chose this size because it was within the average seasonal movement range for bobwhites (Fies et al. 2002, Terhune et al. 2010) and was the scale at which bobwhite habitat dynamics likely occur (Howell et al. 2009).

Statistical Analysis

Local restoration effects—To determine if restoration treatments had a significant effect on the probability of a sample unit being occupied by bobwhites, I used treatment as the variable in a logistic regression and limited the analysis to sample units where restoration treatments were prescribed to occur (i.e. no control units were used in this portion of the analysis). A sample unit was designated as treated if restoration activities had been conducted anywhere within the unit before the survey was done. All other sample units were designated as untreated. To control for possible year effects, I included year in the model as a covariable and combined results from all years. I used the *P*-value of the treatment variable in the model, at $\alpha = 0.05$, as my criterion for determining if treatment had a significant effect on occupancy.

Habitat and landscape effects on occupancy—I analyzed the effect of habitat variables on bobwhite occupancy using multiple logistic regression. I used Principal Components Analysis (PCA) to determine which habitat variables were correlated with each other so as to reduce multicolinearity in the data set (Winter and Faaborg 1999, Crawley 2007). I chose variables for my models based on the strength of correlation to both the PCA axis scores and to each other. There were 3 variables strongly correlated with PCA axis 1: percent overstory canopy cover (CANOPY), percent grass cover (GRASS), and percent cover of standing dead vegetation (STD) (Fig. 1.3). There were 4 variables strongly correlated with PCA axis 2: percent bare ground (GROUND), percent litter cover (LITT), percent shrub cover (SHRUB), and visuals obstruction as an index of vegetation height (VOBS) (Fig. 1.3).

I initially evaluated 40 candidate models, using only the habitat variables within the 50-ha sampling unit, with variables selected according to the following criteria:

1. I assumed a negative exponential relationship between overstory canopy cover and bobwhite occupancy, and therefore used ln(CANOPY+1) as the variable describing canopy cover.
2. I did not include variables that were highly correlated along the same PCA axis (|Correlation| > 0.4) in the same model.
3. I assumed a quadratic relationship may exist, wherein there is a unimodal relationship between axis 2 variables and bobwhite occupancy, and therefore included models with quadratics of variables correlated with axis 2.
4. I assumed an interaction may exist between the axis 1 and axis 2 variables and included models with these interaction terms.

5. I included a null model (intercept as the only variable) in the initial set of candidate models. I did not include a global model as many of the variables are highly correlated and thus could result in non-sensical parameter estimates (Guthery 2008).

I ranked the initial set of candidate models using Akiake's Information Criterion adjusted for small sample sizes (AIC$_c$) and included all models with a ΔAIC$_c \leq 4$ as candidates for the next step in the model selection process (Anderson 2008). The next step involved adding the area of habitat, in ha, within 1 km of the sampling unit (HAB1K) as a landscape variable and sample year (YEAR) as a covariable, both separately and together, to each of the top-ranked models. I evaluated the addition of these variables by including all of the top-ranked models, with and without the additional variables, in a new model set and ranking them using AIC$_c$. I again chose all models with ΔAIC$_c \leq 4$ for inclusion in the final set of candidates for the best approximating model. I evaluated the goodness-of-fit for each model in the final set by computing the ratio of the residual deviance to the null deviance:

$$Deviance\ Explained = \left(1 - \frac{Residual\ Deviance}{Null\ Deviance}\right) * 100$$

where Deviance Explained was the amount of deviance in bobwhite occupancy, expressed as a percentage, explained by the model.

The issue of independence of sample units within a given property, and the fact that the 1-km habitat buffers overlapped on many properties, resulted in a concern about spatial dependence of the results. Therefore, I tested for an effect of spatial dependence of sample units occurring within the same property on the probability of bobwhite occupancy by using a 2-level hierarchical linear model (Crawley 2007, Royle and Dorazio 2008, Howell et al. 2009). Hierarchical modeling can be used for dealing with processes that operate at multiple spatial scales and for addressing the issue of pseudoreplication that is prominent in many ecological field studies (Crawley 2007, Royle and Dorazio 2008). I used all models with $\Delta \mathrm{AIC}_c < 4$ (see above) as my first-level models, which took the form:

$$y_{iz} \sim bernoulli(p_{iz})$$

where y_{iz} is the occupancy status of sample unit *i* in property *z*. I used the logit link function to express this as a linear model where:

$$logit(p_{iz}) = \beta_0 + \ \beta_1(x_1)_{iz} + \cdots \beta_n(x_n)_{iz}$$

where p_{iz} was the probability of sample unit *i* within property *z* being occupied by a bobwhite, β_0 was the intercept, $(x_1)_{iz} \ldots (x_n)_{iz}$ were the *n* fixed effects of local habitat variables measured for sample unit *i* within property *z*, including the amount of habitat in the 1-km buffer surrounding the sample unit, and $\beta_1 \ldots \beta_n$ were the estimated coefficients.

Next, I added a hierarchical effect of property to the model with the assumption that it modified the intercept of the first level model, and so my second level model was expressed as:

$$logit(p_{iz}) = \beta_0 + \ \beta_1(x_1)_{iz} + \cdots \beta_n(x_n)_{iz} + u_z$$

where:

$$u_z \sim N(0, \sigma_z^2)$$

where u_z was the random effect of property z that modified the overall intercept. A meaningful hierarchical effect was indicated if σ_z^2 was sufficiently >0 to have a substantial effect on β_0 (Moore et al. 2005). I compared $\Delta \mathrm{AIC}_c$ between each hierarchical model and the corresponding first-level model to determine if adding the hierarchical term improved the ranking. All statistical analyses were done using program R (R version 2.13.1, http://cran.r-project.org, accessed 1 Sep 2011).

RESULTS

Restoration Effects

Of the 23 sample units where restoration was prescribed to occur, I sampled 10 treated sample units and 13 untreated sample units in 2009, 13 treated sample units and 10 untreated sample units in 2010, and 14 treated sample units and 7 untreated sample units in 2011, for a total of 67 sample unit by year combinations. Differences in the numbers of treated and untreated sample units between years were due to ongoing habitat restoration work and removal of 2 sample units from sampling in 2011 because of loss of access to private land. Three sample units became occupied by bobwhite after undergoing restoration treatments and 2 were occupied in at least one of the years without undergoing any treatment. I found no significant effect of treatment on the probability of bobwhite occupancy ($P = 0.521$).

Habitat and Landscape Effects

I obtained habitat variables from 31 sample units (treatment and control) in 2009, 28 sample units in 2010, and 29 sample units in 2011. The difference in the number of sample units in each year was due to the loss of access to one property in 2010 before sampling habitat variables and the abandonment of 1 sample unit in 2010 due to disturbance during the sampling season. I detected bobwhites at 7, 6, and 9 sample units in 2009, 2010, and 2011, respectively. Of the 40 models compared in the initial selection procedure, there were 13 containing the PCA axis 1 variable ln(CANOPY+1), and these were the 13 top-ranked models, indicating that percent overstory canopy cover was the strongest habitat variable driving bobwhite occupancy at the sample unit level. Of these, there were 4 models with $\Delta\text{AIC}_c \leq 4$. The models ranked 1–3 also contained the linear, quadratic, and interaction term for visual obstruction, respectively. The fourth-ranked model contained the linear term for shrub cover. The top 4 models accounted for 79% of the AIC_c weight, and evidence ratios suggested substantial support for all of these models. The amount of deviance explained by the top 4 models was 39–50% (Table 1.1). The null model was ranked lowest, with $\Delta\text{AIC}_c = 44.6$.

Addition of the landscape variable for the amount of habitat within 1 km of the sample unit improved the performance of all 4 models retained from the initial model set, in that models containing this variable performed better than models that did not (Table 1.2). The addition of year, however, did not have a consistent effect on model performance. There were 5 models having $\Delta\text{AIC}_c \leq 4$. All of these models contained the landscape variable and the linear, quadratic, or interaction term for visual obstruction in addition to ln(CANOPY+1), while only 2 of these models contained year as a covariable (Table 1.2). There was a consistent negative relationship between bobwhite occupancy and ln(CANOPY+1) and a positive relationship to visual obstruction and habitat within 1 km. Year had only a minimal effect on all models in which it appeared, and did not improve the ranking of any of these models. The top 5 ranked models accounted for 87%

of the AIC_c weights. Adding the level-2 hierarchical effect showed no evidence for a random effect of property on the probability of bobwhite occupancy that was not already explained by the fixed effects, as the standard error of the intercept was at or near 0 when property was added to the top 5 selected models, and all hierarchical models were ranked lower than the corresponding model without the effect of property by $\Delta AIC_c > 2$ (Table 1.2). Thus, there was no evidence for an effect of property in my study.

A *post hoc* analysis of the main effects of overstory canopy and habitat within 1 km of the sample unit revealed a threshold response of the predicted probability of bobwhite occupancy to both variables. The probability of bobwhite occupancy increased dramatically when canopy cover fell below 60% (Fig. 1.4 A), and likewise increased when the amount of habitat within 1 km of the sample unit exceeded 150 ha (Fig. 1.4 B).

DISCUSSION

The purpose of this study was to quantify the success or failure of habitat restoration treatments for bobwhites in the context of the habitat conditions created within individual properties and the landscape surrounding them. Because most of the restoration work began prior to the initiation of monitoring, it was not possible to collect before/after data in most of these areas. Additionally, issues of time, manpower, and property access prevented me from being able to estimate bobwhite densities on the properties. Therefore, I used occupancy as the state variable of interest to determine the effect of restoration treatments and model the effects of local habitat and landscape variables. My study shows that local and landscape variables act in concert to determine the probability of bobwhite occupancy within a given sample unit, and therefore the success of habitat restoration efforts. I showed that, at the level of the 50-ha sample unit, 59% of the variation in bobwhite occupancy can be predicted by overstory canopy cover, visual obstruction, and the amount of suitable bobwhite habitat within 1 km of the sample unit. Bobwhite population dynamics are driven by many ecological factors operating at multiple spatial scales and are only partially responsive to local management activities, and so the predicted response of bobwhites to management activities is subject to uncertainty (Howell et al. 2009). If the proper conditions are not created within the appropriate landscape context, it is unlikely that habitat restoration will be successful.

The results of my habitat analysis at the local level showed that overstory canopy cover is the strongest variable determining bobwhite occupancy in the eastern Oklahoma region. I found a threshold effect of canopy cover, where the probability of bobwhite occupancy increases dramatically when canopy cover falls below 60%. Measurements of canopy cover only considered average cover within the sample unit, and did not account for the arrangement of the cover. For example, a measurement of 50% canopy cover could indicate that half of the sample unit had 100% canopy cover and half had 0% canopy cover, or that the entire sample unit was open woodland with 50% canopy cover throughout. Therefore, I have no evidence as to whether the arrangement of canopy cover affects bobwhite occupancy.

I found visual obstruction to be an important secondary variable, although in my analysis the magnitude of the effect was confounded by the level of overstory canopy cover. Within my sample units, visual obstruction was most strongly correlated with shrub cover, but showed very little correlation to overstory canopy cover. In other words, high levels of visual obstruction could occur in both closed canopy forests and open grasslands, and so the main effect of visual obstruction on bobwhite occupancy cannot be separated from overstory canopy and thus was not interpretable based on my models. My results, however, agree with those of Cram et al. (2002), who found that overstory canopy and visual obstruction are strong driving factors in the number of calling male bobwhites heard during breeding season call counts in western Arkansas. Other habitat metrics that have been found to be important for bobwhites, such as cover of grasses, litter, and bare ground (Guthery 2002), were likely not included in the best-performing models because of a correlation to visual obstruction or because of my relatively small sample size. This is not to say that these factors are not important, but rather visual obstruction was a good predictor of these other variables and/or the sample size was not large enough to differentiate their effects with enough certainty to include them in the best models as determined by AIC_c (Anderson 2008).

My analysis showed a strong effect of the amount of habitat within 1 km of the sample unit on the probability of bobwhite occupancy. My finding of a threshold effect when the amount of habitat exceeds 150 ha corresponds with those of Guthery et al. (2001), who found a similar effect when the amount of permanent cover (brushy prairie and native prairie) exceeded 50–100 ha within 800 m of a call count station, and Cram et al. (2002), who found a strong effect of the amount of usable space for bobwhites within 400 m of a sampling unit. Howell et al. (2009), in a study of bobwhite habitat restoration in Georgia, also found strong support for models containing a landscape effect of the 3-x-3-km grid in which management units were nested, although the nature of the effect was unclear.

In several bobwhite studies, researchers have used a variety of metrics to study the relationship between bobwhite abundance and landscape pattern (Guthery et al. 2001, Cram et al. 2002, Veech 2006, Twedt et al. 2007, Duren et al. 2011). Some of these metrics include percentages of various landcover types (e.g. grassland, forest, urban, etc.), number of patches of a given landcover type, length of edge between types, contagion, interspersion, and diversity. Suitable habitat area has been shown to be the main driving factor in most species declines (Fahrig 2003). Studies also have found that percent cover of a given habitat type was a better predictor of species occurrence than other more complex landscape metrics (Cunningham and Johnson 2011), and this has been found to be true specifically for bobwhites (Guthery et al. 2001, Cram et al. 2002). Cunningham and Johnson (2011), in a comparison of landscape metrics for forest birds, found that percent tree cover out-performed other metrics and was by far the most important predictor of forest bird occurrence, and suggested that this is also true for grassland bird species. Their conclusion was that, at landscape scales, other measures of landscape pattern can become redundant and that examining these other metrics may confound results (Cunningham and Johnson 2011). Thus, it appears for bobwhite, total amount of usable space is more important than the arrangement of patches across the landscape. Therefore, we chose to focus on amount of suitable habitat at larger scales.

My second-level hierarchical models did not find evidence that a random effect of the property in which a sample unit occurred influenced the probability of bobwhite occupancy beyond the fixed effects of habitat and landscape. Nevertheless, it has been hypothesized that landscape factors acting at larger spatial scales may have an impact on the long-term maintenance of local bobwhite populations (Veech 2006, Twedt et al.

2007). The fact that my hierarchical analysis at the property level did not show an effect may be due to small sample size or that measuring habitat within 1 km of the sample unit accounted for the potential effect of property. Previous studies have indicated that large-scale landscape patterns may have more to do with persistence than occupancy (Guthery et al. 2000, Twedt et al. 2007), and more detailed analyses in fragmented landscapes, using larger sample sizes, could shed more light on this issue.

It should be noted that my habitat and landscape analyses are only interpretable within the bounds of the 50-ha sample units used in the survey design. An examination of histograms of the 24 sample units containing habitat restoration polygons showed that, while the predicted landscape threshold of >150 ha was exceeded by the majority of the sampling units (Fig. 1.5 B), seldom was enough of the overstory canopy removed to meet the predicted threshold of <60% (Fig. 1.5 A). Only 4 of the 24 sample units had a predicted probability of occupancy > 0.5 according to our AIC_c best model (Fig. 1.5 C). This suggests that the majority of properties chosen for habitat restoration were within the appropriate landscape context and that the limiting factor in the success of the QHRI program in Oklahoma was the creation of sufficient habitat characteristics within the sample unit.

MANAGEMENT IMPLICATIONS

Habitat loss and fragmentation have been blamed for the decline in many bird species that rely on early-successional and grassland habitats (Brennan and Kuvlesky 2005), including bobwhite. It is now commonly accepted that the processes driving many species declines are occurring at the landscape scale, and that if conservation is going to be successful, it must focus on preserving or restoring habitat at the regional level (Askins 2000, Williams et al. 2004, Brennan and Kuvlesky 2005). This is the strategic approach adopted by the National Bobwhite Conservation Initiative (NBCI) (Dimmick et al. 2002) and attempted through programs like the QHRI. Nevertheless, sufficient habitat conditions must be restored at the local level in many areas if the desired population increases at the regional level are to be realized. The failure of the QHRI to significantly increase bobwhite occupancy within the areas designated for restoration does not appear due to errors in planning or strategy, but rather on-the-ground execution. In this case, habitat restoration polygons were generally too small and/or too isolated to be effective in increasing bobwhite occupancy. If habitat restoration is to be effective in increasing bobwhite populations, significant reductions in canopy cover must occur in areas surrounded by suitable amounts of existing habitat.

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Table 1.1 Model variables, deviation in Akiake's Infromation Criterion adjusted for small sample sizes (AIC_c) scores from the model with the lowest AIC_c score (ΔAIC_c), number of parameters in the model (K), model weight (w_i), evidence ratio (w_i/w_{max}), and the amount of deviance explained by the model expressed as a percentage, from models of the local habitat variables affecting the probability of northern bobwhite occupancy in eastern Oklahoma, USA from mid-May to late July 2009–2011. Only models with $\Delta AIC_c \leq 4$ and the null model are reported.

Variables[a]	**ΔAIC_c**	**K**	**w_i**	**Evidence Ratio**	**Deviance Explained**
ln(CANOPY)+VOBS	0	3	0.368	1.000	48.82
ln(CANOPY)+VOBS+VOBS^2	0.9	4	0.229	1.608	50.06
ln(CANOPY)*VOBS	2.2	4	0.124	2.966	48.84
ln(CANOPY)+SHRUB	3.4	3	0.067	5.527	39.41
Intercept	44.6	1	< 0.001	> 368	0.00

[a] ln(CANOPY) = log percent overstory canopy cover; VOBS = visual obstruction as an index of vegetation height; SHRUB = percent shrub cover

Table 1.2 Model variables, deviation in Akiake's Infromation Criterion adjusted for small sample sizes (AIC_c) scores from the model with the lowest AIC_c score (ΔAIC_c), number of parameters in the model (K), model weight (w_i), evidence ratio (w_i/w_{max}), amount of deviance explained by the model expressed as a percentage, variance of the intercept in the second-level hierarchical model when allowed to vary based on the property where the sampling unit occurred (s^2 Int.), and the difference in the AIC_c score between the hierarchical and first-level models (ΔAIC_c*), for models containing the habitat, landscape, and year variables effecting the probability of northern bobwhite occupancy in eastern Oklahoma, USA from mid-May to late July 2009–2011.

	First Level					**Hierarchical**	
Variables[a]	**ΔAIC_c**	**K**	**w_i**	**Evidence Ratio**	**Deviance Explained**	**s^2 Int.**	**ΔAIC_c***
ln(CANOPY)+VOBS +HAB1K	0	4	0.337	1.00	57.978	9.938E-14	2.2
ln(CANOPY)+VOBS + $VOBS^2$+HAB1K	0.7	5	0.233	1.44	59.487	2.493E-12	2.3
ln(CANOPY)*VOBS +HAB1K	2.2	5	0.110	3.07	57.978	0.000	2.3
ln(CANOPY)+VOBS +HAB1K+YEAR	2.3	6	0.105	3.22	60.177	1.512E-18	2.4
ln(CANOPY)+VOBS + $VOBS^2$+HAB1K+YEAR	2.8	7	0.081	4.16	62.020	0.000	2.5

[a] ln(CANOPY) = log percent overstory canopy cover; VOBS = visual obstruction as an index of vegetation height; HAB1K = amount of potential bobwhite habitat, computed from the 2006 National Land Cover Database, within 1 km of the edge of the sample unit; YEAR = year in which sampling occurred.

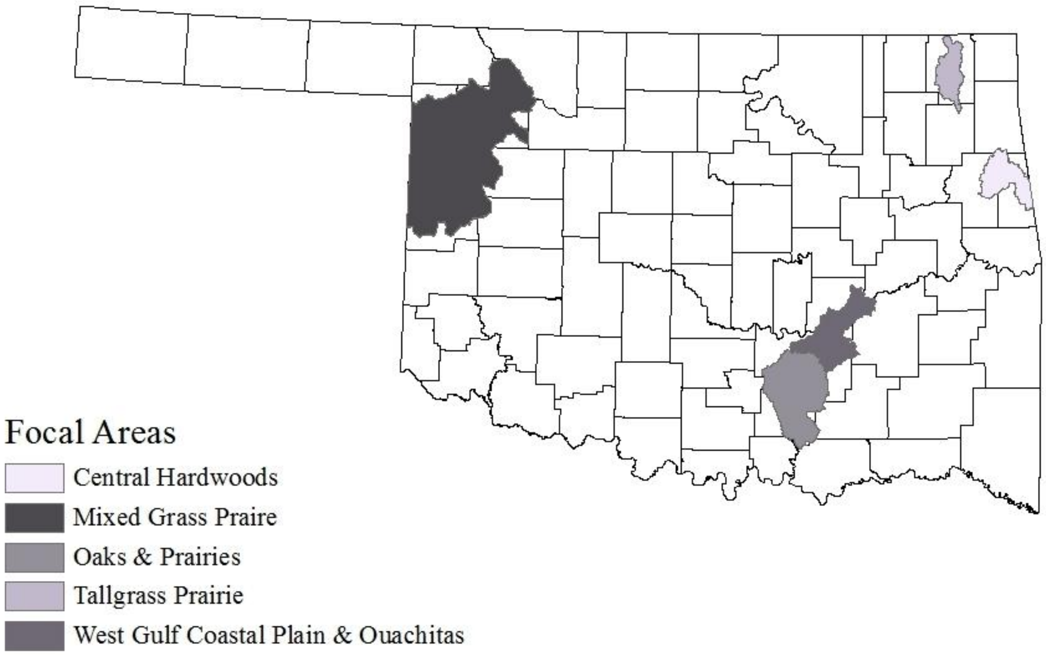

Figure 1.1 Focal areas designated by the Oklahoma Department of Wildlife Conservation for northern bobwhite (*Colinus virginianus*) habitat restoration through the Quail Habitat Restoration Initiative.

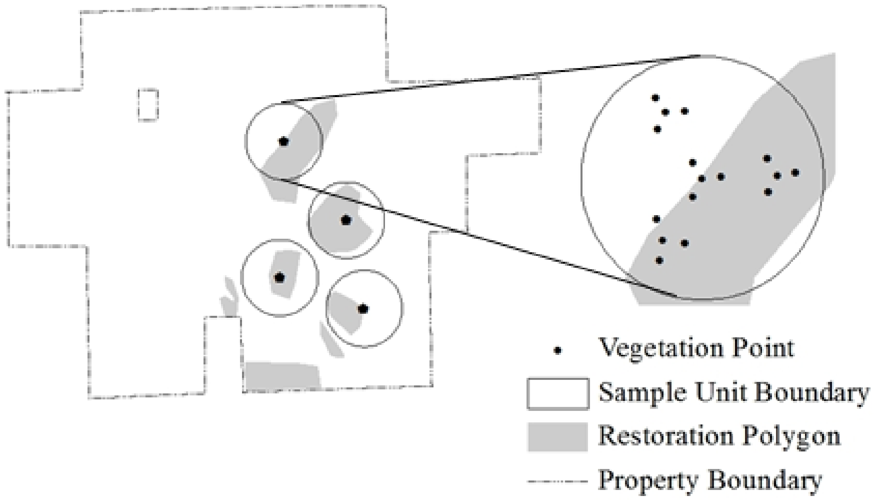

Figure 1.2 Placement of 400-m-radius sample units and systematically located vegetation sampling points for northern bobwhite (*Colinus virginianus*) and habitat surveys in eastern Oklahoma, USA, from mid-May to late July (2009–2011). Clusters of vegetation points were located at the center of each sample unit and 250 m from the center at angles of 90°, 210°, and 330°.

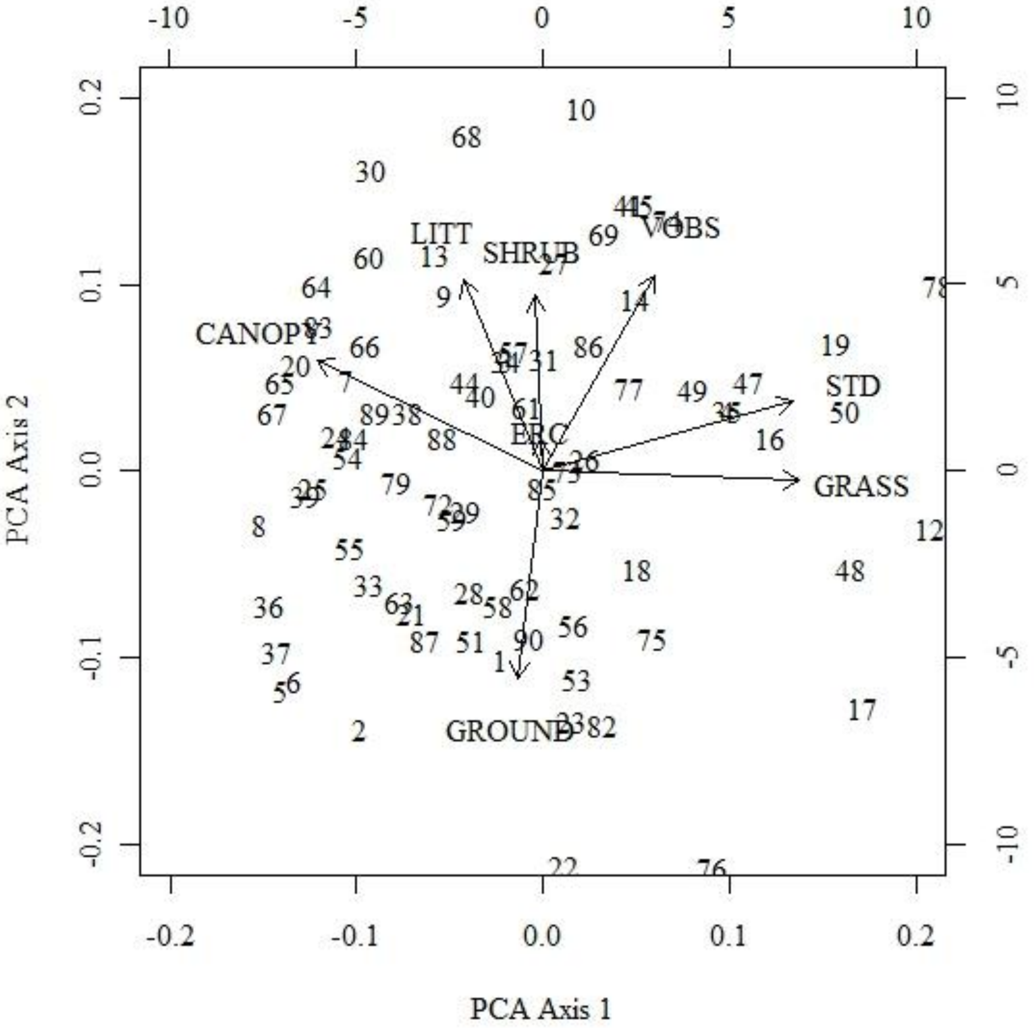

Figure 1.3 Principal Components Analysis (PCA) biplot of habitat variables measured for each northern bobwhite (*Colinus virginianus*) sample unit in eastern Oklahoma, USA (2009–2011). Numbers represent individual observations (each sample unit in each year), and arrows represent the correlation of each variable to the PCA axis. Variables tested were: % overestory canopycover (CANOPY), % grass cover (GRASS), % bare ground (GROUND), % litter cover (LITT), % woody cover < 2 m high (SHRUB), visual obstruction as an index of vegetation height (VOBS) and % cover of Eastern Redcedar (ERC).

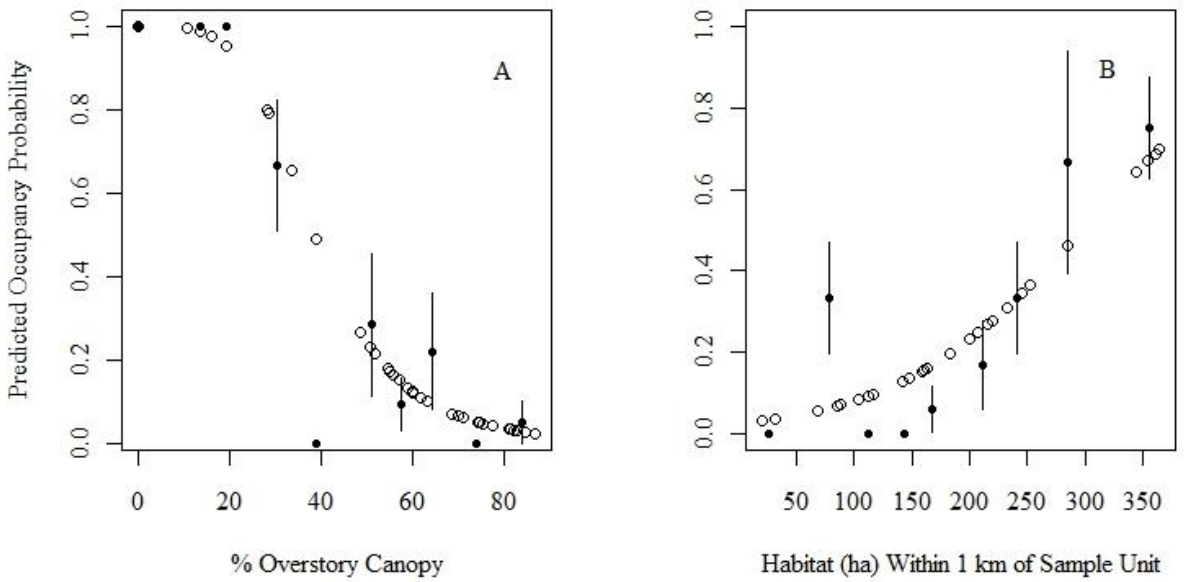

Figure 1.4 The main effects of the back-transformed log of percent overstory canopy cover (A) and the amount of habitat within 1 km of each sampling unit (B) on the predicted probability of bobwhite occurrence within a sample unit from eastern and central Oklahoma, USA (2009–2011). Open circles represent the predicted probabilities for each sampling unit in each year; closed circles rperesent empirically derived probabilities with standard error bars.

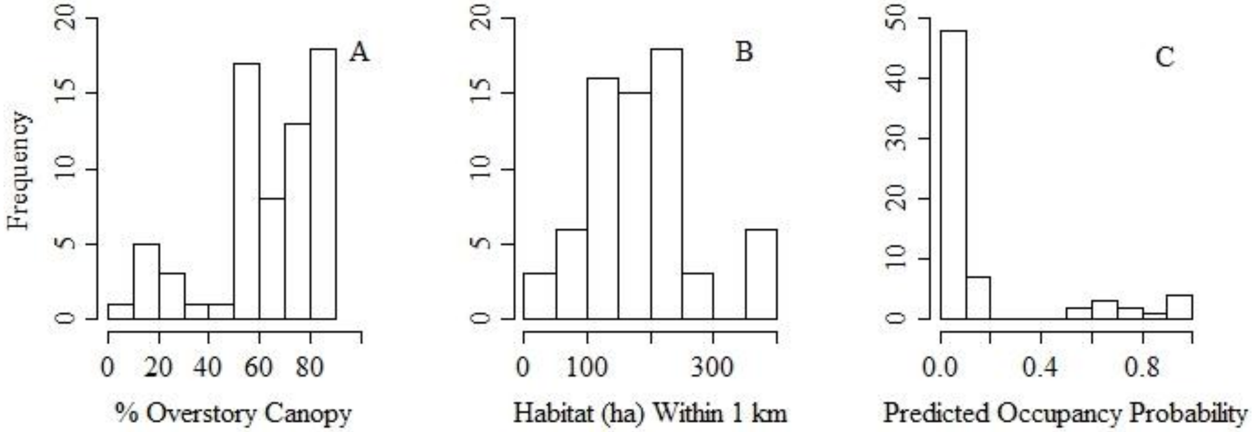

Figure 1.5 Histograms of habitat conditions (A), landscape context (B), and occupancy probability (C) for 67 sample unit (each 50 ha) by year combination containing areas designated for habitat restoration treatments in eastern Oklahoma, USA (2009–2011).

CHAPTER II

BIRD COMMUNITY EFFECTS OF HABITAT RESTORATION FOR NORTHERN BOBWHITES

ABSTRACT Range-wide declines in northern bobwhite (*Colinus virginianus*, hereafter bobwhite) populations have prompted efforts to restore habitat for this socially and economically important game bird across large areas of the landscape. Large-scale habitat restoration for bobwhites is likely to have positive effects on other bird species that rely on early-successional habitats. To assess effects of habitat restoration for bobwhites, I surveyed bird communities and habitat variables in areas of habitat restoration and control areas in eastern Oklahoma, USA in 2009–2011. I used multivariate community analysis and linear regression to identify specific habitat gradients related to habitat restoration that affected bird community composition, assess the effects of those gradients, and define species groups associated with the habitat variables. I found overstory canopy cover to be the dominant variable effecting bird community composition within my sample units, with visual obstruction acting as a strong secondary variable. Species groupings where bobwhite was dominant also included brushy prairie and grassland bird species as codominants. My research confirms that bobwhites may act as an umbrella species in the conservation of declining grassland and shrubland obligate bird species in Oklahoma.

INTRODUCTION

In the Cross Timbers and central hardwoods regions of eastern Oklahoma, frequent fires formerly maintained habitat for many bird species that rely on early-successional habitats such as grasslands and shrublands (Foti and Glenn 1990, Bidwell et al. 2002). In recent decades, however, human activity and secession of fire, and the consequent conversion of large areas of grasslands and open woodlands into closed-canopy forest, have caused a substantial reduction in early-successional habitats in Oklahoma and throughout the southeastern United States (Brennan 1991, Bidwell et al. 2002, Brennan and Kuvlesky 2005). As a result, many species of grassland birds have undergone significant declines in abundance in this region (Brennan and Kuvlesky 2005, Sauer et al. 2011). These declines include the northern bobwhite (hereafter bobwhite), a socially and economically important game bird whose restoration is considered important to many hunters and wildlife managers (Brennan 1991, Williams et al. 2004). The Quail Habitat Restoration Initiative (QHRI) in Oklahoma is a program initiated by the Oklahoma Department of Wildlife Conservation (ODWC) to restore bobwhite populations throughout the state. This 5-year program began in 2008 through the U.S. Department of Agriculture’s Environmental Quality Incentive Program (EQIP) to provide cost-share for private landowners to restore bobwhite habitat on their properties. The primary restoration activities are overstory tree removal and prescribed fire to create the early-successional habitat that bobwhites rely on. Because it focuses on the large-scale restoration of these habitats, the QHRI has the potential to cause changes in the overall bird community. Specifically, restoration is likely to have positive effects on the abundance of other grassland and shrubland obligate bird species and negative impacts to forest obligates.

Bird community composition has been shown to change along ecological gradients related to overstory canopy cover and understory vegetation structure (Wilson et al. 1995, Chapman et al. 2004, Brawn 2006, Au et al. 2008, Coppedge et al. 2008). The effect of overstory canopy cover on individual bird species is well documented (Annand and Thompson 1997, Brawn 2006, Cunningham and Johnson 2006), and threshold effects of overstory canopy cover on forest bird extinction, colonization, and persistence have been demonstrated (Zuckerberg and Porter 2010). Grassland and shrub/scrub birds have also been shown to respond to variations in vertical and horizontal vegetation structure that can be controlled by management activities such as grazing and prescribed fire (Wilson et al. 1995, Chapman et al. 2004, Fuhlendorf et al. 2006, Coppedge et al. 2008). Studies of the response of birds to overstory canopy cover have generally focused on individual bird species responses in an environment that is either mainly forest or mainly grassland. Effects of changes in habitat characteristics on the bird community as a whole, in the context of the transition from forest to grassland, have not been well investigated outside of the oak savannas of the midwestern United States (Davis et al. 2000, Brawn 2006, Au et al. 2008)

To evaluate effects of habitat restoration for bobwhites on bird community composition, I monitored birds within sample units on QHRI restoration areas and control areas in the central hardwoods and Cross Timbers regions of eastern Oklahoma. My objectives were to describe the change in the composition of the bird community along ecological gradients related to bobwhite habitat restoration, test for a non-linear response of bird community composition to overstory canopy cover, and ascertain which bird species are positively affected by habitat restoration for bobwhites. The potential for bobwhites to act as an umbrella species for other grassland and shrubland birds could lend weight to the justification for spending limited conservation money on habitat restoration for this species (Lambeck 1997).

STUDY AREA

To implement the QHRI, the ODWC established focal areas within the state that were deemed to have good potential for increasing bobwhite populations through habitat restoration. Focal areas were designated according to the Bird Conservation Region (BCR) in which they occurred, as established by the North American Bird Conservation Initiative (Fitzpatrick 2002) and a modeling analysis based on bobwhite habitat (Sams 2006). Landowners within the focal areas were enrolled in the program and restoration activities prescribed. I limited this analysis to 3 focal areas in eastern Oklahoma: Central Hardwoods (CH; Cherokee and Adair counties), West Gulf Coastal Plains and Ouachitas (WG; Coal and Hughes counties), and Oaks and Prairies (OP; Pontotoc and Johnston counties), because these areas represented a transitional zone between forest and prairie where habitat restoration is likely to have the biggest effect on declining grassland bird species.

The CH area has rolling topography and is dominated by oak (*Quercus* spp.) and hickory (*Carya* spp.) forests interspersed with areas of native and introduced pasture, hayfield, and row crops. The WG and OP areas are characterized by a mosaic of tallgrass prairie and cross timbers forest. Dominant tree species are post oak (*Q.stellata*.), blackjack oak (*Q. marilandica*) and hickories, and the most prominent grasses include big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), and indiangrass (*Sorghastrum nutans*). The main land uses in the all three focal areas are ranching and row-crop agriculture (Natural Resource Conservation Service 2012).

Among the properties enrolled within the 3 eastern focal areas, there were 55 management units that received restoration treatments. These management units ranged in size from < 1 ha to 192 ha, with 50% being <2 ha in size and 78% <5 ha. There were 38 management units totaling 135 ha in the CH focal area, 16 management units totaling 325 ha in the WG focal area, and 1 management unit totaling 57 ha in the OP focal area. Treatments included various amounts of overstory tree removal, prescribed fire, and reseeding with native warm-season grasses.

METHODS

Study Design and Site Selection

This analysis was part of a larger study evaluating the effectiveness of habitat restoration in increasing bobwhite populations within QHRI management units. Because of the necessity to specifically sample habitat restoration areas, study site selection was not random. To describe the relationship between bobwhite habitat restoration and bird community composition, I conducted bird community surveys concurrently with bobwhite surveys within sample units located in portions of the enrolled properties where bobwhite habitat restoration was prescribed to occur, and in control areas where no restoration would take place. Control areas were either in closed canopy forest with some small areas of prairie or in areas of early-successional habitat with small clumps of trees, ensuring that our sample units covered the full range of natural upland habitat types. Each sample unit was a 400-m-radius circle covering ~ 50 ha and was large enough to survey one or more management units designated for restoration. I did not include agricultural fields or human development in any of the sample units. In 2009, I established 31 sample units, 10 of which contained management units that had already received restoration treatments, 14 that had not yet received restoration treatments, and 7 that were designated as controls. Three additional sample units had received treatments by the 2010 breeding season, and 2 more were treated by 2011.

Bird and Habitat Surveys

I used standard avian point counts (Ralph et al. 1995) to survey the bird community by systematically locating 4 100-m-radius point count stations within each sample unit, with the initial station being in the center of the unit and 3 others located 250 m from the center at 90°, 210°, and 330°. This design ensured that all parts of the sample unit were represented and the spacing ensured that point count stations within a sample unit were independent of each other (Ralph et al. 1995). I conducted 2–3 point counts at each station during the breeding season (May–July) in 2009–2011, recording all birds seen or heard within 100 m of the station during a 5-min period. I began sampling 30 min before sunrise and continued until 4.5 hr after sunrise. I did not sample while it was raining or when wind speeds exceeded 20 kph (Winter et al. 2005). I grouped sample units based on geographic proximity and surveyed one group per day, alternating the order in which they were surveyed to avoid detection bias due to time of day. I collapsed all data into presence/absence in each sample unit in each year and used sample unit by year combinations as the basic unit for analysis because habitat restoration activities were ongoing, which would cause alterations in habitat from one year to the next and likely effect bird community composition.

To measure habitat characteristics, I systematically located 4 vegetation sampling points within the 100-m area defined by each point count station in a design modified from Wilson et al. (1995) and Smith et al. (2008). I used a Global Positioning System (GPS) unit to locate the initial vegetation point at the center of the point count station and 3 additional points 63 m away from the initial point at angles of 90°, 210°, and 330°. I measured percent overstory canopy cover at each point in 2009 using a hemispheric camera and WinSCANOPY canopy analysis software (Regents Instruments Inc., Canada). Canopy was re-measured in subsequent years (2010–2011) only if coverage had changed due to fire or other restoration activities. To avoid including ground-level vegetation in the photograph, I placed the camera on a tripod and took photos from a height of 1 m above the ground. From each vegetation point I extended a 20-m transect in a random direction. At 5, 10, 15, and 20 m along the transect I estimated percent coverage of grass using a 1-m^2 quadrat (Daubenmire 1959). I used the coefficient of variation of grass cover (CVGRASS) as an index of horizontal structure (Chapman et al. 2004). The coefficient of variation is a standardized measurement used to compare the amount of variation in populations with different means (Sokal and Rohlf 1969), and was used here as a measure of the variability in grass cover within sample units. My measurement of CVGRASS was the standard deviation divided by the mean of grass cover from all vegetation points within the sample unit, expressed as a decimal.

Along the same transect, I also measured visual obstruction (VOBS) at 10 and 20 m using a profile board (Guthery et al. 1981). My metric of visual obstruction was the average of the visual obstruction values from each stratum of the profile board (Harrell and Fuhlendorf 2002) and was used as an index of vertical habitat structure (Chapman et al. 2004). I also measured percent shrub cover (SHRUB) along the entire transect using the line-intercept method (Canfield 1941), as modified by Harrell and Fuhlendorf (2002). The transect measurements were taken each year that point counts were done (2009–2011). I averaged all vegetation points within each sample unit to describe habitat conditions within that unit for each individual year.

Statistical Analysis

I used canonical correspondence analysis (CCA) within the program CANOCO v4.5 to assess the influence of habitat structure (CANOPY, CVGRASS, VOBS, and SHRUB) on bird community composition. CCA is a constrained ordination technique that presents the ordination axes as linear combinations of the weighted sums of the measured habitat variables (Lepš and Šmilauer 2003, Chapman et al. 2004). I downweighted the influence of rare species and included year and focal area as covariables in partial CCA (pCCA) to reduce their influence on the analysis as recommended by Lepš and Šmilauer (2003). In a CCA biplot, the correlation of a species to a vector representing a habitat variable is indicated by the species' location in ordination space relative to that variable (Palmer 1993). Species that are closer together in ordination space also have similar habitat requirements. We tested the significance of the relationship of habitat variables to bird community composition using 9,999 (the maximum allowed by CANOCO software) Monte Carlo permutations (Lepš and Šmilauer 2003). I excluded raptors (*Families: Accipitridae, Cathartidae, Falconidae, Strigidae*) and large corvids (*Corvus* spp.) from the analysis because their large home ranges and ubiquitous distribution may cause them to be unreliable as habitat or community indicators.

I tested for a non-linear response of bird community composition to overstory canopy cover by calculating an index of bird community composition in each sample unit and then regressing the index against models for CANOPY (Chapman et al. 2004). I used partial detrended correspondence analysis (pDCA) in CANOCO v4.5 , where year and focal area were added as covariables, to compute the axis 1 site scores for community composition and used these scores as the index of community composition (Chapman et al. 2004). Detrended correspondence analysis is an unconstrained ordination technique that shows changes in community composition along environmental gradients (Lepš and Šmilauer 2003). The axis 1 site scores reflect differences in the community in relation to the strongest environmental influence. I created 3 linear regression models using the linear, quadratic, and log of CANOPY. I interpreted a P-value < 0.05 to mean that there was a significant relationship between the variable CANOPY and the axis 1 site scores. I compared the 3 models using Akiake's Information Criterion adjusted for small sample sizes (AIC_c) and interpreted a $\Delta AIC_c > 4$ to mean that one model was significantly better than the other (Anderson 2008). I considered that higher AIC_c rankings for the quadratic and logarithmic models over the linear model would indicate support for a non-linear relationship.

I used cluster analysis (k-means partitioning) to identify groups of sample units with similar bird community composition (Berg 2002, Borcard et al. 2011). K-means partitioning uses an iterative process that calculates the Euclidean distances between sample sites within a pre-defined number of groups (k), then sums the squares of the distances within each group and divides them by the number of species in that group, with the objective of finding the grouping that minimizes the total sum of the squares from all groups combined (Borcard et al. 2011). I transformed data using a chi-square transformation, which is appropriate for computing Euclidean distances based on presence/absence data (Borcard et al. 2011). I used the CASCADEKM command from the package VEGAN within program R (R version 2.13.1, http://cran.r-project.org, accessed 1 Sep 2011) to test models with 2–10 groups using 10000 permutations. My criterion for choosing the optimum number of groups was the number with the maximum Simple Structure Index (SSI) (Borcard et al. 2011). For this part of the analysis, species with <10 total detections over the 3-year period were considered incidental and were eliminated from analysis.

RESULTS

I surveyed 31 sample units in 2009, 30 in 2010, and 29 in 2011 resulting in 90 sample unit by year combinations. Differences in the number of samples in each year was the result of restoration activities in one sample unit during the breeding season (2010) and loss of access to one of the properties (2011). Histograms of habitat variables within sample units for all years showed that 50% of surveys occurred in sample units with CANOPY > 60% with the other 50% ranging from 0–10% to 50–60%, while the range of VOBS was distributed normally among the sample units and SHRUB and CVGRASS were slightly right-skewed (Fig. 2.1). Palmer (1993) found that CCA is robust to skewed distributions of habitat gradients and that DCA showed only slight distortions, mostly along the second axis, and so skewed distributions were not considered an issue in the analysis.

Bird community composition was correlated with both CANOPY and VOBS among my study sites (Fig. 2.2). CANOPY was the variable most strongly correlated with axis 1 of the pCCA, indicating that it is the main variable defining bird community composition within my sample units. VOBS was orthogonal to CANOPY, which suggests that vertical habitat structure strongly affects community composition beyond the effects of overstory canopy (Fig. 2.2). CVGRASS was more highly correlated with axis 1 than VOBS, and VOBS and SHRUB were highly correlated with each other. Axis 1 explained 65% of the variance in the species-habitat relationship, and axes 1 and 2 combined explained 88%. Forward selection of the variables showed that CANOPY explained the largest amount of variation in the data ($F = 8.57$, $P \leq 0.001$).

Inspection of the pCCA graph (Fig. 2.2) shows shrubland specialists such as bobwhite, bell's vireo (*Vireo bellii*), and dicksissel (*Spiza americana*) were clustered together and correlated with low levels of canopy cover, while their position towards the middle of axis 2 correlated with moderate levels of visual obstruction and shrub cover. At the same time, shrub scrub species such as white-eyed vireo (*Vireo griseus*) and yellow-breasted chat (*Icteria virens*) were clustered around the middle of axis 1 but towards the lower end of axis 2, correlated with moderate levels of canopy cover (axis 1 scores near 0) and higher levels of visual obstruction and shrub cover.

Regression of the pDCA axis 1 site scores against CANOPY revealed a strong relationship between bird community composition and overstory canopy cover ($P \leq 0.001$). AIC$_c$ showed strong support for both the quadratic and logarithmic models, giving evidence for a non-linear relationship between canopy cover and community composition (Fig. 2.3). The quadratic model was selected as the AIC$_c$ best, but model selection also showed strong support for the logarithmic model ($\Delta AIC_c = 1.8$). There was little support for the linear model over the others ($\Delta AIC_c = 6.2$ for the linear model).

After eliminating incidental species from the analysis, there were 50 species included in the k-means cluster analysis. The results suggested 4 main groupings based on the maximum SSI criterion and the dominant species within each group. These grouping were: Forest, Forest/Scrub, Brushy Prairie, and Grassland (Table 2.1). The Forest and Forest/Scrub groups were similar in CANOPY, VOBS, and SHRUB and shared several bird species (Table 2.2, Fig. 2.4); however, the Forest/Scrub group contained several shrub/scrub species such as painted bunting (*Passerina ciris*), field sparrow (*Spizella pusilla*), and white-eyed vireo (*Vireo griseus*) that did not appear in the Forest group. CVGRASS was higher in the Forest than in the Forest/Scrub group, indicating higher variability in grass cover among sample units within this group. Bobwhite occurred as a dominant species in both the Brushy Prairie and Grassland groups but was ranked higher and had a higher mean index of abundance in Brushy Prairie (Table 2.1). Declining grassland and shrubland obligate species occurring with bobwhites were bell's vireo (*Vireo bellii*), dicksissel, lark sparrow (*Chondestes grammacus*), rufous-crowned sparrow (*Aimophila ruficeps*), grasshopper sparrow (*Ammodramus savannarum*), painted bunting, and eastern meadowlark (*Sturnella magna*). The mean of CANOPY was lower in both the Brushy Prairie and Grassland group than in the other 2 groups, and VOBS and SHRUB were slightly lower in Grassland than in Brushy Prairie (Table 2.2, Fig. 2.4).

DISCUSSION

Variation in the extent of restoration activities on individual properties enrolled in the QHRI, mainly in the level of overstory canopy removal, has resulted in gradients in habitat among areas designated for restoration from closed canopy forest to brushy prairie and open grassland. This fact provided an opportunity to study the response of the bird community to gradients of overstory canopy cover and understory vegetation structure related to bobwhite habitat restoration. My results confirm that habitat restoration for bobwhites can have a strong positive effect on many grassland bird species in Oklahoma and show multiple lines of evidence pointing to the fact that bird community composition begins to shift from forest and shrub/scrub birds to brushy prairie and grassland birds when overstory canopy cover falls below 60%. Numerous other studies have shown that tree cover is an important influence on individual bird species (e.g. Wilson et al. 1995, Brawn 2006, Cunningham and Johnson 2006, Zuckerberg and Porter 2010), but I know of none that has tested for a non-linear relationship between overstory canopy cover and community composition. Bird community composition is also affected by understory vegetation structure and heterogeneity (Chapman et al. 2004, Fuhlendorf et al. 2006), but these appear to be secondary to overstory canopy cover in eastern Oklahoma.

Overstory canopy cover is clearly the main influence on bird community composition among the natural upland habitats included in my investigation. Other studies in naturally heterogeneous landscapes have shown similar results for communities and individual species alike (Cram et al. 2002, Cunningham and Johnson 2006, Au et al. 2008). Au et al. (2008) found strong relationships between percent canopy cover and an index of community composition in savanna and oak woodland habitats in central

Minnesota, USA, but they did not test for a non-linear relationship. They did, however, separate oak forest from savanna habitats at 65% canopy cover and found significant differences based on habitat type. The change in community composition indicated by my results did not relate to a sharp breakpoint in the index but a gradual increase in the slope of the line when canopy cover fell below 60%, according to the top-ranked quadratic model (Fig. 2.3). Painted bunting, generally considered a shrub/scrub species occurred as a dominant in all groups except Forest, but was most dominant in the Forest/Scrub group which also included forest species such as red-eyed vireo (*Vireo olivaceus*) and white-breasted nuthatch (*Sitta carolinensis*) as co-dominants, so clearly there is not a sharp boundary between the habitat types. In contrast to my results, bobwhites have been found in areas with canopy cover close to 70% in pine-bluestem habitats in western Arkansas and eastern Oklahoma, USA (Wilson et al. 1995, Cram et al. 2002), which suggests that individual response to habitat may be different based on the specific type of habitat involved for some bird species.

Among my sample units overstory canopy cover, visual obstruction, and shrub cover did not differ appreciably between Forest and Forest/Scrub in the cluster analysis. Effects of visual obstruction and shrub cover on community composition were strongly evident in the pCCA across the range of overstory canopy cover, and they showed in the difference between Brushy Prairie and Grassland in the cluster analysis, in contrast to Forest and Forest/Scrub. The fact that Forest and Forest/Scrub were very similar in these habitat variables but had different bird communities suggests that there is another variable affecting the community composition that was not considered in my analysis. This variable may be related to the arrangement of habitat patches on the landscape, which has been shown to effect bird community composition in heterogeneous habitats (Herkert 1994, Helzer and Jelinski 1999, Coppedge et al. 2001). Horizontal structure (CVGRASS) was marginally correlated with overstory canopy and visual obstruction in the pCCA, and was also much higher in Forest than Forest/Scrub in the cluster analysis, but I could not interpret this in ecological terms.

Bird communities of shrubland and grassland habitats showed sensitivity to vertical vegetation structure in the pCCA and cluster analysis. This is consistent with the findings of other researchers (Wilson et al. 1995, Cram et al. 2002, Chapman et al. 2004). The reason for these differences in vegetation structure is almost certainly related to management actions such as grazing and prescribed fire, which have been shown to effect both species composition and structure of grassland habitats (Fuhlendorf et al. 2006, Derner et al. 2009). Au et al. (2008) found distinct differences in bird community composition between oak savannas in Minnesota that had been restored through mechanical tree removal and prescribed fire and those that had used mechanical thinning alone, with no fire. As in my study, they did not measure species composition of the vegetative community and considered that this, along with the structural heterogeneity created by fire, may have had an effect on the difference.

Of the 14 shrubland and grassland species that were grouped with bobwhites in the Brushy Prairie and Grassland groups, 11 have been declining in one or more of the Bird Conservation Regions involved in my study (Sauer et al. 2011). Of these, the only one considered to be a species of special conservation need in Oklahoma is Bell’s vireo (Sams 2006). Further, Wilson et al. (1995) found that shrub/scrub birds such as prairie warbler (*Dendroica discolor*) and yellow-breasted chat (*Icteria virens*) had higher densities in areas that had been treated for the endangered red-cockaded woodpeckers (*Picoides borealis*) in pine-bluestem communities in Arkansas, which also favored bobwhites in that region. Relatedly, it is clear from my results that habitat restoration for bobwhites can improve conditions for some declining grassland and shrubland obligate bird species.

Not all species that might be predicted to occur with bobwhite were found to be related. For example the red-headed woodpecker (*Melanerpes erythrocephalus*), considered a species of greatest conservation need in Oklahoma, did not appear to be associated with bobwhites habitats in either the pCCA or the cluster analysis. Considered to be a bird of open woodlands and savannas that is dependent on disturbance-maintained ecosystems (Smith et al. 2000, Brawn 2006, Au et al. 2008), my cluster analysis results grouped it in the Forest habitat. In contrast, Wilson et al. (1995) found this species only in burned areas associated with pine–bluestem community restoration in Arkansas, and Brawn (2006), in a study in Illinois, found that red-headed woodpecker was the most important species for differentiating restored oak savanna from closed forest. My results may be due to the fact that burning was rarely used in the restoration treatments within my sample units, and thus the standing dead trees required by this species were not created (Smith et al. 2000). Of the 9 sample units where this species was detected, 6 had received prescribed fire as part of the treatment and all were in either the Forest or Forest/Scrub group. It is likely that mechanical removal of trees alone does not create the habitat conditions necessary for this species and that some sort of disturbance, such as prescribed fire or herbicide treatment that creates standing dead timber, is required for the red-headed woodpecker to thrive (Smith et al. 2000).

MANAGEMENT IMPLICATIONS

The potential for the bobwhite to act as an umbrella species for other grassland and shrubland birds is clearly demonstrated by my results. The threshold level of canopy cover for bobwhites of 60% (see Chapter 1) is also relevant to changes in bird community composition from woodland and forest species to those of shrubland and grassland. Bobwhite habitat restoration in the Cross Timbers and central hardwoods regions of Oklahoma has the potential to create the structurally diverse, early-successional habitats that will support declining bird species reliant on grassland and brushy prairie. Thus, the focus of programs like the QHRI on restoring early-successional habitat over large areas of the landscape may prove to be effective in stemming the decline of grassland and shrubland bird species.

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Table 2.1 Species and mean abundance index (based on a chi-square transformation of presence/absence data) for the 10 most dominant species within species groups defined by k-means cluster analysis for bird surveys conducted from May–July in eastern Oklahoma (2009–2011).

Forest		**Forest/Scrub**		**Brushy Prairie**		**Grassland**	
Spp	$\bar{x}$	**Spp**	$\bar{x}$	**Spp**	$\bar{x}$	**Spp**	$\bar{x}$
Northern Parula	0.40	Painted Bunting	0.28	Bewick's Wren	0.54	Grasshopper Sparrow	1.56
Acadian Flycatcher	0.29	Northern Cardinal	0.26	Brown Thrasher	0.49	Eastern Meadowlark	0.76
Red-eyed Vireo	0.28	Great-crested Flycatcher	0.26	Lark Sparrow	0.49	Northern Mockingbird	0.76
Summer Tanager	0.26	Tufted Titmouse	0.25	Northern Mockingbird	0.46	Dicksissel	0.59
Eastern Wood-pewee	0.25	Carolina Wren	0.25	Rufous-crowned Sparrow	0.43	Eastern Bluebird	0.58
Indigo Bunting	0.25	Indigo Bunting	0.25	Northern Bobwhite	0.42	Northern Cardinal	0.35
Blue-gray Gnatcatcher	0.24	Blue-gray Gnatcatcher	0.25	Bell's Vireo	0.42	Blue Jay	0.35
Pine Warbler	0.24	Carolina Chickadee	0.23	Painted Bunting	0.36	Tufted Titmouse	0.35
Yellow-throated Vireo	0.23	Field Sparrow	0.23	Field Sparrow	0.36	Northern Bobwhite	0.34
Brown-headed Cowbird	0.23	Yellow-billed Cuckoo	0.22	Northern Cardinal	0.32	Painted Bunting	0.31

Table 2.2 Means and 95% confidence intervals for habitat variables within each species grouping, as defined by k-means cluster analysis, on bird community data collected from mid-May to late July in eastern Oklahoma (2009–2011).

	Habitat Variables							
	CANOPY[a]		**CVGRASS**[b]		**SHRUB**[c]		**VOBS**[d]	
Species Group	$\bar{x}$	**95% CI**	$\bar{x}$	**95% CI**	$\bar{x}$	**95% CI**	$\bar{x}$	**95% CI**
Forest	0.684	(0.617−0.752)	1.370	(1.088−1.652)	0.153	(0.116−0.190)	0.370	(0.309−0.432)
Forest/Scrub	0.653	(0.617−0.752)	0.980	(0.891−1.071)	0.156	(0.122−0.191)	0.421	(0.378−0.463)
Brushy Prairie	0.245	(0.617−0.752)	0.749	(0.626−0.872)	0.105	(0.038−0.172)	0.348	(0.236−0.461)
Grassland	0.142	(0.617−0.752)	0.640	(0.203−1.076)	0.057	(-0.006−0.120)	0.244	(0.063−0.242)

[a] Overstory canopy cover.

[b] Coefficient of variation of grass cover ($\mathit{standard\ deviation}_{GRASS}/\mathit{mean}_{GRASS}$).

[c] Shrub cover.

[d] Visual obstruction.

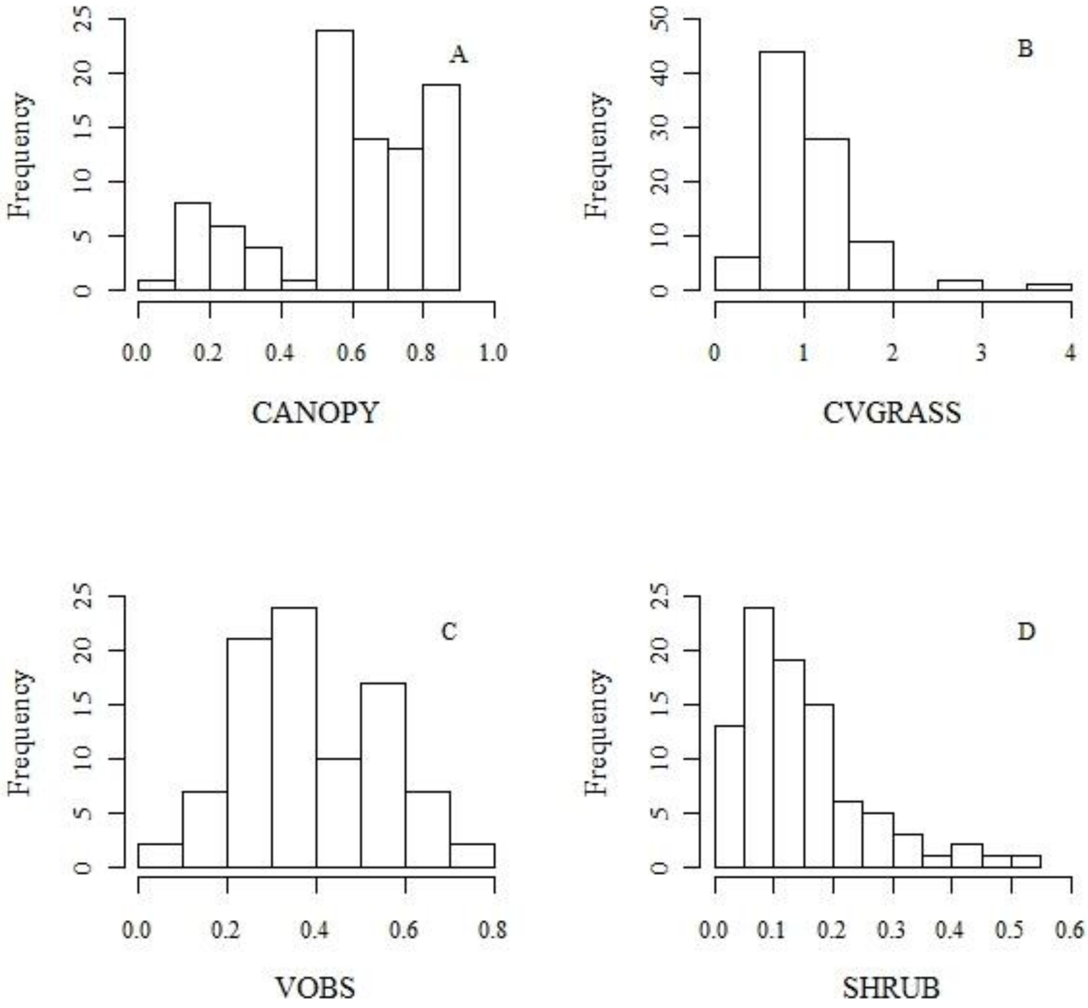

Figure 2.1 Histograms of the frequency of sample unit by year combinations with levels of (A) overstory canopy cover, (B) coefficient of variation of grass cover, (C) visual obstruction, and (D) percent shrub cover, evaluated for bird community analysis in eastern Oklahoma, USA (2009–2011).

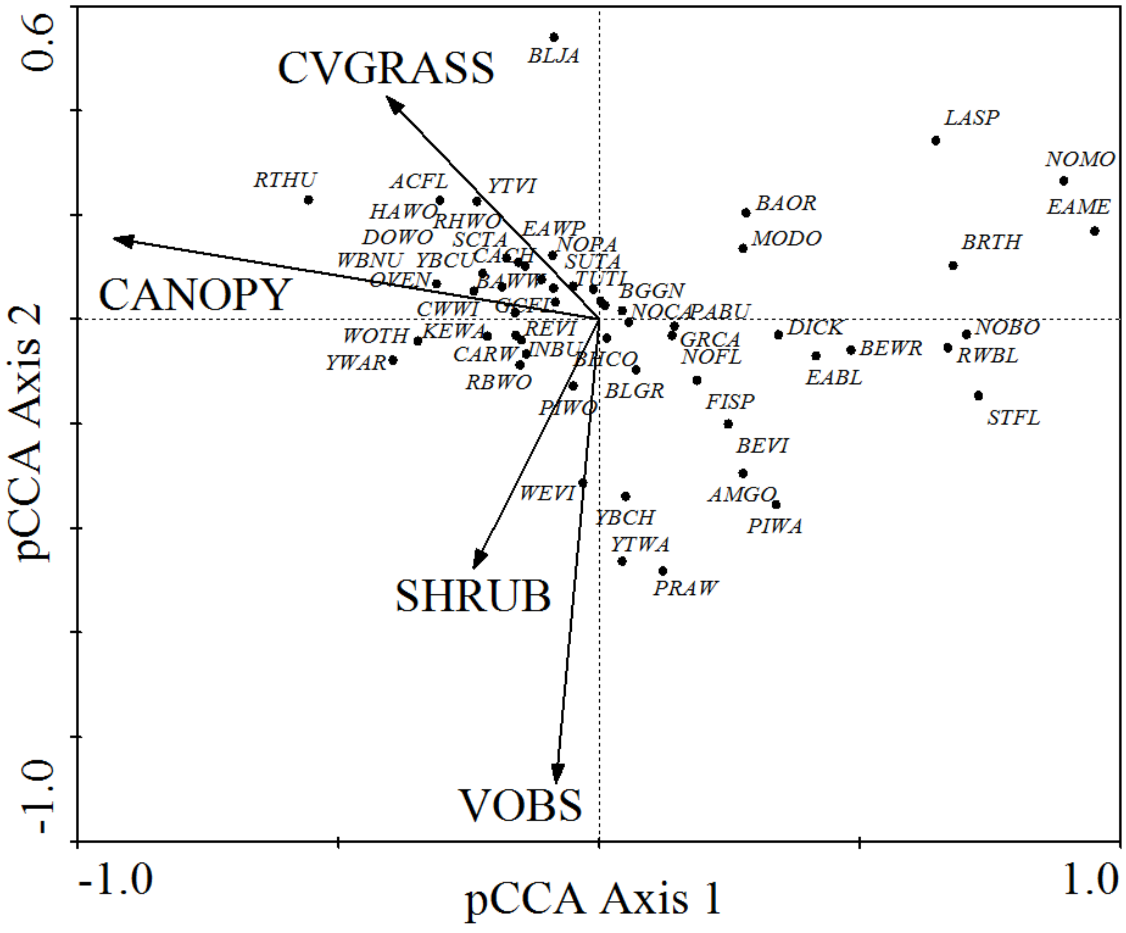

Figure 2.2 Partial canonical correspondence analysis (pCCA) bi-plot of bird species and environmental variables from bird community data collected in eastern Oklahoma from May–July (2009–2011), using year and focal area as covariables. Direction of a vector indicates its correlation with an axis, and length indicates its importance. CANOPY: percent overstory canopy cover; VOBS: visual obstruction; CVGRASS: coefficient of variation of percent grass cover; SHRUB: percent shrub cover. Species codes follow American Ornithologists Union (AOU) convention.

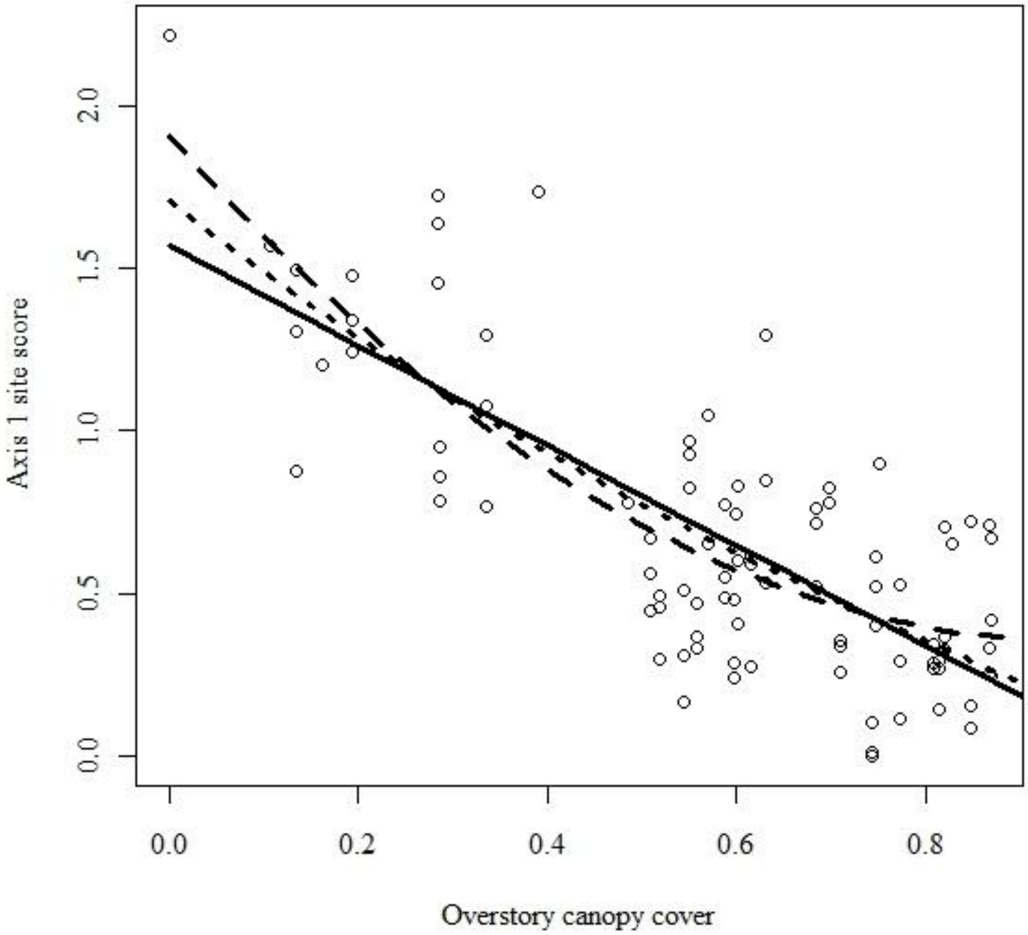

Figure 2.3 Plot of overstory canopy cover versus axis 1 site scores from partial detrended correspondence analysis (pDCA) of bird community composition at 90 sample unit by year combinations in eastern Oklahoma from May–July (2009–2011) using year and focal area as covariables, and predicted scores from the linear, logarithmic, and quadratic models of overstory canopy cover. The solid line represents the linear model, the short dashes represent the logarithmic model, and the long dashes represent the quadratic model.

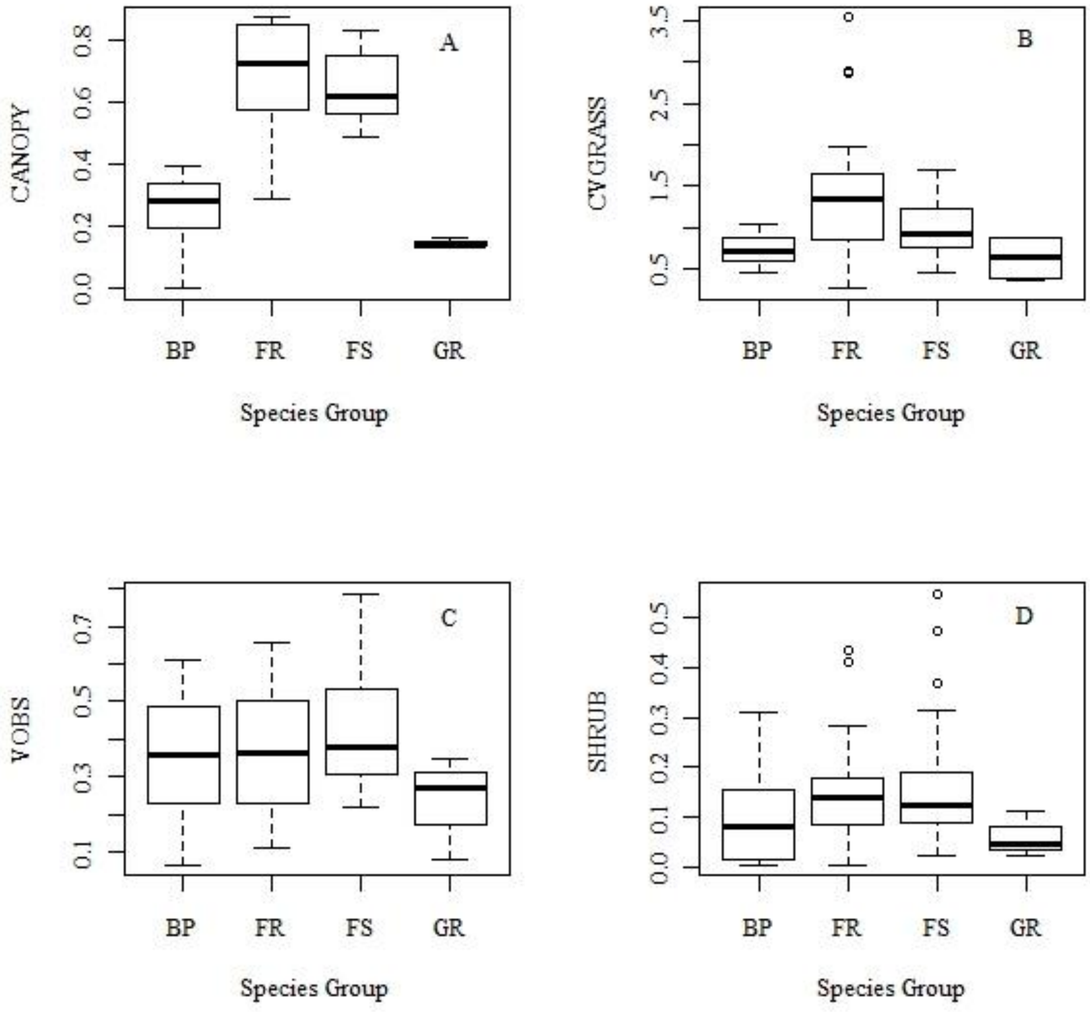

Figure 2.4. Box-and-whisker plots of (A) overstory canopy cover, (B) coefficient of variation of grass cover, (C) visual obstruction, and (D) percent shrub cover within bird species groups defined by k-means cluster analysis on bird community data from surveys done May–July in eastern Oklahoma (2009–2011). The thick horizontal bar represents the median, the box represents the first and third quartiles, and the dashed lines show either the maximum range of the data or 1.5 times the interquartile range, whichever is smaller.

CHAPTER III

THE EFFECT OF ABUNDANCE AND SURVEY PROTOCOL ON OCCUPANCY ESTIMATES FOR NORTHERN BOBWHITES IN OKLAHOMA

ABSTRACT One of the biggest challenges in management for northern bobwhites (*Colinus virginianus*, hereafter bobwhite) has been the collection of reliable, long-term data on population changes. Occupancy-based models allow inferences about populations based on presence-absence data rather than counts. Nevertheless, the failure to account for false absences can negatively bias results of these surveys. New methods for modeling occupancy allow for explicit accounting of the probability of a false absence in the model while also incorporating site- and survey-specific variables, resulting in more accurate estimates of species occurrence. I compared estimates of occupancy from survey protocols using 1, 2, and 3 sampling occasions per year, both with and without accounting for detection probability, between an area where bobwhites were common and an area where they were uncommon. My results showed significant increases in estimates of occupancy when >1 sampling occasion per year was used, and that in areas where bobwhites are uncommon estimates of occupancy may be biased low if the analysis does not account for detection probability.

INTRODUCTION

Many long-term monitoring programs for northern bobwhites (hereafter bobwhite) use the number of calling males heard as an index of bobwhite abundance. Additionally, many published reports of bobwhite population dynamics rely on the number of calling males heard during breeding bird survey (BBS) or state-run surveys as their source of data (Church et al. 1993, Lusk et al. 2002, Veech 2006, Twedt et al. 2007, Spinola and Gates 2008). Unfortunately, there is no well-defined relationship between the number of bobwhites heard during a call-count survey and the actual number of bobwhites in the population (Hansen and Guthery 2001), and such surveys are normally conducted only once per year and do not take into account the probability of failing to detect bobwhites even when they are present (Veech 2006). The number of bobwhites heard on a given survey, and indeed the probability of detecting even a single individual, can vary substantially due to survey-specific factors such as time of year, time of day, cloud cover, temperature, and wind speed (Hansen and Guthery 2001), as well as by simple random chance. Given the deficiencies in using call-counts as an index of bobwhite abundance, it may be useful to consider an alternative state variable (the metric used to describe the state of the population at a given point in time [(MacKenzie et al. 2006)]) in monitoring efforts aimed at detecting changes in bobwhite populations. Proportion of area occupied (PAO), or occupancy, is commonly used as the state variable of interest in monitoring efforts for various species (Zielinski and Stauffer 1996, Trenham et al. 2003, Rhodes et al. 2006), and may offer such an alternative.

Proportion of area occupied is defined as the proportion of the area or sample sites under study occupied by the species of interest (MacKenzie et al. 2006) and is often estimated from repeated or unrepeated presence-absence surveys. Estimates of occupancy can also be derived from other types of surveys, such as point counts or call counts that were originally aimed at estimating either actual or relative abundance. Traditionally, estimates of occupancy assume that when a species is not detected at a given site it is absent from that site (Mackenzie and Royle 2005, MacKenzie et al. 2006), and the estimate of PAO is simply the proportion of sites where the species was detected. This method does not take into account the possibility that the species was present but not detected (a “false absence”), and consequently the PAO estimate may be biased low (MacKenzie et al. 2002). When a species is common and/or easily detected, the chance of getting a false absence is low and therefore traditional surveys that do not account for detection probability may be appropriate. However, when a species is rare and/or not easily detected, the probability of getting a false absence will be much higher and consequently the PAO estimate will be biased low if detection probability, defined as the probability of detecting a species given that it is present, is not accounted for (MacKenzie et al. 2005). Even species such as bobwhites, which are normally considered easy to detect, may have lower detection probabilities in areas where they are uncommon.

Theoretical advances over the last decade have addressed the issue of estimating occupancy when detection probabilities are <1 (MacKenzie et al. 2002, MacKenzie 2005, MacKenzie et al. 2006). The methods that have been developed use repeat visits to survey sites to estimate the probability of detection (p) of the target species with the goal of estimating the proportion of sites that are occupied (ψ) knowing that the species can be present but go undetected (Bailey et al. 2004).

In the context of this analysis, I will use the term “occupancy modeling” to refer to the method introduced by MacKenzie (2002), and the term “presence-absence” to refer to the traditional method that does not account for detection probability. I wished to explore whether in certain cases occupancy modeling may give substantially different estimates of PAO whereas in others the simpler presence-absence method of estimation might be adequate. An investigation of when occupancy modeling may be the appropriate method for estimating PAO would be useful to wildlife managers and researchers seeking the most efficient method for predicting bobwhite occurrence or monitoring changes in the population.

The objectives of this analysis were to compare estimates of occupancy (ψ) and probability of detection (p) from both standard presence-absence surveys and occupancy models, using both single- and multiple-survey protocols, in an area where bobwhites are common and an area where bobwhites are uncommon. Additionally, I wanted to determine how time during the breeding season affected probability of detection. I hypothesized that: 1) protocols where each sample site was surveyed multiple times would have significantly higher estimates of ψ than those that were surveyed only once for both areas, 2) estimates of p would be much higher in areas where bobwhites are common than where they are uncommon, and 3) estimates of p would change significantly as the breeding season advanced.

STUDY AREA

My study was conducted in portions of Oklahoma, USA, in areas where bobwhite populations have been declining (eastern Oklahoma) and where they have remained stable (western Oklahoma) over recent decades (Figure 3.1; Sauer et al. 2007). The eastern area consisted of portions of Adair, Cherokee, Hughes, Coal, Johnston, and Pontotoc counties. These areas are characterized by a mosaic of tallgrass prairie and cross-timbers or central hardwoods forest (Duck and Fletcher 1943). Dominant tree species are oaks (*Quercus* spp.) and hickories (*Carya* spp.), and the most prominent grasses include big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), and indiangrass (*Sorghastrum nutans*). The main land uses in the region are ranching and row-crop agriculture (Natural Resource Conservation Service 2012). Bobwhite populations in this region have decreased at a rate of >1.5% per year between 1966 and 2003 (Sauer et al. 2011).

The western area contained portions of Ellis and Dewey counties and is a characteristic sand-shinnery oak plant community. Vegetation is dominated by shinnery oak (*Quercus havardii*), which is a low-growing clonal shrub, sand sagebrush (*Artemisia filifolia*), and grasses and forbs such as little bluestem, indiangrass, and western ragweed (*Ambrosia psilostachya*). Land use is mainly ranching and row-crop agriculture (Natural Resource Conservation Service 2012). Bobwhite populations in this region remained stable between 1966 and 2006 (Sauer et al. 2007).

METHODS

Bobwhite Surveys

My study was conducted mainly on private properties where habitat restoration for bobwhites was scheduled to take place via the Environmental Quality Incentives Program (EQIP). In the eastern portion of the study area, there were select areas scheduled for restoration on small, isolated properties, and this precluded a random placement of study sites. Therefore, I subjectively located sample sites in these areas and added control sites so that I could survey the range of habitat types from closed-canopy forest to open prairie. I sampled 31 sites in this area in 2009, 30 in 2010, and 29 in 2011. Properties in the western study area were large enough to allow for the random location of sample sites. I sampled 27 sites in this area in 2009 and 2010, and 26 sites in 2011.

Each sample site consisted of a point from which call-counts were conducted for bobwhites within a 400-m radius (Stoddard 1931, Hansen and Guthery 2001). I conducted surveys at each point 3 times during the breeding season (mid-May–late July) at intervals of 2–3 weeks in 2009–2011. Each survey consisted of a 5-min call-count, done between 0.5 hr before sunrise and 4.5 hr after sunrise, where all bobwhites heard within 400 m during the survey were recorded. I did not survey when it was raining or when wind speeds exceeded 20 km per hr (Ralph et al. 1995).

PAO Estimation and Survey-specific p

My methods in this study were similar those used by Bailey et al. (2004) in an assessment of occupancy and detection probabilities for salamanders in the eastern United States. For the purposes of the analysis, I began with the assumption that probabilities of occupancy and detection were constant across times and sites, $\psi(.)p(.)$. Although this constant model is not necessarily the most accurate representation of the system, as my objective was to compare the impacts of different sampling protocols on the parameters of interest the inclusion of additional variables may have confounded my results (Bailey et al. 2004). Occupancy modeling is based on closed-population capture-recapture methods and therefore assumes that sample sites are closed to changes in occupancy status during the course of the surveys (MacKenzie et al. 2006). Given the limited movements of bobwhites during the breeding season (Fies et al. 2002, Townsend et al. 2003, Lohr et al. 2011), it was reasonable to assume that sample sites would not be colonized or abandoned during the survey period. For all statistical comparisons, I split the data into 2 categories and analyzed each category separately. The western area represented a region where bobwhites were common, and the eastern area represented a region where bobwhites were uncommon. These areas will be referred to as “western” and “eastern,” respectively, for the remainder of this manuscript. I treated year as a random variable, and thus combined data for all years (Mark Payton, Oklahoma State University, personal communication).

I compared estimates of ψ and p using 3 different “sampling protocols” reflecting different survey intensities (1, 2, or 3 surveys per season), and 2 different estimation procedures for ψ (listed below). In order to simulate the different survey intensities, I randomly selected first one and then 2 of the survey occasions from each sampling unit in each year to represent the 1-survey and 2-survey protocols, respectively. All 3 sampling occasions combined were used to represent the 3-survey protocol. I estimated: ψ(obs), a “naïve” estimate of occupancy that does not account for detection probability, using 1, 2, and 3 sampling occasions per year; and $\psi(.)$ and $p(.)$ from occupancy models accounting for detection probability using both 2 and 3 sampling occasions. My estimate of the precision of $\psi(.)$ and $p(.)$ was [SE(estimate)/estimate] (Bailey et al. 2004). I calculated ψ(obs) from each protocol separately between the 2 areas and compared the results using

McNemar’s Chi-square test for paired samples (Conover 1999). I compared $p(.)$ between the 2 areas using a Chi-square test on proportions.

Additionally, I assumed that probability of detection would vary within the breeding season as a function of day, and thus I modeled probability of detection based on Julian day, where each day of the year is assigned a consecutive number with 1 corresponding to January first. I compared this model to the model assuming probability of detection to be constant, $p(\text{day})$ to $p(.)$, using Akaike’s Information Criterion (AIC) (Anderson 2008). Estimations of ψ and p, as well as AIC model comparison, was done using program PRESENCE (Presence Version 4.0, http://www.mbr-pwrc.usgs.gov/software/presence.html, accessed 4 Apr 2011). I conducted all other statistical analyses using program R (R version 2.13.1, http://cran.r-project.org, accessed 1 Sep 2011).

RESULTS

From 2009 to 2011, I detected bobwhites on 96 out of 174 sampling occasions at 58 individual survey sites. Twenty-one of these detections occurred in the area where bobwhites were uncommon (east) and 75 occurred in the area where they were common (west). Results from the standard presence-absence analysis showed that $\psi(\text{obs})$ increased substantially as survey intensity increased (Table 3.1). The McNemar’s test showed statistically significant increases between 1 survey and 2 or 3 surveys, but not between 2 and 3 surveys for both areas. In areas where bobwhites were uncommon, $\psi(\text{obs})$ increased by 201% between the 1-survey and 3-survey protocols ($P \leq 0.001$), but only increased by 16.5% between the 2-survey and 3-survey protocols ($P = 0.248$).

Results were similar but less drastic in the western focal area, with an increase in ψ(obs) of 32% between the 1-survey and 3-survey protocols ($P \leq 0.001$) and an increase of 4% between the 2-survey and 3-survey protocols ($P = 0.480$).

Comparison of $\hat{\psi}(.)$ to ψ(obs) showed different results between the eastern and western survey areas. When comparisons were done using the 3-survey protocol there was a 31% increase in the estimate of $\psi(.)$ in the eastern area but an increase of only 1.9% in the western area. Estimates of $p(.)$ were significantly higher in the western area than in the eastern area ($P < 0.05$), and showed a marked difference between the 2-survey and 3-survey protocols in the eastern area (Table 3.1). Of note is the extremely low $\hat{p}(.)$ for the 2-survey protocol resulting in an extremely high estimate of $\psi(.)$ (Table 3.1). Differences in the estimates of $\psi(.)$ between the 2-survey 3-survey protocols were nearly identical in the western area, where $\hat{p}(.)$ was also significantly higher (Table 3.1). Precision for both $\hat{\psi}(.)$ and $\hat{p}(.)$ were considered good, with [SE(estimate)/estimate] < 0.23 (Bailey et al. 2004), except for the 2-survey protocol in the eastern area ([SE(estimate)/estimate] = 0.897).

Comparison of the model using Julian day as a survey-specific variable, $\psi(.)p(\text{day})$, to the constant model, $\psi(.)p(.)$, indicated that the $\psi(.)p(\text{day})$ model was much better at describing the data (ΔAIC = 11.17). The plot of Julian day vs. $\hat{p}$ showed a large increase in detection probability as the breeding season advanced (Figure 3.2).

DISCUSSION

My results indicate that survey protocols using more than one sampling occasion per year are important in obtaining good estimates of bobwhite occupancy and, particularly in areas where bobwhites are uncommon, estimates may be biased very low if the analysis does not account for detection probability. Hansen and Guthery (2001) came to the same conclusion about using call counts as an index of abundance. This would seem to indicate that studies of bobwhites where call counts are done only once per year likely give unreliable estimates of the state of the population. Duren (2010), in a study that developed a landscape-based occupancy model for bobwhites in the eastern United States, may have encountered this problem in trying to test the model using BBS data. Occupancy estimated from the BBS data was likely biased low because of the lack of repeat surveys, and this might have confounded the predictive ability of the model (Duren 2010). Thus, the issue of detectability must be taken into account when designing surveys aimed at describing the state of a population or detecting changes in that population.

Monitoring programs that seek to establish the status of a population and detect changes over time can use either of 3 state variables: 1) abundance, 2) an index of abundance such as raw counts of calling male birds, and 3) occupancy (Hansen and Guthery 2001, Manley et al. 2004, MacKenzie et al. 2006, Johnson 2008). The choice of which state variable to use depends on the system under study, the specific objectives of the program, and the resources available (Bailey et al. 2004, Mackenzie and Royle 2005, MacKenzie et al. 2006). Getting good estimates of abundance can be very costly in terms of both time and money, and indexes of abundance may not be a reflection of actual abundance (Hansen and Guthery 2001, Bailey et al. 2004). Estimates of occupancy are generally much less costly to obtain than abundance estimates (Manley et al. 2004), and may be a more reliable alternative metric to the call-count index for monitoring trends in bobwhite populations.

In the case of bobwhites, values of ψ(obs) based on only 1 or 2 sampling occasions may seriously underestimate the proportion of area occupied. Especially in areas where bobwhites are uncommon, detections probabilities can be so low that 2 surveys will not give an accurate estimate even when accounting for this factor. MacKenzie et al. (2002) and Baily et al. (2004) both found that detection probabilities <0.15 can yield unreasonable estimates of occupancy, and their findings were consistent with my results for the 2-survey protocol in the area where bobwhites were uncommon. Using 3 surveys in this area increased the estimate of p(.) and reduced the standard error and estimate of accuracy. Conversely, in the area where bobwhites were common there was a much smaller difference in estimates of ψ(obs), ψ(.), and p(.) between the 2-survey and 3-survey protocols, although there was a large increase in ψ(obs) when using multiple surveys instead of just one.

Maximizing detection probabilities is important in increasing the reliability and utility of occupancy models, and it is better to deal with the issue of low detection probabilities through design-based approaches rather than by increasing the complexity of models (Royle 2006). One possible way to increase detection probabilities for bobwhites is by sampling during peak calling periods. In testing this, my results agree with those of Hansen and Guthery (2001) showing that detection probabilities vary temporally throughout the breeding season. Therefore, considering time during the breeding season may be a more efficient way to increase detection probabilities as opposed to adding more survey occasions, but this should be carefully evaluated before sampling is begun.

Some studies have shown that local density may be the most important source of differences in detection probability between different sample sites or areas (Royle and Nichols 2003, Smith et al. 2007). It would seem to follow that the probability of detecting a single individual increases as local density increases (Bailey et al. 2004). My results clearly indicate that this might be true, but the relationship of $\hat{\psi}$ and $\hat{p}$ to abundance of bobwhites is undefined and researchers should use caution in relating these metrics to actual abundance. On the other hand, the greater detection probability that I found in the area where bobwhites were common shows that estimates of p based on multiple survey occasions are likely a good predictor of relative abundance.

In deciding whether to use occupancy as the state variable of interest in a monitoring program, the question that must be asked is whether changes in occupancy reflect actual changes in the population. It is probable that changes in the estimate of bobwhite occupancy are reflecting changes in the amount of usable space for bobwhites (Guthery 1997). It has been shown that the total amount of usable space is likely the main factor in determining bobwhite abundance (Guthery et al. 2001, Cram et al. 2002, Veech 2006, Twedt et al. 2007). Therefore, a significant change in usable space should result in a change in the estimates of occupancy, and thus be a reliable estimate of trends in bobwhite populations.

MANAGEMENT IMPLICATIONS

Using occupancy as the state-variable of interest for detecting changes in bobwhite populations is a viable alternative to the call-count index, but occupancy may be seriously underestimated if probability of detection is not accounted for, particularly in areas where the species in uncommon. Sampling protocols in areas where bobwhites are uncommon should include ≥3 sampling occasion per year so that detection probability can be estimated with a high degree of confidence and then used to improve estimates of occupancy. Additionally, sampling design should be carefully considered. In my study, surveys conducted later in the breeding season (June and July) had higher detection probabilities. This may vary by location. I suggest that occupancy modeling may be particularly appropriate in areas where bobwhites are uncommon because low detection probabilities will have a much larger effect on estimates of occupancy in these locations. The accuracy of the estimates can likely be improved by the addition to the models of site- and survey- specific variables and testing the predictive ability of the models on independent datasets.

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Table 3.1 Occupancy estimates calculated from presence absence data [ψ(obs)], and estimates of occupancy [ψ(.)] and detection probability [p(.)]and their associated standard errors from occupancy models, using 1, 2, and 3 survey occasions per year for northern bobwhites in an area where they were uncommon (Eastern) and an area where they were common (Western) in Oklahoma, USA (2009–2011).

	Area	**ψ(obs)**						
One Survey[a]	Eastern	0.075					**Precision[b]**	
	Western	0.711	**ψ(.)**	**SE**	**p(.)**	**SE**	**ψ(.)**	**p(.)**
Two Surveys	Eastern	0.194	0.9704	0.87	0.105	0.097	0.897	0.924
	Western	0.901	0.997	0.046	0.708	0.047	0.046	0.066
Three Surveys	Eastern	0.226	0.296	0.066	0.396	0.082	0.223	0.207
	Western	0.938	0.956	0.028	0.732	0.032	0.029	0.044

[a] *p* cannot be estimated from only one survey occasion, so only the *ψ(obs)* values were calculated.

[b] Precision = [SE(estimate)/estimate]

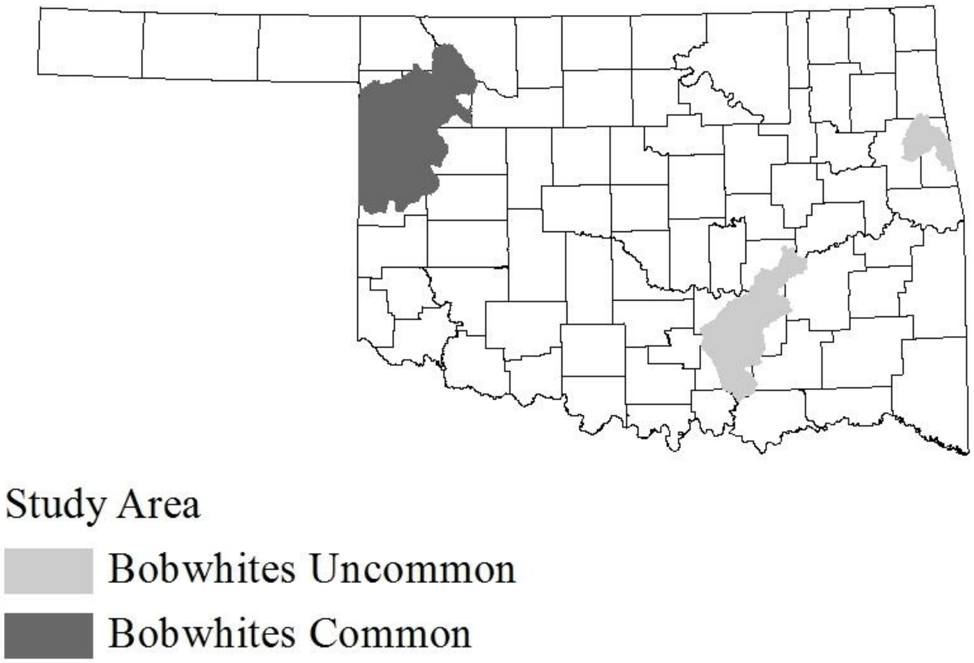

Figure 3.1 Study area where Northern bobwhite surveys were conducted from 2009-2011 in an area where they were common and an area where they were uncommon in Oklahoma, USA.

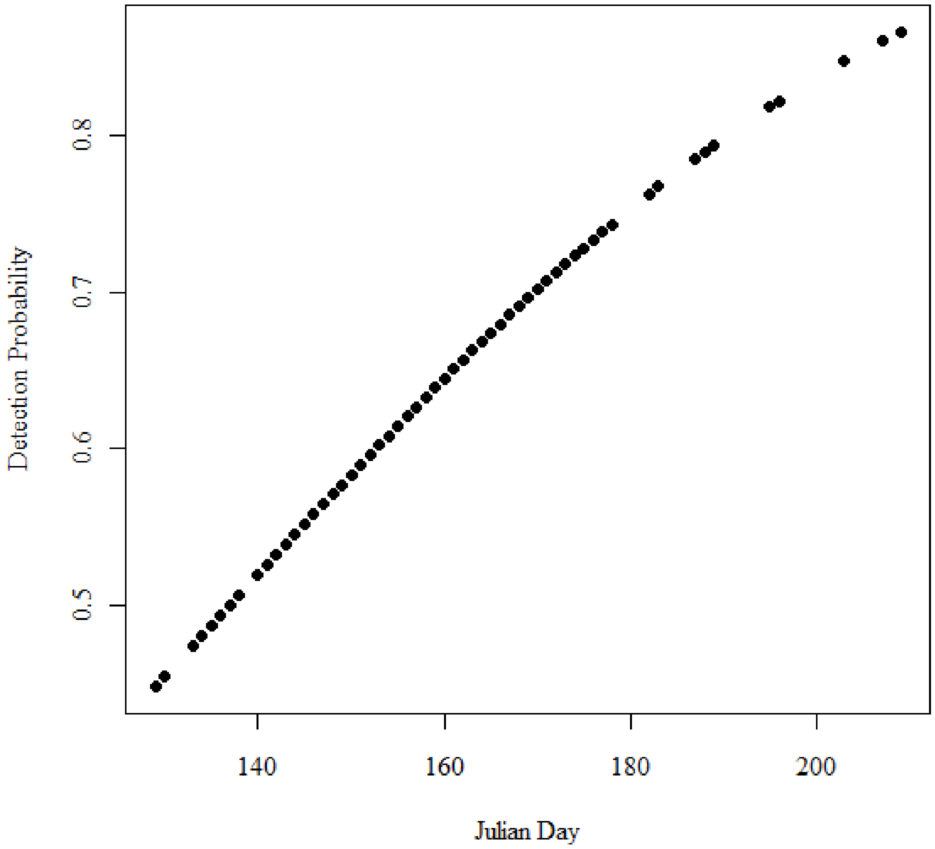

Figure 3.2 Predicted detection probabilities for Northern bobwhite call count surveys as a function of Julian day in Oklahoma, USA, (2009–2011).

APPENDIX A

Table A.1. Species and mean within-group abundance index (based on chi-square transformation of presence/absence data) for species groups defined by k-means cluster analysis from surveys done May–July in eastern Oklahoma (2009–2011). FR=Forest, FS=Forest/Scrub, BP=Brushy Prairie, and GR=Grassland. Bold numbers indicate species mean > group mean within each group.

	Mean within-group Abundance Index			
Species	**FR**	**FS**	**BP**	**GR**
Acadian Flycatcher	**0.29**	0.01	0.00	0.00
Bell's Vireo	0.00	0.06	**0.42**	0.00
Bewick's Wren	0.01	0.07	**0.54**	0.00
Black-and-white Warbler	**0.21**	**0.19**	0.10	0.09
Blue Grossbeak	**0.19**	**0.19**	**0.10**	**0.20**
Blue Jay	**0.15**	0.06	0.06	**0.35**
Blue-grey Gnatcatcher	**0.24**	**0.25**	0.30	0.15
Brown Thrasher	0.02	0.05	**0.49**	0.00
Brown-headed Cowbird	**0.23**	**0.22**	**0.22**	0.07
Carolina Chickadee	0.07	**0.23**	**0.17**	0.09
Carolina Wren	**0.18**	**0.25**	0.05	0.09

Table A.1 Continued

	Mean within-group Abundance Index			
Species	**FR**	**FS**	**BP**	**GR**
Cassin's Sparrow	0.00	0.00	**0.23**	0.00
Chuck-will's Widow	0.05	0.12	0.00	**0.22**
Common Yellowthroat	0.12	0.00	0.00	0.00
Dicksissel	0.03	0.12	**0.15**	**0.59**
Downy Woodpecker	**0.16**	**0.14**	0.04	0.12
Eastern Bluebird	0.09	0.06	0.00	**0.58**
Eastern Meadowlark	0.07	0.01	**0.30**	**0.76**
Eastern Wood Pewee	**0.25**	0.11	0.04	**0.18**
Field Sparrow	0.12	**0.23**	**0.36**	0.16
Grasshopper Sparrow	0.00	0.00	0.00	**1.56**
Gray Catbird	**0.14**	0.09	**0.19**	0.00
Great-crested Flycatcher	**0.15**	**0.26**	0.09	**0.17**
Indigo Bunting	**0.25**	**0.25**	0.06	0.00
Kentucky Warbler	**0.14**	0.12	0.00	0.00
Lark Sparrow	0.02	0.06	**0.49**	0.16
Mourning Dove	0.10	0.06	**0.30**	0.00
Northern Bobwhite	0.05	0.03	**0.42**	**0.34**
Northern Cardinal	**0.17**	**0.26**	**0.32**	**0.35**
Northern Mockingbird	0.01	0.05	**0.46**	**0.76**
Northern Parula	**0.40**	0.04	0.00	0.00
Painted Bunting	0.03	**0.28**	**0.36**	**0.31**
Pileated Woodpecker	**0.16**	0.12	0.00	0.00

Table A.1 Continued

	Mean within-group Abundance Index			
Species	**FR**	**FS**	**BP**	**GR**
Pine Warbler	**0.24**	0.00	0.00	0.00
Prairie Warbler	**0.15**	0.02	0.00	0.00
Red-bellied Woodpecker	**0.16**	**0.14**	0.04	0.00
Red-eyed Vireo	**0.28**	**0.20**	0.05	0.00
Red-headed Woodpecker	**0.16**	0.05	0.00	0.00
Ruby-throated Hummingbird	0.10	0.08	0.00	0.00
Rufous-crowned Sparrow	0.00	0.00	**0.43**	0.00
Summer Tanager	**0.26**	**0.21**	0.10	**0.25**
Tufted Titmouse	**0.21**	**0.25**	**0.22**	**0.35**
Whitebreasted Nuthatch	**0.14**	**0.18**	0.00	0.00
White-eyed Vireo	0.12	**0.20**	**0.17**	0.00
Wood Thrush	0.00	**0.14**	0.00	0.00
Yellow Warbler	0.04	0.11	0.00	0.00
Yellow-billed Cuckoo	**0.15**	**0.22**	0.06	**0.19**
Yellow-breasted Chat	**0.15**	0.07	**0.16**	0.00
Yellow-throated Vireo	**0.23**	0.09	0.00	0.00
Yellow-throated Warbler	**0.15**	0.06	0.00	0.00

APPENDIX B

Table B.1. Bird pecies and number of detections in each focal area in each year for surveys done May–July in eastern Oklahoma (2009–2011). Focal area codes are as follows: CH=Central Hardwoods, WGCPO=West Gulf Coastal Plains and Ouachitas, and OP=Oaks and Prairies.

	CH			**WGCPO**			**OP**		
Species	**2009**	**2010**	**2011**	**2009**	**2010**	**2011**	**2009**	**2010**	**2011**
Acadian Flycatcher	8	9	8	1					
American Crow		1		1		1			
American Goldfinch	3	3	2						
American Robin	2	2		1					
Baltimore Oriole			1	1	4			1	

Table B.1 Continued

	CH			WGCPO			OP		
Species	**2009**	**2010**	**2011**	**2009**	**2010**	**2011**	**2009**	**2010**	**2011**
Barn Swallow									1
Black-and-white Warbler	10	8	7	18	15	11	3	4	3
Bell's Vireo							17	20	17
Bewick's Wren	2			8	8	2	11	10	2
Blue-gray Gnatcatcher	38	29	43	75	55	67	50	47	44
Brown-headed Cowbird	8	37	24	12	42	26	8	21	21
Blue Grossbeak	42	12	5	24	11	3	17	5	2
Blue Jay	1	4	3	2	3	3		1	2
Brown Thrasher		1		7	4	4	2		3
Bullock's Oriole				1					1
Broad-winged Hawk		1				1		1	
Blue-winged Warbler	1	1	2	1					

Table B.1 Continued

Species	**CH** 2009	**CH** 2010	**CH** 2011	**WGCPO** 2009	**WGCPO** 2010	**WGCPO** 2011	**OP** 2009	**OP** 2010	**OP** 2011
Carolina Chickadee	6	1	6	12	10	17	14	4	13
Carolina Wren	34	20	2	30	21	11	19	24	23
Cassin's Sparrow									12
Chipping Sparrow	2	3	3						
Chimney Swift		1		1					
Cooper's Hawk									1
Common Nighthawk						2			
Common Yellowthroat	6	7	3						
Chuck-will's Widow	1	1	1	5	5	1	2	4	
Dicksissel	1	4	6		2	6	16	29	28
Downy Woodpecker	4	7	6	7	6	1	4	9	6
Eastern Bluebird	6	2	2	1	1	1	1	5	1

Table B.1 Continued

	CH			WGCPO			OP		
Species	**2009**	**2010**	**2011**	**2009**	**2010**	**2011**	**2009**	**2010**	**2011**
Eastern Kingbird	2	1	3						
Eastern Meadowlark	5	6		3		2	11	5	10
Eastern Phoebee	1	1					1		
Eastern Towhee		1	1						
Eastern Wood Pewee	9	24	13	11	7	6			2
European Starling								1	
Fish Crow					2			1	
Field Sparrow	29	23	12	39	20	28	47	46	39
Great-crested Flycatcher	14	11	5	23	24	17	20	16	13
Gray Catbird	18	1		7			13	2	
Grasshopper Sparrow						1	4	6	1
Hairy Woodpecker	3	1	1						1

Table B.1 Continued

	CH			WGCPO			OP		
Species	**2009**	**2010**	**2011**	**2009**	**2010**	**2011**	**2009**	**2010**	**2011**
House Finch			1	2					
Hooded Warbler		1			1	1			1
House Wren	1		1			1			
Indigo Bunting	25	69	51	14	51	31	16	32	22
Kentucky Warbler	6	1	4	3	4	1	2	4	3
Killdeer				1	1	1			
Lark Sparrow		2		2	5	9	3	2	7
Mourning Dove	9	1			1	3	2	1	2
Northern Bobwhite	14	1	3	5	6	15	44	17	23
Northern Cardinal	12	20	8	54	63	48	56	59	39
Northern Flicker	1			2	1	1	1	1	
Northern Mockingbird		1		11	6	20	6	4	5

Table B.1 Continued

	CH			**WGCPO**			**OP**		
Species	**2009**	**2010**	**2011**	**2009**	**2010**	**2011**	**2009**	**2010**	**2011**
Northern Parula	41	40	38	3	2			1	
Orchard Oriole					1				1
Ovenbird	1	3		1					
Painted Bunting	1		2	53	50	59	56	48	39
Pine Warbler	3	8	4						
Pileated Woodpecker	4	6	5	3	4	3	1	3	1
Prairie Warbler	5	6	6						1
Red-bellied Woodpecker	6	8	7	11	6	5	5	2	2
Rufous-crowned Sparrow				1			8	1	
Red-eyed Vireo	77	57	66	29	33	24	3	1	2
Red-headed Woodpecker	3	1	3	3	1		1		
Red-shouldered Hawk			1	1	1				1

Table B.1 Continued

	CH			WGCPO			OP		
Species	**2009**	**2010**	**2011**	**2009**	**2010**	**2011**	**2009**	**2010**	**2011**
Red-tailed Hawk						1			1
Ruby-throated Hummingbird		1	3	1	3	1		2	
Red-winged Blackbird			1	2	1	2	1		
Scarlet Tanager	2		1	6					
Scissor-tailed Flycatcher			1				3	1	3
Summer Tanager	22	29	25	36	30	19	13	8	4
Tufted Titmouse	29	31	29	69	64	48	33	35	22
Turkey Vulture				2		1			1
Warbling Vireo				1	5				
White-breasted Nuthatch	3	8	11	10	13	3	3	1	1
Western Kingbird	1								

Table B.1 Continued

		CH			WGCPO			OP	
Species	**2009**	**2010**	**2011**	**2009**	**2010**	**2011**	**2009**	**2010**	**2011**
White-eyed Vireo	15	8	10	9	11	6	21	31	11
Wild Turkey	1			4	1				
Wood Thrush				19			3		
Whip-poor-will	2								
Yellow-breasted Chat		20	26			1		7	16
Yellow-billed Cuckoo	7	2	15	27	21	16	11	15	7
Yellow-throated Vireo	10	11	4	3	3	2		1	1
Yellow-throated Warbler	4	4	3	3	1		2		
Yellow Warbler		1		6	1	2			
Number of Species	**53**	**56**	**50**	**57**	**48**	**48**	**42**	**45**	**49**
Total		**69**			**68**			**64**	

VITA

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Scope and Method of Study: Reversing the population decline of Northern Bobwhites (*Colinus virginianus*, hereafter bobwhite), an economically important gamebird, in Oklahoma, is a priority for wildlife managers in the state. The Quail Habitat Restoration Initiative (QHRI) was initiated in 2008 to address this issue by doing cost-share with private landowners for the restoration of bobwhite habitat. The purpose of my study was to evaluate the effect of this program on bobwhites and other grassland bird species of conservation concern, and evaluate the key factors affecting the outcome of the program.

Findings and Conclusions: There was very little bobwhite response to restoration treatments, and occupancy of restoration areas did not significantly increase. The main habitat factor effecting bobwhite occupancy on a sample unit was overstory canopy cover, with a secondary effect of visual obstruction. Bobwhite occupancy was also significantly affected by the amount of habitat within 1 km of the sample unit. Most restoration areas were within the appropriate landscape context for bobwhites to recolonize the site, but proper local habitat condition were only created within a few sample units and this was the limiting factor in the success of the QHRI program. Community analysis showed that bird community composition responded most strongly to overstory canopy cover and visual obstruction, and many declining grassland bird species were strongly associated with bobwhites in species groupings from cluster analysis. Bobwhites show the potential to act as an "umbrella species" for declining bird species that rely on early-successional habitat. Occupancy modeling showed that estimates of bobwhite occupancy may be biased low by as much as 30% if detection probability is not accounted for, especially in areas where they are uncommon. Maximizing detection probability in the study design, and accounting for it in the analysis, must be done if estimates of bobwhite occupancy are to be accurate.

ADVISER'S APPROVAL: Dr. R. Dwayne Elmore