

Articles

Northern Bobwhite Occupancy Patterns on Multiple Spatial Scales Across Arkansas

Ellery V. Lassiter,* Marcus Asher, Grace Christie, Connor Gale, Andrhea Massey, Cody Massery, Christopher R. Middaugh, John T. Veon, Brett A. DeGregorio

E.V. Lassiter, G. Christie, C. Gale, A. Massey, J.T. Veon

Department of Biological Sciences, University of Arkansas, Fayetteville, Arkansas 72701

M. Asher, C. Massery, C.R. Middaugh

Arkansas Game and Fish Commission, Little Rock, Arkansas 72205

B.A. DeGregorio

U.S. Geological Survey, Fish and Wildlife Cooperative Research Unit, University of Arkansas, Fayetteville, Arkansas 72701

Abstract

Northern bobwhite *Colinus virginianus* populations have been rapidly declining in the eastern, central, and southern United States for decades. Land use change and an incompatibility between northern bobwhite resource needs and human land use practices have driven declines. Here, we applied occupancy analyses on two spatial scales (state level and ecoregion level) to more than 5,000 northern bobwhite surveys conducted over 6 y across the entire state of Arkansas to explore patterns in occupancy and land use variables, and to identify priority areas for management and conservation. At the state level, northern bobwhite occupied 29% of sites and northern bobwhite were most likely to occur in areas with a high percentage of early successional habitat (grassland, pasture, and shrubland). The statewide model predicted that northern bobwhite were likely to occur ($\geq 75\%$ predicted occupancy) in $< 20\%$ of the state. Arkansas is comprised of five distinct ecoregions, and analyses at the ecoregion spatial scale showed that habitat associations of northern bobwhite could vary between ecoregions. For example, early successional habitat best predicted northern bobwhite occupancy in both the Arkansas River Valley and Ozark Mountains ecoregions, and other habitat associations such as the proportion of herbaceous habitat and hay-pasture habitat, respectively, further refined predictions. Contrastingly, richness of land cover classes alone best predicted northern bobwhite occupancy in the Ouachita Mountains ecoregion. Ecoregion-level models were thus more discerning than the state-level model and should be more helpful to managers in identifying priority conservation areas. However, in two of five ecoregions, surveys too rarely encountered northern bobwhite to accurately predict their occurrence. We found that likely occupied northern bobwhite habitat lay primarily on private properties (95%), but that numerous public entities own and manage land identified as suitable or likely occupied. We conclude that management of northern bobwhite in Arkansas could benefit from cooperation among state, federal, and military partners, as well as surrounding private landowners and that ecoregion-specific models may be more useful in identifying priority areas for management. Our approach incorporates multiple landscape scales when using remote sensing technology in conjunction with monitoring data and could have important application for the management of northern bobwhite and other grassland bird species.

Keywords: landscape; occupancy modeling; *Colinus virginianus*; remote sensing; multi-scale analysis

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* Corresponding author: evlassit@uark.edu



Introduction

Northern bobwhite *Colinus virginianus* (hereafter, bobwhite) populations have been rapidly declining across their natural range in the eastern, central, and southern United States for decades (e.g., Brennan 1991; Burger et al. 1999; Sauer et al. 2005). Estimates of range-wide decline calculated by the Breeding Bird Survey indicate an annual loss of 3%, with the most dramatic losses reported from the southeastern United States (Bowling et al. 2014). Regional variation in the severity of the population losses indicates locality-specific causes of decline. However, the combined effects of habitat conversion, degradation, and fragmentation have resulted in a decrease of total suitable landscape space available to bobwhite (Guthery 1997). Specifically, practices such as establishment and maintenance of dense stocking of forests, fire suppression, conversion of grassland and edge habitats to large-scale monoculture agriculture, and an increasing rate of development are all responsible for widespread bobwhite habitat and population loss (Duren et al. 2011; Bowling et al. 2014). The diversity of habitats they occupy complicates successful monitoring of bobwhite. While the species is generally associated with early successional habitat, that can include a variety of land cover types such as prairies, shrublands, agricultural fields, rangeland, and park-like pine or mixed hardwood forests with open understories (Brennan et al. 2020). These habitat-use patterns can vary regionally, greatly impeding efforts to monitor bobwhite at local or larger state-level scales (Williams et al. 2004). Understanding occupancy at multiple spatial scales will be necessary to inform monitoring strategies and identify best management decisions and priority areas for management and protection (Veech 2006).

Bobwhite occur across the entire state of Arkansas, where populations have been declining steadily over the last several decades (Twedt et al. 2007; Hernández et al. 2013). Wildlife habitat management in Arkansas is often conducted using an ecoregion framework (modified from Omernik 1987), with the state divided into five ecoregions based on covarying topography, geology, and vegetation type (Table 1). Managers tasked with monitoring or recovering bobwhite across large and diverse areas, such as in Arkansas, understand that what constitutes bobwhite habitat in one ecoregion is likely to be different in the others. Thus, managers must know how habitat associations vary across regional scales, what locality-specific factors most influence bobwhite occupancy, and what disturbances and management techniques are necessary to create and maintain habitat

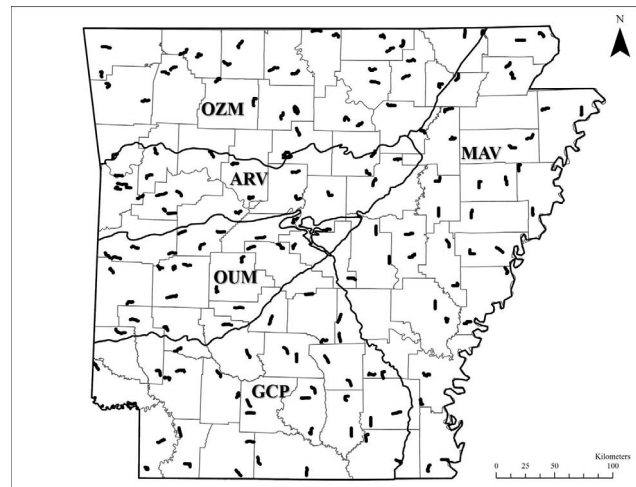


Figure 1. Location of northern bobwhite *Colinus virginianus* survey points conducted across the counties and the five Level 3 Environmental Protection Agency ecoregions of Arkansas in 2014–2019. Ecoregions include: Arkansas River Valley (ARV), Gulf Coastal Plain (GCP), Mississippi Alluvial Valley (MAV), Ouachita Mountains (OUM), and Ozark Mountains (OZM).

in each region. They need this information to implement monitoring protocols to account for this variability.

Understanding the distribution and habitat associations of bobwhite across a large spatial extent should rely on a robust, repeated occupancy framework that incorporates detection probability (MacKenzie et al. 2017). Here, we use multiyear call survey data to explore patterns of bobwhite occupancy across the entirety of Arkansas and also within specific ecoregions. Our specific objectives were to 1) explore how inferences regarding bobwhite occupancy patterns differed when analyzed at a coarse state level compared to analyses at finer, ecologically meaningful regional scales (i.e., ecoregion), 2) use these findings to guide prioritization of habitat management strategies, and 3) evaluate how bobwhite occupancy within each ecoregion changed during the 6-year study period.

Methods

Study site

Our study occurred across the entire state of Arkansas, which is 137,942 km² and divided into 75 counties (Figure 1). The state has five Level 3 Environmental Protection Agency ecoregions (Table 1). The Arkansas River Valley (ARV) ecoregion occurs along the Arkansas

Table 1. The five Level 3 Environmental Protection Agency ecoregions present and surveyed for northern bobwhite *Colinus virginianus* in Arkansas 2014–2019.

Ecoregion	Dominant land cover(s)	Size (km ²)
Arkansas River Valley	Diverse mix of savannah, pasture, lowland forest, and agriculture	15,957
Gulf Coastal Plain	Timber plantations	33,664
Mississippi Alluvial Valley	Row-crop agriculture, bottomland hardwood forest	39,722
Ouachita Mountains	Upland pine hardwood	16,405
Ozark Mountains	Upland hardwood, pasture	32,194

River drainage; a diverse mosaic of savannah, lowland forests, pasture, and agriculture characterize this region. The Gulf Coastal Plain ecoregion (GCP), dominated primarily by privately owned pine plantations, occurs in the southernmost lowlands of the state. The Mississippi Alluvial Valley ecoregion (MAV) occurs along the western drainage of the Mississippi River and primarily consists of row-crop agriculture with bottomland hardwood forest in riparian areas. The Ouachita Mountain ecoregion (OUM), characterized by upland pine hardwood forests, occurs along the Ouachita Mountains in the west-central portion of the state. The Ozark Mountain ecoregion (OZM) is in the northwestern portion of the state and includes a mixture of upland hardwood forest and pasture.

Bobwhite surveys

Our study design consisted of conducting point surveys in most counties to ensure coverage across the entire state. From May 15 to June 1 of each year from 2014 to 2019 Arkansas Game and Fish Commission regional staff conducted point count surveys for bobwhite following standardized protocols. We spread out survey locations to establish approximately 30 survey points in each county with each survey point separated by 500 m along gravel roads to ensure closure between points. Staff conducted surveys along both private and public lands. During each survey, a trained observer listened for and recorded all bobwhite heard or seen within a 2-min period at each location. We conducted surveys only on clear, calm days with wind speeds of no more than 11 km/h. Surveys began at sunrise, ended by 1000 hours, and were conducted at least 10 m from parked vehicles. Survey points were located along roads that traversed habitat historically suitable for bobwhite as determined by local Arkansas Game and Fish Commission personnel familiar with the county.

Remote sensing

We quantified landscape variables that we hypothesized would influence bobwhite presence across the state and in each ecoregion. Researchers had previously identified these variables as important in other studies of bobwhite occupancy (e.g., Duren et al. 2011; Bowling et al. 2014) or they were a priori predicted to be important for bobwhite presence. Variables related to human disturbance, land use and land cover, and landscape composition (Table 2; Data S1, *Supplemental Material*). We derived all landscape variables in a geographic information system (ArcGIS Pro, ESRI Inc, Redlands, CA) using layers available from the 30-m resolution National Land Cover Database (NLCD 2016; produced by U.S. Geological Survey) and 1-m resolution digital elevation model (produced by U.S. Geological Survey). We calculated all variables within a 500-m buffer around each survey point. We chose 500-m to align with the detection distance of calling bobwhite (Duren et al. 2011) and to reduce the overlap among buffers of

Table 2. Variables included in dynamic occupancy models of northern bobwhite *Colinus virginianus*. We used variables for estimation of bobwhite occupancy probability unless otherwise noted. We calculated all variables within 500 m of northern bobwhite survey points collected in Arkansas 2014–2019.

Proportion land cover types derived from National Land Cover Database 2016	Land use and landscape composition variables derived using remote sensing
% Early successional habitat	Aspect
% Barren land	Biomass index (1–45) ^a
% Crops	Density of forest edge
% Developed open space	Distance to nearest Conservation Reserve Program (m) ^b
% Developed: low, medium, and high	Distance to nearest divided highway (m)
% Emergent herbaceous wetlands	Distance to nearest early successional habitat (m)
% Forest	Distance to nearest fire perimeter ^c
% Hay or pasture	Ecoregion
% Herbaceous	Fire density
% Open water	Land cover evenness
% Scrub-shrubland	Land cover richness
% Woody wetland	Size of nearest early successional habitat patch (ha)
	Slope

^a Included both overall mean (occupancy) and yearly mean (colonization).

^b Included in the Arkansas state model and Mississippi Alluvial Valley ecoregion models only.

^c Calculated per year only (colonization).

adjacent points. Because bobwhite habitat can be ephemeral, we restricted our analyses to 3 y before and 3 y after the 2016 NLCD layer to ensure that the landscape variables we quantified accurately reflected the current land cover.

We created 500-m radius buffers around each survey point and derived the proportion cover of woody wetland, scrub-shrub, open water, herbaceous land cover, hay and pasture, forest (mixed, hardwood, and coniferous), emergent wetland, developed (low, medium, and high intensity were grouped together), agriculture crops, open space, and early successional habitat (ESH: a land cover created by combining herbaceous, scrub/shrub, and hay/pasture). We also quantified the straight-line distance from each survey point to the nearest patch of ESH and the size (km²) of the nearest ESH patch. We created a feature called forest edge using the NLCD layer. We developed the forest edge feature by delineating a buffer of 15 m inward and outward from each polygon of deciduous, mixed, or coniferous forest. We then summed the amount of forest edge available within 500 m surrounding each survey point. In addition to calculating percentages of each land cover type, we also derived richness (the number of different land cover types present within 500 m of a survey point) and evenness values (Shannon's equitability index, $E_H = H / \ln[S]$; Shannon and Weaver 1949; Forman 1995). We calculated the distance from each survey point to the nearest available polygon of Conservation Reserve Program property (Provided by U.S. Department of



Agriculture–Farm Service Agency). We only included Conservation Reserve Program properties enrolled in conservation practices predicted to influence bobwhite presence (i.e., in the creation or maintenance of early successional habitat). Because nearly all Conservation Reserve Program enrollment within the state of Arkansas occurs within the MAV, we only used this variable for the overall state and that ecoregion's analysis. We used Landsat imagery with a Normalized Difference Vegetation Index from 2016 to calculate average plant biomass within a 500-m radius surrounding each survey location point (available from ESRI Living Atlas). We used the fire point layer from Global Forest Watch and created a kernel density estimate to create a layer of fire density across the entire state. In addition to these land cover variables, we derived the slope, aspect, distance to nearest divided highway, and ecoregion for each survey point.

Additionally, we included two annually varying variables to capture potential change in vegetative structure between years within the study period. Following the same procedure as above, we used Normalized Difference Vegetation Index data to calculate average plant biomass for each survey point for each year. We used National Interagency Fire Center historical point data to calculate distance to nearest fire using a spatial join between these point data to the 500-m buffers around each point in each year.

Analytical methods

We constructed dynamic occupancy models (MacKenzie et al. 2003) in a Bayesian framework (Carpenter et al. 2017; Kellner 2021) to estimate the probability of bobwhite occurrence and turnover at sampling locations and to explore the influence of covariates on occupancy probability. Temporal replication was not possible within sampling years because we surveyed each point only once per year, though we surveyed sites across most or all years. Sites that we did not resample during a given sampling year remained in the analysis but we censored them for that year.

For the state overall and each ecoregion, we fit single-variable dynamic occupancy models (MacKenzie et al. 2003) in a Bayesian framework (Carpenter et al. 2017; Kellner 2021) with colonization and extinction probabilities held constant. We used county as the detection variable for all analyses. For all comparisons, we first standardized covariates by centering on the mean and scaling by standard deviation. We performed all model fitting in R (R Core Team 2020) with the *ubms* package (Kellner 2021), which fits occupancy models in a Bayesian framework using Stan (Carpenter et al. 2017) instead of maximum likelihood as with other packages (e.g., unmarked; Fiske and Chandler 2011). For each model we specified three chains run for 1,000 warmup and 2,000 post-warmup iterations, for a total of 3,000 simulation draws. We reviewed R-hat values and trace plots to check for Markov chain Monte Carlo chain

convergence and used MacKenzie–Bailey χ^2 tests (MacKenzie and Bailey 2004) to assess model goodness-of-fit. We conducted model selection using leave-out cross-validation (Vehtari et al. 2017). Interpretation is similar to that of Akaike's Information Criterion (Burnham and Anderson 2002), in which the model with the largest expected predictive accuracy (elpd) performed the best (Vehtari et al. 2017). We also included uncertainty intervals alongside parameter estimates, which may be interpreted similar to that of a confidence interval, but instead gives a range of posterior values that includes 95% of the probability. To improve clarity in presenting model selection tables, we only display models that were competitive with the highest elpd values in the set and whose standard error was larger than the Δ elpd (Vehtari et al. 2017), though full model selection tables are available in supplemental materials (Table S1, *Supplemental Material*). For ecoregions with more than one top candidate model, we averaged parameter values and calculated standard deviation. For the state and each ecoregion, we then reran candidate models with a single colonization variable, distance to fire and yearly mean biomass, respectively, though neither variable was significant and therefore not included for additional analysis.

We generated occupancy probability across each sampling year by calculating posterior distributions of latent occupancy. We generated a 500 × 500 m sampling grid across the entire state of Arkansas and interpolated spatial predictions of occupancy using occupancy predictions from candidate models for the state and each ecoregion. Prior to interpolation, we checked for collinearity by performing Spearman's rank correlation coefficient (none were over 0.7 correlation). We derived the occupancy probabilities for the state and each ecoregion from predictive state and ecoregion maps, respectively. From the state-level interpolation, we derived occupancy probability across private and public land categories. We broke public land categories into parks and public use (combination of local and county parks, public use areas, and recreational areas), military, national forest, national park, national wildlife refuge, natural area and easements, state parks, wilderness area, and wildlife management area.

Results

From 2014 to 2019, Arkansas Game and Fish Commission staff conducted 5,714 bobwhite surveys at 1,648 survey points across the state of Arkansas (Data S1, *Supplemental Material*). In total, staff conducted 1,282 surveys in the OZM, 913 in the OUM, 728 in the ARV, 1,457 in the GCP, and 1,457 in the MAV (Table 3). We detected bobwhite at 628 of 5,714 surveys (11%) statewide (naïve occupancy = 0.11). The proportion of sites where surveyors detected bobwhite varied by ecoregion with the highest occurring in ARV (bobwhite detected in 28% of surveys) and the lowest occurring in GCP (bobwhite at 3% of surveys; Table 4).



Table 3. Number of survey points and surveys conducted for northern bobwhite *Colinus virginianus* from 2014 to 2019 across the entire state of Arkansas broken down by ecoregion.

Ecoregion	No. of survey points	No. of surveys
Arkansas River Valley	208	728
Gulf Coastal Plain	390	1,457
Mississippi Alluvial Valley	435	1,334
Ouachita Mountains	225	913
Ozark Mountains	390	1,282
Total	1,648	5,714

At the state level, bobwhite occupancy probability was 0.29 and detection 0.05 (Table 4). Percentage of ESH land cover most influenced occupancy probability (Table 5). Model predictions indicated high occupancy probabilities (> 0.90) when a large amount of ESH was present adjacent to the survey point (> 90%; $\beta = 0.77$; UI = 0.41, 1.20; Figure 2). Rates of colonization (0.18) and extinction (0.16) were low, half that of occupancy (Table 4). During the course of the study occupancy probability remained low and relatively constant (Figure 3).

When we evaluated bobwhite occupancy at the ecoregion level, different patterns emerged in some areas (Table 5). The ARV had higher mean occupancy (mean = 0.49; SD = 0.12) and detection probabilities (mean = 0.34; SD = 0.06) than the state overall (Table 4). Percentage of emergent herbaceous wetland, ESH, forest, and herbaceous land covers most influenced occupancy probability (Table 5). Predictions from this model indicated avoidance of herbaceous wetland ($\beta = -8.6$; UI = -22.54, -1.43) and forested habitats ($\beta = -0.81$;

UI = -1.44, -0.23), with high occupancy probabilities (> 0.90) when ESH land cover proportions were high (> 0.75; $\beta = 1.15$; UI = 0.43, 2.19) and herbaceous habitat was available ($\beta = 3.06$; UI = 0.76, 7.98; Figure 2). Mean rates of colonization (mean = 0.11; SD = 0.03) and extinction were low (mean = 0.08; SD = 0.03; Table 4), and occupancy probability fluctuated greatly across the sampling years (Figure 3).

Bobwhite detection probabilities in the OUM and OZM were similarly high, while occupancy probability was much larger in the OUM than OZM. In the OUM, occupancy probability was 0.73 and detection was 0.65 (Table 4). Land cover richness was the best predictor of bobwhite occupancy with bobwhite more likely to occur in patchier landscapes ($\beta = 6.04$; UI = 1.68, 19.16; Figure 2; Table 5). Colonization (0.35) was higher than extinction (0.12) rates (Table 4), though occupancy probability showed some evidence of decrease across the sampling years (Figure 3). Occupancy probability was much lower in the OZM (mean = 0.18; SD = 0.03), though detection probability (mean = 0.90; SD = 0.05) was higher than OUM (Table 4). Percentage ESH, hay-pasture, and developed open-space land covers and biomass were the best predictors of bobwhite occupancy (Table 5). Bobwhite strongly avoided developed open spaces ($\beta = -0.50$; UI = -0.98, -0.03), and were only moderately (occupancy 50–75%) influenced by ESH ($\beta = 0.69$; UI = 0.29, 1.09), hay-pasture ($\beta = 0.49$; UI = 0.11, 0.87), and biomass ($\beta = 0.56$; UI = 0.11, 1.02; Figure 2). Mean rate of colonization was low (mean = 0.23; SD = 0.83), while mean extinction was high (mean = 0.83; SD = 0.01; Table

Table 4. Naïve occupancy (percentage of points where northern bobwhite were detected), and occupancy (psi), colonization (gamma), extinction (epsilon), and detection (p) probabilities from dynamic occupancy models of northern bobwhite *Colinus virginianus* across Arkansas from 2014 to 2019. Lower and upper 95% uncertainty intervals are in parentheses. We only included models that converged and provided meaningful predictors of bobwhite occupancy. Variables in top candidate models include percentage of early successional (PESH), percentage of emergent herbaceous wetland (PEHW), percentage of forest (PForest), percentage of herbaceous (PHerb), percentage of barren land (PBL), percentage of developed open space (PDevOS), and percentage of hay-pasture (PHP) National Land Cover Database land cover classes within 500 m of survey point; richness (Rich) of NLCD land cover classes within 500 m; mean biomass within 500 m; and distance to nearest divided highway (DistHwy).

Model	Naïve occupancy	Occupancy probability	Colonization probability	Extinction probability	Detection probability
Arkansas					
psi(PESH)gam(.)eps(.)p(route)	0.11	0.29 (0.21–0.40)	0.18 (0.11–0.31)	0.16 (0.07–0.33)	0.05 (0.01–0.28)
Arkansas River Valley					
psi(PEHW)gam(.)eps(.)p(route)	0.28	0.66 (0.09–0.87)	0.10 (0.01–0.21)	0.06 (0.01–0.16)	0.25 (0.08–0.49)
psi(PESH)gam(.)eps(.)p(route)	—	0.41 (0.24–0.64)	0.09 (0.01–0.20)	0.06 (0.01–0.15)	0.37 (0.09–0.76)
psi(PForest)gam(.)eps(.)p(route)	—	0.41 (0.23–0.63)	0.10 (0.03–0.22)	0.07 (0.02–0.17)	0.38 (0.11–0.80)
psi(PHerb)gam(.)eps(.)p(route)	—	0.47 (0.27–0.69)	0.16 (0.06–0.31)	0.12 (0.01–0.34)	0.36 (0.13–0.73)
Gulf Coastal Plain					
psi(PBL)gam(.)eps(.)p(route)	0.03	—	—	—	—
Mississippi Alluvial Valley					
psi(DistHwy)gam(.)eps(.)p(route)	0.05	—	—	—	—
Ouachita Mountains					
psi(Rich)gam(.)eps(.)p(route)	0.17	0.73 (0.41–0.93)	0.35 (0.15–0.93)	0.12 (0.10–0.38)	0.65 (0.34–0.99)
Ozark Mountains					
psi(PESH)gam(.)eps(.)p(route)	0.13	0.15 (0.09–0.22)	0.23 (0.14–0.33)	0.84 (0.57–0.98)	0.95 (0.48–0.99)
psi(PHP)gam(.)eps(.)p(route)	—	0.16 (0.09–0.34)	0.23 (0.13–0.35)	0.83 (0.51–0.98)	0.91 (0.33–0.99)
psi(Biomass)gam(.)eps(.)p(route)	—	0.17 (0.11–0.26)	0.23 (0.13–0.35)	0.82 (0.52–0.98)	0.83 (0.53–0.99)
psi(PDevOS)gam(.)eps(.)p(route)	—	0.22 (0.14–0.32)	0.23 (0.13–0.34)	0.83 (0.53–0.99)	0.84 (0.24–0.99)

Table 5. Top-ranked occupancy models influencing occupancy of northern bobwhite *Colinus virginianus* for the state of Arkansas and each ecoregion from 2014 to 2019. Models were ranked with expected predictive accuracy (elpd) values calculated using a leave-one-out cross-validation approach. Variables in top candidate models include percentage of early successional (PESH), percentage of emergent herbaceous wetland (PEHW), percentage of forest (PForest), percentage of herbaceous (PHerb), percentage of barren land (PBL), percentage of developed open space (PDevOS), and percentage of hay-pasture (PHP) National Land Cover Database (NLCD) land cover classes within 500 m of survey point; richness (Rich) of NLCD land cover classes within 500 m; mean biomass within 500 m; and distance to nearest divided highway (DistHwy).

Model	K	elpd	Δelpd	ΔSE	Weight
Arkansas					
psi(PESH)gam(.)eps(.)p(route)	49.24	-922.72	0.00	0.00	0.86
Arkansas River Valley					
psi(PEHW)gam(.)eps(.)p(route)	12.13	-238.96	0.00	0.00	0.37
psi(PESH)gam(.)eps(.)p(route)	12.91	-240.05	-1.09	3.95	0.11
psi(PForest)gam(.)eps(.)p(route)	12.11	-241.64	-2.68	3.96	0.08
psi(PHerb)gam(.)eps(.)p(route)	17.39	-241.73	-2.77	5.17	0.13
Gulf Coastal Plain					
psi(PBL)gam(.)eps(.)p(route)	12.71	-99.00	0.00	0.00	0.27
Mississippi Alluvial Valley					
psi(DistHwy)gam(.)eps(.)p(route)	7.36	-52.14	0.00	0.00	0.07
Ouachita Mountains					
psi(Rich)gam(.)eps(.)p(route)	15.81	-318.67	0.00	0.00	0.22
Ozark Mountains					
psi(PESH)gam(.)eps(.)p(route)	7.38	-195.20	0.00	0.00	0.26
psi(PHP)gam(.)eps(.)p(route)	7.53	-198.04	-2.83	2.73	0.05
psi(Biomass)gam(.)eps(.)p(route)	7.97	-198.15	-2.94	2.60	0.005
psi(PDevOS)gam(.)eps(.)p(route)	8.22	-198.87	-3.67	4.31	0.12

4), though occupancy probability over time was constant (Figure 3).

Surveyors detected bobwhite in only 3% of surveys in the GCP and 5% of surveys in the MAV. Due to the rarity of the species in these regions, model goodness of fit was

poor and model-averaged predictions had extremely large confidence intervals around the estimate and provided little explanatory power (Tables 4 and 5). Given the uncertainty and low explanatory power of model results from the GCP and MAV, we do not show results in figures.

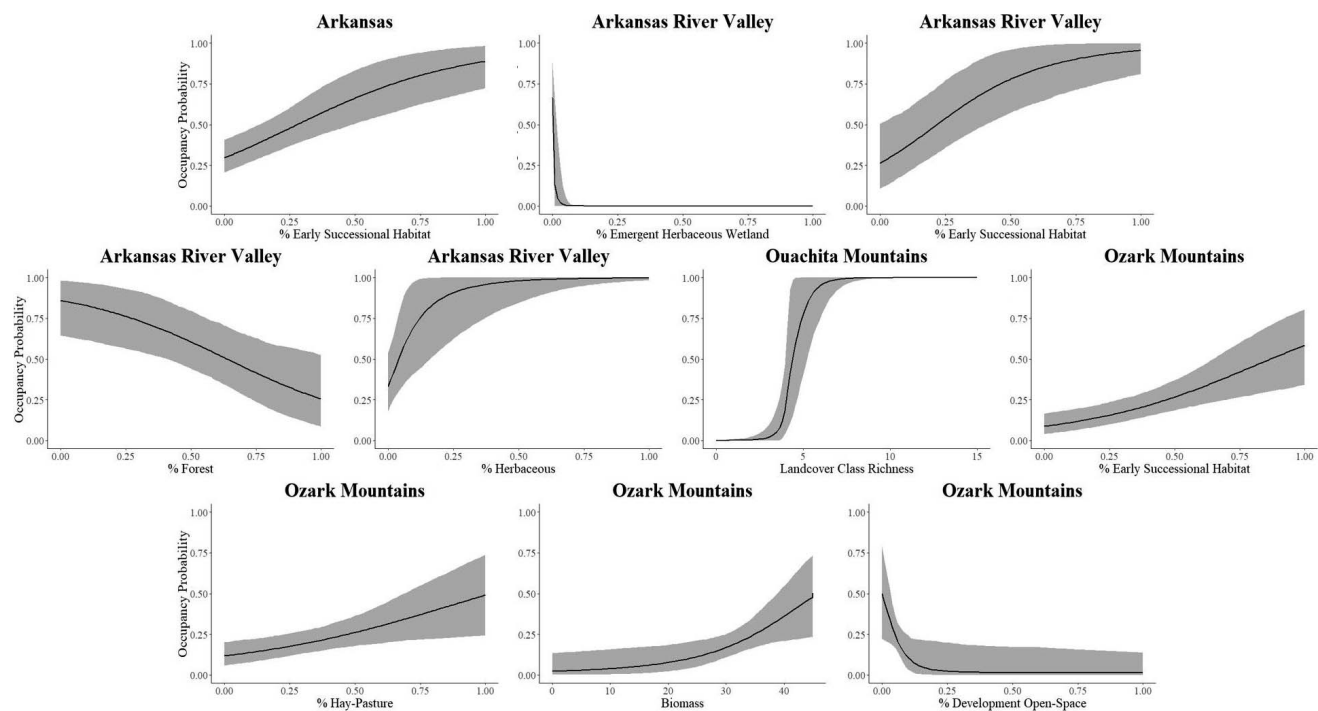


Figure 2. Relationship between northern bobwhite *Colinus virginianus* occupancy probability and top-ranked landscape models for Arkansas and each ecoregion for which model goodness-of-fit was confirmed. Upper and lower 95% uncertainty intervals are presented in the gray band.

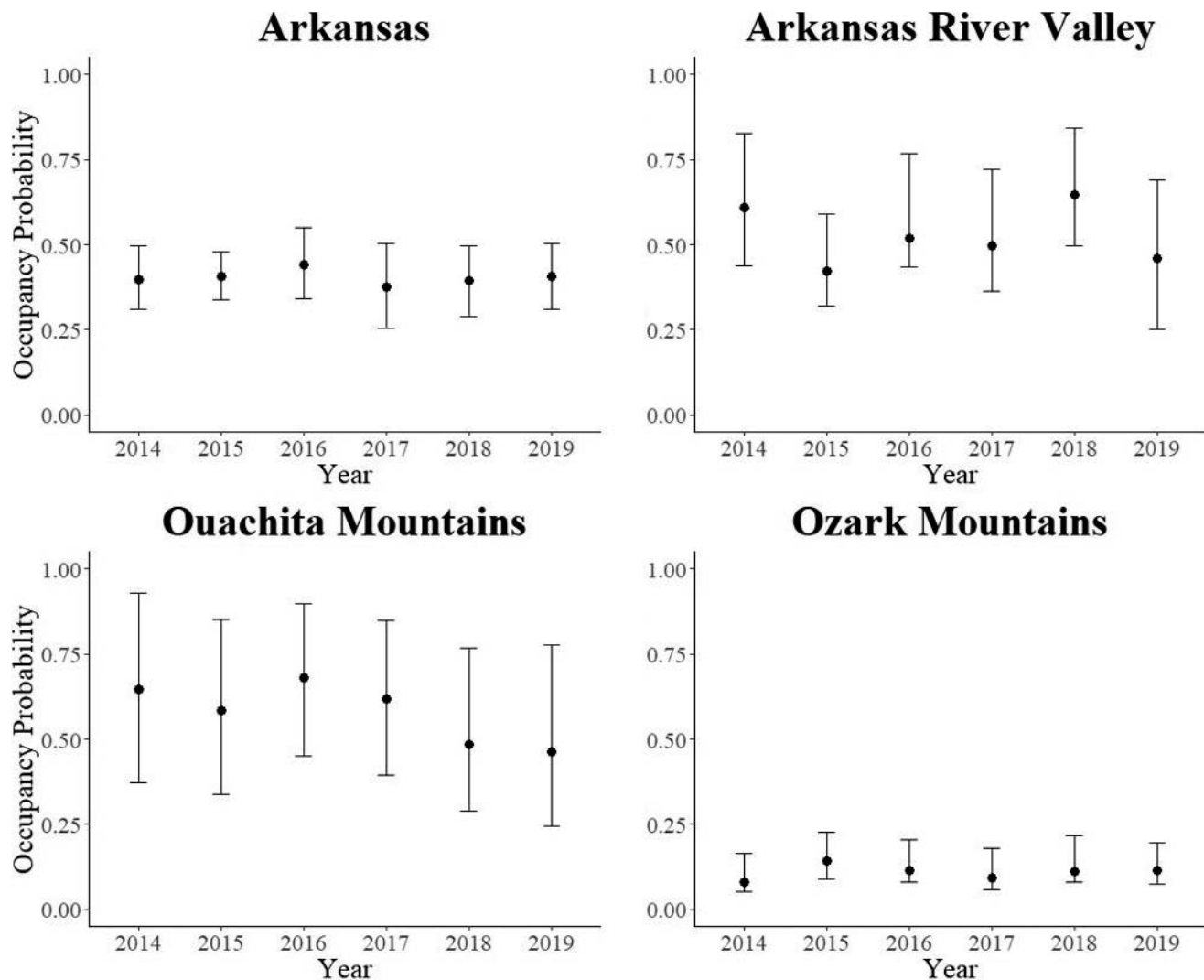


Figure 3. Occupancy probability of northern bobwhite *Colinus virginianus* from 2014 to 2019 estimated from posterior distribution using top candidate model for each ecoregion. Upper and lower 95% uncertainty intervals are presented in the black vertical lines.

The predictions of occupancy across the entire state of Arkansas illustrate how the distribution of early successional habitat and related herbaceous cover throughout the state jointly influence the probability of bobwhite occurrence (Figure 4). Based on state-level predictions, the state of Arkansas had 17.2% likely occupied habitat ($\geq 75\%$ occupancy; Table 6). The ARV had the highest percentage of habitat likely occupied by bobwhite (40.0%) and the MAV had the lowest percentage (1.9%; Table 6). Using the ecoregions predictions (Figure 4), ARV only had 20.8% likely occupied habitat and OZM had less than 1%, while OUM had 52.8% likely occupied habitat (Table 6). Of the likely occupied habitat available in the state, 22,527 km² occurred on private land and 1,195 km² on public. Within the public land properties, national forests had a large percentage of habitat (66.8%), followed by wildlife management areas (16.5%) and military properties (11.9%), while less than 10% of habitat likely occupied by bobwhite was available in each of the remaining property types (Table 7).

Discussion

Bobwhite are generally associated with ESH, although this can take many different forms across the range of the species, from grassland to shrubland to early seral stages of forests and to actively grazed pastures (Taylor et al. 2000; Howell et al. 2009; Brennan et al. 2020). Our top model predicting occupancy at a state scale indicated that bobwhite were most likely to be present when a large proportion of the adjacent landscape was composed of ESH land cover. These results support what researchers know about bobwhite preference for patchy habitats with access to open ESH. Habitat quality is essential for maintaining viable bobwhite populations and a small area with a mixture of all necessary microhabitat features is capable of maintaining bobwhite (Guthery 1997; Taylor et al. 1999; Collins et al. 2009). However, large connected patches of habitat are likely necessary for long-term stability (Gomez and Reyna 2017).

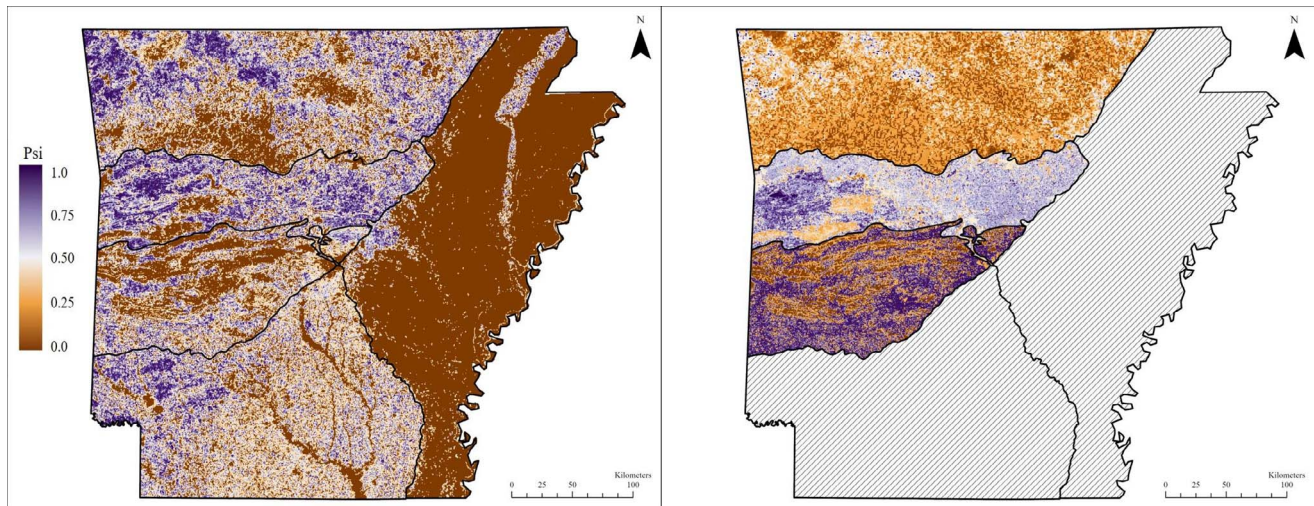


Figure 4. Occupancy probability of northern bobwhite *Colinus virginianus* for the entire state of Arkansas (left) and each ecoregion (right) from 2014 to 2019. Only models for the Arkansas River Valley, Ouachita Mountains, and Ozark Mountains ecoregions converged and provided meaningful predictors of northern bobwhite occupancy.

Our state-level occupancy approach confirmed the importance of ESH in predicting bobwhite occupancy, but the ecoregion-level models provided finer precision. Arkansas is a diverse state and, unsurprisingly, we found differences in patterns of bobwhite occupancy between the ecoregions (Table 6). Identifying trends at the ecoregion level could provide higher resolution in identifying priority areas for management or acquisition. However, the downside of finer-scale approaches is the reduction in sample size, which in conjunction with low detections resulted in an inability to predict occupancy for two of the five ecoregions in Arkansas.

We detected the greatest rate of occupancy in the ARV. The proportion of ESH and herbaceous land cover surrounding survey points positively influenced bobwhite occupancy in this region. The ARV is a diverse region and contains both savannah and remnant tallgrass prairie (Brye et al. 2004). The highest concentration of bobwhite reliably detected in the ARV was on Fort Chaffee Maneuver Training Center, a > 26,300-ha military reserve that actively manages large expanses of savannah and grassland. Fort Chaffee alone contains 14.5% of the public land area that bobwhite are reliably identified to occupy (Table 7). Additionally, Fort Chaffee

is in proximity to several tallgrass prairie patches including Cherokee Prairie and H.E. Flanagan Prairie. These large, highly managed properties represent the largest contiguous patches of herbaceous grassland in the state. The size and close proximity of these properties likely explains why bobwhite occupancy is consistently high in this region. Our predicted occupancy map for the ARV identified few areas of high occupancy probability outside of this cluster (Figure 4). Because bobwhite do not typically disperse long distances (Kassinis and Guthery 1996, Townsend et al. 2003) land acquisition and habitat restoration in the vicinity of these hotspots could improve metapopulation viability of bobwhite for the region.

The proportion of surrounding ESH and hay-pasture most influenced bobwhite occupancy in the OZM. Likely occupied bobwhite habitat was limited to a few core areas, though much of the ecoregion was characterized by moderate habitat (25–75% occupancy), mostly occurring in the form of glades, open woodlands, scattered remnant prairies, and pasture. The survey points where bobwhite were most consistently detected in this region were in proximity to Harold E. Alexander Wildlife Management Area, a state-managed property

Table 6. Area of habitat likely occupied ($\geq 75\%$ occupancy) by northern bobwhite *Colinus virginianus* based on predicted occupancy for the state of Arkansas and each ecoregion. Area (km²) and percentage of the total area (in parentheses) are included for the state and each ecoregion. Estimates are derived from predictive state-level map for the entire state and each ecoregion. Only models for the Arkansas River Valley, Ouachita Mountains, and Ozark Mountains converged and provided meaningful predictors of northern bobwhite occupancy for ecoregion estimates. Values are presented as km² (%).

Occupancy probability	AR	ARV	ARV ^a	MAV	GCP	OUM	OUM ^a	OZM	OZM ^a
0–25%	63,270 (46.0)	2,647 (16.6)	108 (0.7)	35,518 (89.4)	8,662 (25.7)	6,919 (42.2)	3,529 (21.5)	9,524 (29.8)	11,375 (35.8)
26–50%	30,118 (21.9)	3,338 (20.9)	3,120 (19.5)	2,112 (5.3)	11,992 (35.6)	4,517 (27.5)	3,646 (22.2)	8,159 (25.5)	18,160 (57.1)
51–75%	20,436 (14.9)	3,603 (22.6)	9,407 (58.9)	1,061 (2.7)	7,004 (20.8)	2,612 (15.9)	579 (3.5)	6,156 (19.3)	1,997 (6.2)
76–100%	23,722 (17.2)	6,376 (40.0)	3,325 (20.8)	755 (1.9)	6,053 (18.0)	2,379 (14.5)	8,661 (52.8)	8,159 (25.6)	246 (0.8)

AR = Arkansas, ARV = Arkansas River Valley; MAV = Mississippi Alluvial Valley; GCP = Gulf Coastal Plain; OUM = Ouachita Mountains; OZM = Ozark Mountains

^a Estimates derived from predictive ecoregion maps.

Table 7. Land ownership and area of habitat likely occupied (\geq 75% occupancy) by northern bobwhite *Colinus virginianus* based on predictions of occupancy for public land categories from 2014 to 2019. Area (km²) and percentage of the total area available in the state (in parentheses) are included for private and public lands, and then further broken down into categories within public land. Estimates derived from predictive state-level map.

Land ownership	Likely occupied habitat, km ² (%)
Private	22,527 (95)
Public	1,195 (5)
National forest	800 (66.8)
Wildlife management area	197 (16.5)
Military	142 (11.9)
National park	18 (1.5)
National wildlife refuge	16 (1.4)
Parks and public use	9 (0.7)
State park	5 (0.5)
Natural area and easements	4 (0.4)
Wilderness area	4 (0.3)

that provides bobwhite habitat in the form of wildlife food plots, maintained open fields, and glades. Other public properties such as Sylamore Wildlife Management Area in the OZM are managed for bobwhite, but we did not conduct surveys on these properties. Other areas of reliable bobwhite occupancy occurred where forestry activity and pastures were in close proximity. The OZM is heavily forested with large tracts occurring in the Ozark National Forest. Silvicultural activities, when occurring near ESH, have the potential to create and improve bobwhite habitat. Several studies have shown that bobwhite incorporate more forest edge than anticipated within their home ranges (Roseberry and Sudkamp 1998) and that forest edge is often valuable for bobwhite, providing food and cover resources (Yoho and Dimmick 1972). Forest management by private timber industries and the U.S. Forest Service in this region can create and maintain suitable bobwhite habitat by incorporating strategic disturbance associated with low- to moderate-intensity logging (Arner 1972). However, these habitats are ephemeral and often harbor bobwhite for 2 or 3 y before regeneration makes the area unsuitable without follow-up management (Arner 1972). Management for bobwhite in this part of the state should also benefit by restoring glades through burning and red cedar removal, managing the remnant prairies to ensure they provide high-quality bobwhite habitat, and incorporating silvicultural practices such as those described above to provide open woodlands and clear-cuts in proximity to ESH. Additional opportunities may exist by incorporating rotational grazing on cattle pastures to improve compatibility between cattle and bobwhite (Hernández and Guthery 2012).

Bobwhite occupancy in the OUM was most influenced by richness of land-cover classes and notably, included no measure of ESH or related herbaceous cover. Thus unsurprisingly, there was a large difference between the amount of likely occupied bobwhite habitat in the state-level map versus the ecoregion-specific predictions (Table 6; Figure 4). In fact, predicting bobwhite occupancy in the OUM led to some of the largest

mismatches between what we know of bobwhite distribution in the state and where our map predicted their occurrence. The Ouachita National Forest constitutes much of the OUM. Managers on this large, publicly owned area use forest thinning and prescribed burning to maintain a diverse habitat structure and species composition. Wildlife managers know several of these areas as bobwhite hot spots and yet because our survey points did not traverse any of the areas currently managed in this way, our model failed to capture the importance of prescribed fire as a predictor of bobwhite occupancy. Future surveys should incorporate both managed and unmanaged portions of the Ouachita National Forest to better understand habitat associations between bobwhite and ongoing management.

Across the state of Arkansas, habitat likely occupied by bobwhite occurred primarily on private land (95%; Table 7). Bobwhite occupancy probability varied across the many public land types in Arkansas and no single public land management entity owns the majority of available bobwhite habitat across the state (Table 7). Based on state-wide models for public lands, the areas of highest likelihood of occupancy were in national forests (66.8%), wildlife management areas (16.5%), and military installations (11.9%; Table 7). Management for bobwhite in Arkansas should benefit from cooperation between these management agencies and private landowners. Thus, landscape-scale planning should ensure connectivity between surrounding private landowners with stable bobwhite occupancy such as Fort Chaffee and Camp Robinson military installations, Ouachita and Ozark national forests, and Sylamore Wildlife Management Area. Additionally, future surveys should occur in and around these properties to better understand patterns in occupancy and refine habitat associations by ensuring surveys capture the full range of land cover variables.

Bobwhite are declining across their range (Sauer et al. 2005, 2008). We found that during the 6 y of this study in Arkansas, predicted bobwhite occupancy was stable, but relatively low. Further, we detected very few bobwhite across large expanses of the state in the GCP and MAV. In the GCP, timber companies privately own > 70% of land and plant forests in short rotations of fast-growing loblolly pines *Pinus taeda* and shortleaf pines *Pinus echinata* (Bragg 2002; Zhang et al. 2010). These dense, short-rotational forests are unsuitable for bobwhite and this form of silviculture is incompatible with bobwhite. Similarly, the industrial agricultural practices that dominate the MAV are unsuitable for bobwhite; research has linked such practices to bobwhite declines across much of the Midwestern United States (Daily 2002). Industrial agriculture presents numerous challenges to bobwhite persistence including increased fragmentation due to increasing agricultural field size and depletion of critical food sources, reduced insect populations due to increased pesticide use, and reduced availability of waste grain due to improved harvest machinery (Daily 2002). The observed low occupancy rate in Arkansas and across much of bobwhite range highlights the urgency of identifying suitable bobwhite habitat for monitoring and conservation purposes.



Using monitoring data in Arkansas, we created occupancy models demonstrating that bobwhite occupancy can be predicted on a large spatial scale (i.e., statewide) based on the availability of ESH and related herbaceous cover, and through avoidance of unsuitable habitat types (wetlands and mature forests). When samples are robust and detections are not rare, managers can also apply these models to smaller spatial scales (e.g., ecoregion) to provide more in-depth information about the influence of land cover variables on bobwhite occupancy regionally. This approach allows managers to use readily available remote sensing data (e.g., NLCD layers) in combination with long-term monitoring to identify areas likely occupied by bobwhite, which in turn could lead to the identification of high-priority areas for management, conservation, and monitoring, and to partnerships between managers on public and private lands. The approach detailed herein could be readily adapted to additional locations to provide managers critical information to improve conservation of bobwhite.

Supplemental Material

Please note: The Journal of Fish and Wildlife Management is not responsible for the content of functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Data S1. Spreadsheet containing data for survey data ($n = 5,714$), location ($n = 1,648$), and occupancy status of northern bobwhite *Colinus virginianus* collected in Arkansas during 2014–2019. The spreadsheet also provides site-specific data collected via remote sensing. We have formatted data for use in analysis of occupancy using the unmarked or ubms packages, or both, in R.

Available: <http://doi.org/10.3996/JFWM-21-002.S1> (660 KB CSV)

Table S1. Document containing complete model selection tables for estimation of occupancy of northern bobwhite *Colinus virginianus* for the state of Arkansas and each ecoregion from 2014 to 2019. We ranked models with expected predictive accuracy (elpd) values calculated using a leave-one-out cross-validation approach.

Available: <http://doi.org/10.3996/JFWM-21-002.S2> (35 KB DOCX)

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