Northern Bobwhite Response to Habitat Restoration in Eastern Oklahoma

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ABSTRACT In response to the decline of northern bobwhite (Colinus virginianus; hereafter, bobwhite) in eastern Oklahoma, USA, a cost-share incentive program for private landowners was initiated to restore early successional habitat. Our objectives were to determine whether the program had an effect on bobwhite occupancy in the restoration areas and evaluate how local- and landscape-level habitat characteristics affect occupancy in both restoration and control areas. We surveyed 14 sample units that received treatment between 2009 and 2011, and 17 sample units that were controls. We used single-season occupancy models, with year as a dummy variable, to test for an effect of restoration treatment and habitat variables on occupancy. We found no significant treatment effect. Model selection showed that occupancy was best explained by the combination of overstory canopy cover and habitat area at both the local and landscape scales. Moran's I revealed positive spatial autocorrelation in the 1,000–3,000-m distance band, indicating that the likelihood of bobwhite occupancy increased with proximity to other populations. We show that creating ≥20 ha of habitat within 1–3 km of existing bobwhite populations increases the chance of restoration being successful. Published 2013. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS area, canopy cover, Colinus virginianus, landscape, occupancy modeling, population.

The northern bobwhite (Colinus virginianus; hereafter, bobwhite) is a socially and economically important game bird species that has experienced range-wide declines throughout most of the 20th 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, Howell et al. 2009). 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 (Roseberry and Sudkamp 1998, Peterson et al. 2002, Brennan and Kuvlesky 2005). Similar to most areas of the country, bobwhites have declined in eastern Oklahoma, USA (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).

In response to the decline of bobwhites, various federal programs (such as the Environmental Quality Incentive Program) have targeted select focal areas in hopes of restoring enough suitable usable space to impact populations of bobwhites in formerly suitable habitat (Sams 2002, Williams et al. 2004). One such program, the Environmental Quality Incentive Program-funded Quail Habitat Restoration Initiative was initiated in 2008 in an attempt to increase bobwhite populations in Oklahoma. Focal areas were identified as those having the best potential for growth and range expansion of local bobwhite populations. Landowner applications within those areas were then ranked based on the size of the area being offered for restoration, proximity to existing habitat, and the type of restoration activities the landowner was willing to conduct.

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 re-colonization from other patches (Hanski and Gilpin 1991, Terhune et al. 2010). Thus, while the probability of bobwhites occupying a restoration area will depend on the local habitat conditions created, the probability that bobwhites will disperse into the restored area, and survive if they do, will depend on both the size of the restored area and the amount of usable space in the surrounding landscape (Fies et al. 2002). If restoration creates only small, isolated habitat patches, the probability of bobwhites dispersing into those patches is low and the probability of individual mortality increases (Fies et al. 2002, Terhune et al. 2010).
areas such as eastern Oklahoma, where bobwhite habitat is highly fragmented, consideration of these factors is critical to the success of restoration efforts.

Our objectives were to ascertain whether the Quail Habitat Restoration Initiative program had a significant effect on bobwhite occupancy within restoration areas, determine how local- and landscape-level habitat factors affected the probability of bobwhite occupancy within sample areas, and test for spatial autocorrelation in the probability of bobwhite occupancy among sample areas. Specifically, we tested whether treatment was a significant factor in models of bobwhite occupancy, and modeled the effects of overstory canopy cover, habitat area, and composition of the surrounding landscape on the probability of bobwhite occupancy within a sample unit. We hypothesized that all 3 variables would significantly affect the probability of occupancy, and that including all 3 together would better explain occupancy than any one of them separately. We also tested for spatial autocorrelation in the probability of occupancy between sample units at 2 spatial scales, hypothesizing that proximity to existing populations would have an effect on occupancy probability. Understanding how these coarse-scale variables affect the success or failure of habitat restoration programs can help make restoration efforts more successful and cost-effective.

STUDY AREA

This study was conducted in 3 focal areas in eastern and central Oklahoma: the Central Hardwoods (Cherokee and Adair counties), West Gulf Coastal Plains and Ouachitas (Coal and Hughes counties), and the Oaks and Prairies (Pontotoc and Johnston counties). The Central Hardwoods area had deeply dissected topography and was 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 was not a significant issue in this area. The West Gulf Coastal Plains and Ouachitas and Oaks and Prairies areas were characterized by a mosaic of tallgrass prairie and cross-timbers forest. Dominant tree species were post oak (Q. stellata), blackjack oak (Q. marilandica) and hickories, and the most prominent grasses included big bluestem (Andropogon gerardii), little bluestem (Schizachyrium scoparium), and indiangrass (Sorghastrum nutans). The main land uses in all 3 focal areas were ranching and row-crop agriculture (Natural Resource Conservation Service 2012). Bobwhite population indices indicate a 1.5%/year decrease between 1966 and 2003 in these areas (Sauer et al. 2011).

There were 10 properties enrolled within the focal areas under study, and within each property there were ≥1 areas designated for habitat restoration, defined as management units. Among the 10 properties there were 92 individual management units totaling 827 ha and ranging in size from <1 ha to 192 ha, with 75% being <5 ha. Fifty-five of these management units received restoration treatments either immediately before or during the study: 38 management units totaling 135 ha in the Central Hardwoods focal area; 16 management units totaling 325 ha in the West Gulf Coastal Plains and Ouachitas focal area; and 1 management unit totaling 57 ha in the Oaks and Prairies focal area. The main treatment prescribed in all areas was overstory tree removal, sometimes followed by prescribed fire and/or re-seeding with native warm-season grasses. Two properties owned by The Nature Conservancy were used for control sample units within the focal areas: the J. T. Nickel Preserve in Adair County and the Pontotoc Ridge Preserve in Johnston and Pontotoc counties.

METHODS

Study Design and Site Selection

Study-site selection was not random because of the necessity to sample habitat restoration areas specifically. Within properties we defined specific areas as sample units for monitoring bobwhite populations and habitat variables. We 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 range of overstory canopy cover from 0% to >90%. This design enabled us to examine habitat variables of interest in a continuous distribution rather than a standard control–treatment design, which was necessary because Quail Habitat Restoration Initiative treatments were not uniformly applied spatially, temporally, or methodologically. We did not include agricultural fields or human development within the sample units because these areas were not eligible to receive treatments. In 2009, we established 31 sample units within the properties: 10 contained management units that had already received restoration treatments; 13 contained management units that had not yet received restoration treatments; and 8 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 approximately 50 ha and was large enough to sample one or more management units designated for restoration. We chose this size because the radius of audibility for bobwhites was considered to be approximately 400 m (Stoddard 1931) and the area was sufficient to sample bobwhites within the management units designated for restoration.

Bobwhite and Habitat Surveys

We conducted breeding-season call-count surveys for bobwhites (Hansen and Guthery 2001) at the center point of each sample unit 3 times during the breeding season (mid-May–late Jul) at intervals of 2–3 weeks in 2009–2011. We grouped sample units based on geographic proximity and surveyed 1 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. We recorded date and time of day at the beginning of each survey. Each survey consisted of a 5-minute call count between 0.5 hour before sunrise and 4.5 hour after sunrise.
All bobwhites heard within 400 m of a plot's center point were recorded. We did not survey when it was raining or when wind speeds exceeded 20 km/hour (Ralph et al. 1995). Count data were converted to presence–absence data for analysis.

We measured 2 habitat variables within each sample unit: proportion of overstory canopy cover and the amount of early successional habitat within the sample unit. Although many other habitat characteristics (e.g., percent cover of shrubs; visual obstruction) are known to be important to bobwhites (Guthery 2002), we focused on the main spatial and structural components being manipulated by the landowners in the restoration process. Greenberg et al. (2011) defined 2 essential elements as necessary for early successional habitat: a well-established ground-cover component, such as grasses, shrubs, and young trees, and lack of a mature, closed tree canopy. Lacking a strict quantitative definition, we defined early successional habitat as any area within the sample unit >0.1 ha in size (approx. 30 m²) with tree cover ≤50%.

To measure overstory canopy cover, we systematically located 16 vegetation sampling points within each sample unit in a design modified from Wilson et al. (1995) and Smith et al. (2008). We used a Global Positioning System 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). We measured overstory canopy cover at each vegetation sampling point, beginning in June of 2009, using a hemispheric camera and WinSCANOPY® canopy analysis software (Regents Instruments, Inc., Quebec City, QC, Canada). Canopy was re-measured in subsequent years (2010–2011) only if coverage had changed due to restoration activities. To avoid including ground-level vegetation in the photograph, we placed the camera on a tripod and took photographs from a height of 1 m above the ground.

To estimate the amount of early successional habitat within each sample unit in each year, we obtained aerial photographs of the properties under study, taken in 2008 and 2010, and digitized all areas of early successional habitat within each sample unit. We used ocular estimates of canopy cover in the aerial photographs and then checked to ensure that the size of the area was large enough. If areas within any sample unit had undergone restoration that was not reflected in the photographs (i.e., after the photograph was taken), the boundary of the restored area was estimated from the ground and drawn onto a paper map, and then the photograph was re-digitized to reflect the new land-cover configuration.

At the landscape scale, we measured the amount of suitable bobwhite habitat within 1 km of the sample unit as a measure of landscape habitat availability. To estimate this, we used land-cover data derived from the 2006 National Land Cover Database, which used 30-m-resolution LANDSAT data to determine land cover throughout the United States (Fry et al. 2011). Because we were only concerned with land-cover classes that could be considered as potential bobwhite habitat, the following classes were considered: Shrub–Scrub, Grassland–Herbaceous, and Pasture–Hay. We computed the total area in km² of these 3 classes combined within 1 km of the outer edge of each sampling unit. We chose this size because it was within the reported average seasonal movement range for bobwhites within a grassland–forest mosaic (Fies et al. 2002) and is the scale at which bobwhite population dynamics likely occur (Howell et al. 2009).

**Figure 1.** Sample-unit design for measuring habitat variables relating to bobwhite habitat in Oklahoma, USA (2009–2011).

**Statistical Analysis**

We combined data for all years and used single-season occupancy models (MacKenzie et al. 2006), controlling for year, to determine bobwhite detection probability (P) and occupancy (psi; ø) for each sample unit × year combination in relation to restoration treatment and habitat variables at both scales. Using single-season models was more appropriate than using multi-season models for 2 reasons. First, multi-season models require large sample sizes (Weir et al. 2009); and second, we were attempting to look directly at habitat effects on occupancy in each year rather than meta-population dynamics (probabilities of extinction and colonization), which are the focus of multi-season occupancy models (MacKenzie et al. 2006). Researchers have recorded a number of variables that affect detection probability of bobwhites during call-count surveys, including day, time, wind, temperature, and light intensity (Robel et al. 1969, Hansen and Guthery 2001). Because we did not survey when it was raining or very windy, and because there are strong daily and seasonal peaks in the calling activity of bobwhites (Hansen and Guthery 2001), we used only the phenological variables Julian day and time of day (recorded as minutes from sunrise) to model detection probability. We assessed model fit with a χ² test that used 10,000 bootstrapped simulations of the data to produce an approximation of the distribution of the fit statistic derived from comparing observed with expected values, and then
calculated a P-value based on the proportion of fit statistic values greater than the observed value (Fiske and Chandler 2011). We considered that model fit was adequate if \( P > 0.05 \). We fit all models using Package UNMARKED (Fiske and Chandler 2011) in Program R (R version 2.15.0, http://cran.r-project.org; accessed 22 May 2012).

To test whether treatments applied as a result of the Quail Habitat Restoration Initiative had a significant effect on bobwhite occupancy within the enrolled properties, we ran 2 single-season occupancy models: a null model using only the detection covariates, controlling for year; and a model using treatment as a binomial variable indicating whether the sample unit had received restoration activities. Only sample units that were scheduled to undergo restoration activities were used in this analysis, because these sites were mainly closed-canopy forest and allowed us to directly test for an effect of treatment without using control sites that already contained significant amounts of usable space and were thus occupied by bobwhites. We did not consider the amount or type of treatment in the analysis because we were only concerned with the overall effectiveness of the Quail Habitat Restoration Initiative program rather than the effect of individual treatments. We compared the 2 models using Akaike’s Information Criterion adjusted for small sample sizes (AICc; Anderson 2008) and considered that treatment was an uninformative parameter if \( \Delta \text{AIC}_c \) was <2 between the treatment and the null models (Arnold 2010).

To assess the effect of habitat and landscape variables on bobwhite occupancy we compared 8 models: each of the 3 variables alone; the 3 possible combinations using 2 variables; a global model using all 3 variables; and a null model. Assuming there would be an exponential relationship between overstory canopy cover and bobwhite occupancy, we used the log of canopy cover in our models. We compared models using AICc, and considered models with \( \Delta \text{AIC}_c < 4 \) to be good candidate models (Anderson 2008). To test whether a sample unit was more likely to be occupied if it was within a certain distance of another occupied unit, we tested for an effect of spatial autocorrelation among the residuals (non-independence of errors) by calculating a Moran’s \( I \) on residuals from the top-ranked model (Moore and Swihart 2005, Duren et al. 2011), using binary neighborhood weights, at 2 different spatial scales: 0–1,000 m because this is within the average seasonal movement distance of bobwhites (Fies et al. 2002, Terhune et al. 2010); and 1,000–3,000 m to cover the average dispersal distance for bobwhites in a grassland–forest mosaic (Cook 2004). We used 999 Monte Carlo permutations to account for potential non-normality of the location values. We tested the Moran’s \( I \) using package SPDEP in Program R (R version 2.15.0, http://cran.r-project.org; accessed 22 May 2012). We considered the existence of spatial autocorrelation within a distance band at \( P < 0.05 \).

We examined the individual effects of the variables of interest, using the AIC, best model, by predicting occupancy probability across the range of an individual variable while holding the other variables constant at their means (Guthery and Bingham 2007). We then visually examined the graphs of these predictions for apparent thresholds where predicted occupancy probability increased substantially. We also created histograms of the frequencies of sample unit \( \times \) year combinations where restoration treatments had occurred to examine the frequencies of different levels of our parameter estimates with respect to the predictions from the top-ranked model.

## RESULTS

Among the 23 sample units where restoration treatments were planned, 3 of them became occupied by bobwhites after undergoing restoration treatments and 2 were occupied in at least one of the years without undergoing any treatment. We found no effect of treatment based on AICc model selection. The null model was chosen as the AICc best and the \( \Delta \text{AIC} \), between the null and treatment models was 1.863, indicating that adding treatment to the model did not reduce the deviance of the model enough to make up for the added penalty for the extra variable in the AICc.

We sampled 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 one sample unit in 2010 due to disturbance during the sampling season that invalidated the bobwhite surveys. We detected bobwhites at 7, 6, and 9 sample units in 2009, 2010, and 2011, respectively. Our top-ranked habitat model contained all 3 of the habitat and landscape variables (Table 1) and was considered better than the second-ranked model by a significant margin (\( \Delta \text{AIC}_c = 9.808 \) for the second-ranked model). The log of canopy cover and the amount of early successional habitat within the sample unit were each contained in 3 of the 4 highest-ranked models. Single-variable models were ranked below the 2-variable models,

### Table 1. Results of model selection procedure using Akaike’s Information Criterion adjusted for small sample sizes (AICc) on models using variables related to detection probability (\( P \)) and occupancy (\( \psi \)) for bobwhites in eastern Oklahoma, USA, in 2009–2011. Reported are the variables used in the model, the number of parameters estimated (\( K \)), the AICc score, the relative difference in score when compared with the top-ranked model (\( \Delta \text{AIC}_c \)), and the model weight (\( w_i \)).

<table>
<thead>
<tr>
<th>Model</th>
<th>( K )</th>
<th>AICc</th>
<th>( \Delta \text{AIC}_c )</th>
<th>( w_i )</th>
</tr>
</thead>
<tbody>
<tr>
<td>psi(CAN)(^a)</td>
<td>7</td>
<td>116.042</td>
<td>0.000</td>
<td>0.985</td>
</tr>
<tr>
<td>psi(CAN + HAB)(^b)</td>
<td>8</td>
<td>125.850</td>
<td>9.808</td>
<td>0.007</td>
</tr>
<tr>
<td>psi(HAB + LAND)(^c)</td>
<td>8</td>
<td>126.420</td>
<td>10.378</td>
<td>0.005</td>
</tr>
<tr>
<td>psi(CAN + LAND)(^d)</td>
<td>8</td>
<td>130.040</td>
<td>13.998</td>
<td>0.001</td>
</tr>
<tr>
<td>psi(CAN)(^e)</td>
<td>7</td>
<td>129.834</td>
<td>13.791</td>
<td>0.001</td>
</tr>
<tr>
<td>psi(HAB)(^f)</td>
<td>7</td>
<td>134.314</td>
<td>18.271</td>
<td>0.000</td>
</tr>
<tr>
<td>psi(LAND)(^g)</td>
<td>7</td>
<td>155.394</td>
<td>39.351</td>
<td>0.000</td>
</tr>
<tr>
<td>psi(.)(^h)</td>
<td>6</td>
<td>168.981</td>
<td>52.938</td>
<td>0.000</td>
</tr>
</tbody>
</table>

\(^a\) Log of percent canopy cover.
\(^b\) The amount of early successional habitat (ha) within the 400-m-radius sample unit.
\(^c\) The amount of potential habitat within 1 km of the outer edge of the sample unit.
\(^d\) Julian day + min from sunrise.
and the null model had $\Delta AIC_c = 52.938$. In the top-ranked model, bobwhite occupancy was negatively correlated with the log of canopy cover and positively correlated with area of early successional habitat and the amount of habitat within 1 km of the sample unit (Table 2). There was no evidence for lack-of-fit in any of the models, with $P$ values between 0.475 and 0.832.

We found no evidence for spatial autocorrelation in the 0–1,000-m distance band (Moran’s $I = 0.112$; $P = 0.109$) but did find a significant positive effect in the 1,000–3,000-m distance band (Moran’s $I = 0.168$; $P = 0.005$), indicating that a sample unit had a higher probability of being occupied if it was located within 3,000 m of another occupied sample unit.

Plots of the predicted individual effects showed apparent threshold levels at 60% for overstory canopy cover, 20 ha of early successional habitat within the sample unit, and 2 km$^2$ of habitat within 1 km of the outer edge of the sample unit.

Table 2. Covariates, estimates, standard errors (SE), and 90% confidence intervals (CI) for occupancy probability of bobwhites in Oklahoma, USA, in 2009–2011.

<table>
<thead>
<tr>
<th>Covariate</th>
<th>Estimate</th>
<th>SE</th>
<th>90% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>CANOPY$^{a}$</td>
<td>$-104.732$</td>
<td>$55.883$</td>
<td>$-196.652$ to $-12.812$</td>
</tr>
<tr>
<td>HAB$^{b}$</td>
<td>$0.344$</td>
<td>$0.209$</td>
<td>$0.00015$ to $0.688$</td>
</tr>
<tr>
<td>LAND$^{c}$</td>
<td>$5.821$</td>
<td>$3.199$</td>
<td>$0.559$ to $11.082$</td>
</tr>
</tbody>
</table>

$^a$ Log of percent canopy cover.
$^b$ The amount of early successional habitat (ha) within the 400-m-radius sample unit.
$^c$ The amount of potential habitat (km$^2$) within 1 km of the outer edge of the sample unit.

DISCUSSION

Although 3 sample units in our study became occupied after undergoing restoration treatments, the Quail Habitat Restoration Initiative did not have an effect on bobwhite occupancy on properties enrolled in the program within the timeframe of our study. 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. Our analyses show that, in most cases, sufficient habitat was not created at the local level to cause restoration areas to become occupied within 3 years. Specifically, there was not enough early successional habitat created within restoration areas to attract bobwhites, and most of the restoration was done in areas without sufficient habitat in the surrounding landscape (Fig. 3).

Different amounts and types of restoration treatments are likely to have varying effects on the probability of bobwhites re-colonizing the restored area. Additionally, different treatments might operate at different temporal scales. In the case of the effectiveness of the Quail Habitat Restoration Initiative program, we were only concerned with whether or not a sample unit had been treated and whether the treatments throughout the study area had an effect on occupancy. In the case of local- and landscape-level habitat variables, we were not concerned with the type of treatment but rather the intended result of that treatment, which was the creation of early successional habitat for bobwhites; and measuring this allowed us to make inferences about the reason that the Quail Habitat Restoration Initiative program was or was not effective. The fact that this was not a before–after-control–impact study did not allow us to directly test the effects of individual treatments or consider the type or amount of treatment within an individual sample unit.
Reducing overstory canopy cover is the critical component in restoring habitat for bobwhites because this is what allows enough sunlight in to facilitate the growth of the grass and shrub components required by this species (Peitz et al. 1997, Cram et al. 2002). We found an apparent threshold of canopy cover where at values above 60%, the occupancy probability for bobwhites was at or near 0 (Fig. 2A). Cram et al. (2002) found bobwhites in pine–grassland restoration areas in Arkansas, USA, where canopy cover was estimated at approximately 80% (using a spherical densitometer), which was much higher than our threshold. Other than Cram et al. (2002), we found no published accounts of bobwhite response to different levels of overstory canopy cover. It would seem, based on our contrasting results, that overstory canopy cover may have different effects based on the particular ecosystem under consideration. We note that Cram et al. (2002) used a spherical densiometer rather than a hemispheric camera to estimate canopy cover; however, it has been shown that there is no significant difference between the estimates obtained using either method (Fiala et al. 2006).

Our histograms of occupancy probability and of each variable (Fig. 3A–D) suggest that the limiting factor in the success of the Quail Habitat Restoration Initiative program was the creation of sufficient habitat characteristics at the local level within the proper landscape context. Because our variable measurements can only be interpreted in terms of the 50-ha sample unit, this likely means that restoration patches were, in most cases, too small to induce colonization by bobwhites even when populations existed nearby. In fact, records of incidental detections of bobwhites show that ≥16 of the 23 sample units where restoration was scheduled to occur (70%) had bobwhites within 1 km, which is well within the average seasonal movement range of bobwhites in patchy habitats (Fies et al. 2002).

One of the primary assumptions of occupancy models is that sample units are closed to changes in occupancy during the survey period (MacKenzie et al. 2006). Our definition of occupancy was such that, although individual bobwhites may move into or out of a sample unit during the season, the social nature and limited movements of bobwhites would cause the occupancy status to remain constant. Thus, although the number of individuals may have changed during the course of sampling, occupancy status would likely remain constant and any change in the number of individuals would have its largest effect on detection probability (Royle and Nichols 2003, Smith et al. 2007). If dispersing bobwhites had colonized sample units after sampling was begun, the effect would have been to bias detection probability low, which can be mitigated by allowing detection probability to vary by sampling occasion (MacKenzie et al. 2006), as we did in our models. It is also likely that the radius of audibility for bobwhites varies by habitat (Guthery et al. 2001, Cram et al. 2002), and so it was possible to detect bobwhites outside the radius of the sample unit in the more open habitats. The issue of false-positive errors can be serious in occupancy models, and this has been addressed in terms of the misidentification of the species (Royle and Link 2006). In our case, we were careful to differentiate between bobwhites inside and outside of the sample unit, and we do not consider false-positive errors to be a significant issue.

As shown by the Moran’s I-test, our sample units were not spatially independent, and this was to be expected. It would have been impossible, under the constraints of our study design, to avoid spatial dependence; and further, it is not necessarily possible or advisable to avoid something that is so

![Figure 3. Frequencies of 400-m-radius sample units in eastern Oklahoma, USA (2009–2011), that had received bobwhite habitat restoration treatments, at different levels of (A) proportion of overstory canopy cover, (B) total area (ha) of early successional habitat within the sampling unit, (C) total area (km²) of potential habitat within 1 km of the outer edge of the sample unit, and (D) estimated occupancy probability using a model containing all 3 variables.](image-url)
inherent to ecological processes (Legendre 1993, Zuckerberg et al. 2012). Because of the clustering of sample units on properties, many of our landscape buffers were overlapping, and this is sometimes a concern (Holland et al. 2004). Nevertheless, it has been shown empirically that there is no relationship between the existence or extent of overlap in landscape buffers and the degree of spatial autocorrelation (Zuckerberg et al. 2012), and non-overlapping landscapes do not ensure spatial independence in any case (Schooley 2006). Thus, we did not consider overlapping landscapes to be an issue of concern in our study.

Bobwhite populations should be spatially dependent because of their limited dispersal distance (Fies et al. 2002, Cook 2004). Thus, our finding of spatial autocorrelation among sample units at the 1,000–3,000-m level was not unexpected given the scale at which population dynamics likely occur (Howell et al. 2009). This finding suggests that spatial clustering of restoration areas may be beneficial to bobwhites. The lack of spatial autocorrelation at the 0–1,000-m level was likely due to the fact that any autocorrelation was already being explained by the inclusion of the landscape variable at that scale. Therefore, the autocorrelation was likely not reflected in the residuals. Although not conclusive, a post hoc analysis using the single-variable model of canopy cover suggested a much stronger, although still not statistically significant, spatial autocorrelation at the 0–1,000-m level (P = 0.072). Our finding of spatial autocorrelation is in contrast to Duren et al. (2011), who found no evidence for spatial autocorrelation in an occupancy model for bobwhites in Delaware, USA. However, Duren et al. (2011) did not report testing for autocorrelation at specific distance bands as in our study.

Our analysis showed a strong effect of the amount of habitat within 1 km of the sample unit on the probability of bobwhite occupancy. The finding of an apparent threshold effect of area of usable space 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 GA, USA, also found strong support for models containing a landscape effect of the 3-km × 3-km grid in which management units were nested, although the nature of the effect was unclear.

MANAGEMENT IMPLICATIONS

Guthery (1997) has asserted that the long-term density of bobwhite populations in any given area is directly related to the amount of area on the landscape that can support the life-history needs of the species. The "usable space" hypothesis has become the underpinning of the effort to restore bobwhite populations throughout their range (Dinnick et al. 2002, Williams et al. 2004). Our results support this hypothesis in both positive and negative terms. Essentially, the majority of the restoration efforts through the Quail Habitat Restoration Initiative created only small, isolated patches of habitat and saw no bobwhite response. Conversely, the sample units that did become occupied had undergone restoration over large areas and were adjacent to existing bobwhite habitat. Therefore, we suggest that restoration efforts should focus on creating a few large areas of usable space rather than many small patches, and that these areas should be within the average dispersal distance of existing populations.

Our analysis shows threshold levels of overstory canopy cover, area of early successional habitat within the 50-ha sample unit, and area of habitat within 1 km of the sample unit at 60%, 20 ha, and 2 km², respectively. We also demonstrated positive spatial dependence of sites within 3 km of each other, suggesting that clustering of restoration areas within this range could make restoration efforts more effective. These levels can be taken as suggestions to guide further habitat restoration efforts and make them more cost-effective. Although meeting these guidelines does not guarantee the success of restoration, it significantly increases the likelihood that bobwhites will begin using the restored areas, according to our models.

ACKNOWLEDGMENTS

Funding was provided by the Pittman–Robertson Federal Aid to Wildlife Restoration Act under project W-161-R (F10AF00180) of the Oklahoma Department of Wildlife Conservation and Oklahoma State University with additional support from The Nature Conservancy's Weaver Grant Program, Oklahoma Ornithological Society, and Payne County Audubon Society. The project was administered through the Oklahoma Cooperative Fish and Wildlife Research Unit (Oklahoma Department of Wildlife Conservation, Oklahoma State University, U.S. Geological Survey, U.S. Fish and Wildlife Service, and the Wildlife Management Institute cooperating). We thank all of the landowners who allowed us to conduct research on their property; M. G. Sams and E. M. Bartholomew of the Oklahoma Department of Wildlife Conservation; R. E. Will and D. S. Wilson of the Oklahoma State University Department of Natural Resource Ecology and Management; R. J. Cervantes, C. Griffin, C. E. Chappell, and N. Hillis for assistance in the field; and M. Payton of the Oklahoma State University Department of Statistics for statistical consulting help. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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