



Original Article

Nesting Ecology of Northern Bobwhite on a Working Farm

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ABSTRACT Creating early successional vegetation on working farms can increase northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) abundance with little reduction in crop production, but specific effects of field border establishment on bobwhite nesting ecology are not well understood. We monitored bobwhite nesting on a 1,740-ha working farm with 19% of property managed for early successional vegetation in southeastern North Carolina, USA. We monitored 133 radio-marked bobwhites from 1 April to 30 September in 2014 and 2015. We modelled nest-site selection by comparing paired nest and random reference sites and modeled effects of habitat covariates on daily nest survival. Forb, shrub, and native warm-season grass cover were greater at nest sites than reference sites with forb cover the strongest predictor of nest-site selection. Bobwhite nested at a greater density in areas managed for fallow vegetation (1 nest/3 ha) than in planted warm-season grasses and forbs (1 nest/5 ha). The daily nest survival rate over 2 years was 0.964 (SE = 0.007), and was not significantly influenced by any modeled covariate. Naïve nest success (nest successes/total nests) was 46.9%. The importance of forbs as nesting cover indicates bobwhite abundance in areas dominated by row-crop agriculture may be limited by low nest initiation from a lack of herbaceous nesting cover. Hence, the creation of fallow herbaceous vegetation on working farms should be prioritized to increase bobwhite reproduction within agricultural landscapes. Furthermore, planting warm-season grasses is not necessary because volunteer forbs and grasses provide as good or better nesting cover and can be less costly to establish. © 2020 The Wildlife Society.

KEY WORDS agriculture, *Colinus virginianus*, early successional, field borders, forbs, nest survival, northern bobwhite, private land management.

Land-use changes have resulted in a continual loss of high-quality early successional plant communities from many landscapes in the eastern United States, furthering a concomitant decline in wildlife associated with early successional plant communities (Samson and Knopf 1994, Best et al. 1997). The continued intensification of farming practices has reduced the amount of fallow land on most agricultural landscapes, and unmanaged woodlands have been allowed to succeed into closed-canopy forest (Brennan 1991, Burger 2001). Additionally, fire suppression has

reduced the effect of a primary natural disturbance to set back succession and influence plant communities (Engstrom et al. 1984). Concurrent with changes to the region's landscape, the northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) has declined 82% since the mid-20th century (Sauer et al. 2014). Its popularity as a game bird has made the bobwhite a flagship species to support the conservation of early successional communities (Riffell et al. 2008, Palmer et al. 2011, Hernandez et al. 2013).

Cropland comprises 198 million ha, 26.8% of the land area within the eastern United States (Nickerson et al. 2011). This large proportion of land area has the potential to provide opportunities for conservation of early successional vegetation on private land. The National Bobwhite Conservation Initiative estimated 78% of their target increase of 2.7 million

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coveys could be attained through conservation on private farmland (Palmer et al. 2011). Creating bobwhite habitat on working farms may reduce the cost of habitat management because unused or unproductive areas can be converted more readily to early successional vegetation than can areas with a large proportion of timber (Brennan 1991, Greenfield et al. 2003, Hernandez et al. 2013). Converting as little as 2–3% of total row-crop area into early successional vegetation can increase bobwhite abundance on working farms while maintaining an economically critical land use (Burger et al. 1990, King and Savidge 1995, Riddle et al. 2008, Bowling et al. 2014). Additionally, agricultural land can be kept in early successional vegetation more easily than can forested lands because the former lacks a substantial woody component, which often can be labor-intensive and costly to reduce to the proper density or successional stage adequate for high-quality bobwhite habitat (Greenfield et al. 2003, Gill et al. 2006).

Though extensive research has been conducted on bobwhite population response to the creation of early successional vegetation on agricultural landscapes (e.g., Riddle et al. 2008, Evans et al. 2013, Bowling et al. 2014), relatively little research has focused on how the creation of early successional vegetation around crop fields affects nesting ecology of bobwhites (but see Puckett et al. 1995, Berger et al. 2017). Additional understanding of how managed early successional vegetation affects nest-site selection, nest initiation rates, and nest survival on working farms is needed to aid bobwhite population recovery in areas of the eastern United States (Brennan 1991, Best et al. 1997, Burger 2001, Riddle et al. 2008). Considerable research has been conducted on nesting ecology of bobwhites in forested systems managed for bobwhites in the southeastern United States, but populations within these systems may be limited by different habitat components (e.g., brood cover) than those residing in areas dominated by agricultural practices (DeVos and Mueller 1993, Hughes et al. 2005, Terhune et al. 2006). Additionally, information on characteristics of productive nesting sites (e.g., vegetation composition and structure) is essential to maximizing benefits from restoration efforts on working farms.

Field borders, linear strips of early successional vegetation either left fallow or planted adjacent to agricultural fields, often are used to restore early successional vegetation on working farms (Palmer et al. 2005, Smith et al. 2005, Riddle et al. 2008). Bobwhite abundance has increased following implementation of field borders (Puckett et al. 1995, Palmer et al. 2005, Riddle et al. 2008, Evans et al. 2013, Bowling et al. 2014). Borders containing a mixture of native warm-season grasses and forbs provide a combination of nesting cover and arthropod prey for broods (Moorman et al. 2013). However, there is concern that potential benefits of improved nesting and brooding cover may be outweighed if nest predator activity is concentrated in borders and nest survival is low (Puckett et al. 1995).

We investigated nesting ecology of bobwhite on a 1,740-ha farm that experienced 9 years of habitat management (e.g., creation of fallow field borders) prior to our study. Our objectives were to use radio-marked bobwhites residing on a working farm to 1) characterize vegetation composition of

nest sites, 2) determine to what extent bobwhites nested in field borders and other managed noncrop vegetation, and 3) identify the relationship between nest-site vegetation composition and bobwhite nest survival. We hypothesized monitored bobwhite would 1) select nest sites with a greater percent cover of grass than at reference sites, 2) select planted native warm-season grasses over fallow vegetation and cropland for nesting cover, and 3) experience greater nest survival in sites with a greater grass and forb cover.

STUDY AREA

We conducted our study on a 1,740-ha commercial swine farm located in Bladen County, North Carolina, USA. This farm was in the southeastern coastal plain physiographic region, which was characterized by low topography and sandy, nutrient-poor soils mottled with areas of highly fertile organic soils that are favorable for row-crop agriculture.

At the time of this study, the farm had 56 ha of fallow field borders averaging 6.1 m (range = 3–18 m) in width on 790 ha of row crops and 21 ha of fallow nonlinear vegetation areas. Managers began establishing borders in 2005 and maintained early successional vegetation within borders by disking or burning every 2–3 years. Managers also planted 19 ha (range = 1.2–2.8 ha) of nonlinear areas in little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), indiangrass (*Sorghastrum nutans*), or switchgrass (*Panicum virgatum*) between 2005 and 2010. Managers planted 49 ha of longleaf pine (*Pinus palustris*) in 2010. Red bay (*Persea borbonia*), red maple (*Acer rubrum*), gallberry (*Ilex coriacea*), swamp cyrilla (*Cyrilla racemiflora*), sweet pepperbush (*Clethra alnifolia*) and maleberry (*Lyonia ligustrina*) were dominant species in the 182-ha of shrubland maintained with periodic roller chopping.

The long-term average minimum and maximum temperatures during bobwhite nesting season at the site were 18.8 C and 30.0 C, respectively, and the average daily precipitation is 0.39 cm. The average minimum and maximum daily temperatures during the nesting seasons in this study were 19.7 C and 30.4 C in 2014, and 20.3 C and 30.9 C in 2015. The average daily precipitation was 0.38 cm in 2014 and 0.35 cm in 2015.

METHODS

We captured bobwhites from 1 February to 4 April, 2014 and 2015 using modified funnel-entrance cage traps baited with soybeans or cracked corn (Stoddard 1931). The North Carolina State University Institutional Animal Care and Use Committee (IACUC) approved the capture and handling procedures used during our study (IACUC Protocol #14-010-O). We placed traps in cleared areas within shrub cover near interfaces with cropland and covered the tops of traps with leafy vegetation to hide captured individuals. We checked trap arrays 3 hours after sunrise and 1 hour before sunset each day. We affixed each individual weighing >150 g with a 320-day very-high-frequency (VHF) radio transmitter containing a 12-hour mortality sensor (model AWE-Q, American Wildlife Enterprises, Monticello, FL, USA). We released captured groups near their original

capture site in the direction of cover to reduce the possibility of postcapture mortality.

We obtained 1 location of each individual each day for ≥ 3 days spread throughout each week from 1 April until 31 July. After 31 July, we reduced the number of collected locations to 1/week on remaining birds until 30 September because of limited resources. We collected location data at various times between 0600 and 1600 hours to increase the likelihood of encountering an individual while it was incubating. We located birds using VHF receivers (model R4000, Advanced Telemetry Systems, Isanti, MN, USA) fixed with 3-element Yagi-style antennas by homing to roughly 50 m of each individual and maintained this distance while recording locations to reduce possibility of pushing individuals into unused cover (White and Garrott 1990). We used handheld Global Positioning System [GPS] navigators (model Oregon 450, Garmin International, Inc., Olathe, KS, USA) to record locations. We then recorded an azimuth and estimated distance to each individual. If we could not locate an individual with Yagi antennas, we searched an approximately 5-km radius from the last known location using a truck-mounted omnidirectional antenna. We declared an individual lost if we could not locate it for 2 weeks.

We located nests by approaching individuals observed via telemetry as being in the same location for 2 consecutive monitoring days. If that individual was determined to be attending a nest, we marked the specific location using a GPS unit. We recorded the nest status (i.e., nest building, egg laying, incubating) based on visual observations of the nest and behavior of the monitored individual. We conducted an egg count on all nests once the nest was visually observed to have reached the incubation stage. After we conducted the egg count, we continued to monitor the presence of the incubating adult with the same frequency from >50 m distance to minimize disturbance. Once the incubating adult left the nesting site, we approached the site to determine nest fate (i.e., successful, depredated, abandoned). We categorized nests as successful if any eggs exhibited pipping. We categorized nests as depredated if broken eggshells were present or all eggs were absent. We

considered nests to be abandoned if intact eggs were left unattended for ≥ 3 consecutive monitoring days.

We documented vegetation cover at nest sites following determination of a final nest outcome. We collected vegetation measurements within 10 days of observing the outcome of a nest to minimize any changes in vegetation from what was experienced by the incubating adult. We measured vegetation at each meter along 2 intersecting 10-m transects. We collected measurements using a 3.18-cm (1.25-in) \times 2-m polyvinyl chloride pole. At each sample point within a plot, we recorded the ground cover (i.e., bare soil, thatch, leaf litter) below the pole and the vegetation species in contact with the pole; we calculated percent cover metrics by dividing the number of sample points with a contact by the total number of sample points (21) at a plot (Moorman and Guynn 2001). We designated vegetation cover types (i.e., woody debris, native warm-season grasses, other grass species, forbs, shrubs, trees, corn, soybeans) by grouping related or structurally similar plant species to create covariates for statistical analysis (Table 1).

To determine nest-site selection, we randomly selected 3 reference points for each nest from a distance between 20 m and 250 m of the nest. We selected the maximum distance between nest and reference points based on the average home range of individuals residing in an area with similar land cover (Lohr et al. 2011). We allowed reference points to fall within any vegetation type in the specified random distance range to evaluate nest-site selection across all vegetation types available to bobwhites on this farm. For any reference point not falling within a vegetated area (i.e., body of water, barn, road), we decreased the random distance measurement until the obstruction was outside of the entire vegetation plot. We compared vegetation composition and structure between each nest and corresponding reference points using lme4 to create a generalized linear model with a binomial outcome that identified nest and reference points (Bates et al. 2015; Program R version 3.6.1, www.r-project.org, accessed 23 Jul 2019). We tested for collinearity of continuous variables using Pearson's correlation coefficients with a ± 0.50 limit. We examined variance inflation factors (VIF) for variables with $VIF > 3$ and tested

Table 1. Covariates used to describe northern bobwhite nest-site selection (SS) and nest survival (NS) in North Carolina, USA (2014–2015).

Description	Analysis
Date of first presence of incubating adult at nest site (± 2 -day accuracy)	NS
Year of study	NS
Distance from nest to nearest mature forest stand ≥ 1 ha	NS
Distance from nest to nearest edge of vegetation patch	NS
Numerical index describing shape of vegetation patch containing nest ^a	NS
Percentage of sample points with bare soil present under the pole	SS, NS
Percentage of sample points in contact with corn	SS, NS
Percentage of sample points in contact with native warm-season grasses (NWSG)	SS, NS
Percentage of sample points in contact with other grasses	SS, NS
Percentage of sample points in contact with forbs	SS, NS
Percentage of sample points in contact with soybean	SS, NS
Percentage of sample points in contact with trees	SS, NS
Percentage of sample points in contact with woody debris	SS, NS
Percentage of sample points in contact with shrubs	SS, NS

^a Patch Shape Index = $P/(2\sqrt{\pi A})$, where P = patch perimeter (m) and A = patch area (m^2).

for nonlinearity using the car package in Program R, adding quadratic terms as needed (Fox 2011). If any variables exhibited correlation $>|0.50|$ or VIF >3 , we removed the variable that would be more difficult to alter through habitat management efforts. We built model selection tables using the reduced set of potentially informative variables and identified the top models by lowest Akaike's Information Criterion, corrected for small sample size (AIC_c ; Zuur et al. 2007). If a model within 2 ΔAIC_c per-parameter difference of the top model was more parsimonious, we selected it as the most informative model (Burnham and Anderson 2002, Arnold 2010).

We estimated effects of vegetation composition and structure on daily nest survival rates using the nest survival model in Program MARK (White and Burnham 1999, Dinsmore et al. 2002). In addition to vegetation cover covariates used in nest-site selection analysis, we included covariates describing date of first presence of an incubating adult at the nest site, study year, linear distance from nest to nearest mature forest stand, linear distance from nest to nearest edge of vegetation patch containing nest, and an index describing the shape of the vegetation patch in the nest survival analysis (Table 1). We used a 2-stage modeling process to first evaluate the effects of year and estimated date of incubation initiation (Table 1). Using the best initial model, we analyzed standardized vegetation cover, distance, and management covariates (Table 1). We ranked nest survival models based on ΔAIC_c and model weights in the same manner as described above for the nest-site selection models.

RESULTS

We captured 104 and 108 individuals during 2014 and 2015, respectively. We captured 9 and 7 individuals/100 trap-nights during the 2 years, respectively. We recaptured 5 individuals in 2015 that originally were captured as juveniles in 2014. We were able to monitor 133 individuals from 1 April to 30 September of 2014 and 2015. During this period, individuals had a naïve survival rate of 37%.

The nesting season spanned from 21 May to 15 September in 2014, and 19 May to 21 September in 2015. We located 39 and 25 nests during the 2014 and 2015 seasons, respectively. We found the majority of these nests to be located in areas consisting of fallow early successional vegetation (Table 2). We located 5 nests (7.8%) during egg laying and 59 nests (92.2%) during incubation. Pooling the number of nests reaching the incubation stage during both years, we observed 1 incubated nest/2 marked individuals alive at the start of the nesting season. Clutch size of nests reaching the incubation stage ranged from 9 to 23 eggs with a mean of 13.58 (SE = 0.36) eggs/nest. Males incubated 36% ($n = 23$) and females 64% ($n = 41$) of all nests. Overall, naïve nest success was 46.9% over both years, with 19 and 10 nests hatching in 2014 and 2015, respectively. Successful nests produced 310 hatchlings (2014 = 202, 2015 = 108), which equates to 2.33 hatchlings/monitored individual.

We censored 2 nests from site selection analysis because the nest-site vegetation was altered prior to data collection,

Table 2. Count and percentage of northern bobwhite nests located within each vegetation type on a working farm in Bladen County, North Carolina, USA (2014–2015).

Vegetation type	Nest count	% Total
Fallow early successional	14	21.8
Nonlinear early successional ^a	13	20.3
Field border ^a	12	18.8
Planted longleaf pine ^a	11	17.2
Mixed forest	4	6.3
Planted native warm-season grass ^a	6	9.4
Row crop	2	3.1
Loblolly pine plantation	0	0.0
Pasture	2	3.1
Total	64	100.0

^a Bobwhite habitat management enacted on this vegetation type.

leaving data from 62 nests for analysis. We removed thatch and leaf litter as variables during analysis because their correlation with other variables exceeded our established threshold. The model that best described the variation in nest-site selection characterized nest sites as exhibiting a greater percentage of area covered in forbs, shrubs, and native warm-season grasses, and a lower percentage of bare soil than random reference sites (Tables 3 and 4). Of the covariates included in the most descriptive model, forb cover had the greatest influence over nest-site selection (Fig. 1). The mean forb cover at nest sites was 52.8% (SE = 4.3%) compared with 15.6% (SE = 1.7%) at reference sites.

We censored 2 nests from nest survival analysis because of alterations to vegetation prior to data collection and 4 additional nests because they failed prior to reaching the incubation stage, leaving 58 nests for analysis. The daily nest survival rate did not differ between years; it was 0.964 (SE = 0.009) in 2014 and 0.962 (SE = 0.010) in 2015. Daily nest survival rate pooled over 2 years was 0.964 (SE = 0.007). Pooled nest survival for the entire incubation period (23 days) was 0.430 (95% CI = 0.309–0.596). No covariate model created for the analysis was determined to better describe the variation in nest survival than the null model (Table 5).

Table 3. Model specification, log-likelihood, AIC_c , and ΔAIC_c , for top 5 and null models of northern bobwhite nest-site selection on a working farm in Bladen County, North Carolina, USA (2014–2015).

Model ^a	Log(L_i) ^b	AIC_c ^c	ΔAIC_c ^d
Bare soil + Forbs + NWSG + Shrubs	−97.01	204.27	0.00
Bare soil + Forbs + NWSG + Shrubs + Woody debris	−95.99	204.33	0.06
Bare soil + Forbs + NWSG + Shrubs + Woody debris + Soy	−95.28	205.01	0.74
Bare soil + Forbs + NWSG + Shrubs + Corn	−96.51	205.35	1.08
Bare soil + Forbs + NWSG + Shrubs + Soy	−96.60	205.45	1.17
Null	−141.71	285.42	81.15

^a 'NWSG' is percentage of sample points in contact with native warm-season grasses.

^b Log(L_i) is log-likelihood.

^c AIC_c is Akaike's Information Criterion corrected for small sample size.

^d ΔAIC_c is difference in AIC_c from top-ranking model.

Table 4. Model parameters, coefficients, and standard errors for top model predicting northern bobwhite nest-site selection on a working farm in Bladen County, North Carolina, USA (2014–2015).

Parameter	β	SE
Bare soil	−0.038	0.021
Forbs	0.043	0.007
Native warm-season grasses	0.020	0.008
Shrubs	0.021	0.008

DISCUSSION

Fallow, early successional vegetation provided nesting cover for northern bobwhite on working farms. Moreover, our results indicate a lack of available nesting cover likely limits bobwhite reproduction on working farms without field borders or other areas of noncrop herbaceous vegetation. Early successional vegetation accounted for just 9% of the farm property, yet 64.1% of nests were located within these areas. An additional 9.4% of nests were located on farm road ditch banks directly adjacent to maintained early successional field borders.

Though we hypothesized that grass cover would drive bobwhite selection of nest sites, individuals may have more strongly selected nesting sites based on greater forb cover because of the multiple benefits afforded to both the incubating adult and the posthatching brood (Harper et al. 2007, Potter et al. 2011). Forb species such as dog-fennel (*Eupatorium capillifolium*), horseweed (*Conyza canadensis*), and goldenrod (*Solidago* spp.) were common throughout fallow areas on our study site. The presence of these species may have created the bunching structural component similar to that typically attributed solely to native warm-season grasses, but provided additional benefits to nesting bobwhites. Senescent material from herbaceous cover likely provided important nest building material (Stoddard 1931, Klimstra and Roseberry 1975). Abundant forbs provided food in the form of seeds as well as large quantities of arthropod prey, which are crucial for brood

Table 5. Model specification, log-likelihood, AIC_c , and ΔAIC_c for top 5 and null models of northern bobwhite nest survival on a working farm in Bladen County, North Carolina, USA (2014–2015).

Model	$\text{Log}(L_i)^a$	AIC_c^b	ΔAIC_c^c
Bare soil + Other grasses + Shrubs	−123.19	254.43	0.00
Bare soil + Other grasses	−124.40	254.83	0.40
Bare soil + First presence	−124.70	255.43	1.00
Bare soil + First presence + Other grasses + Shrubs	−122.80	255.68	1.25
Bare soil + Other grasses + Soy	−123.84	255.73	1.17
Null	−127.28	256.55	2.12

^a $\text{Log}(L_i)$ is log-likelihood.

^b AIC_c is Akaike's Information Criterion corrected for small sample size.

^c ΔAIC_c is difference in AIC_c from top-ranking model.

development and egg-laying females (Brennan and Hurst 1995, Moorman et al. 2013). The combination of adequate overhead cover from predators, open space at ground level to facilitate movement, sufficient nesting material, and abundant food resources for adults and broods likely are the reason nesting locations with greater forb cover were selected (Taylor et al. 1999, Collins et al. 2009, Moorman et al. 2013).

Herbaceous vegetation for nesting occurred in both the fallow and planted areas managed for bobwhite nesting cover; however, bobwhites nested more frequently within areas of naturally occurring grasses and forbs than those of planted native warm-season grasses. We located 1 nest/3 ha in fallow field borders and nonlinear areas, whereas we located 1 nest/5 ha in the nonlinear sites planted with native grasses and forbs, suggesting planting was not required to provide adequate nesting cover. Furthermore, not all areas of planted grasses were used equally. In particular, a 2-ha area of planted switchgrass grew dense and unsuitable for bobwhite nesting cover despite regular management with fire and herbicide. We did not observe any nesting attempts within planted switchgrass, which is rhizomatous and a heavy seed producer that allows the stand to easily become too dense over time. Conversely, we observed bobwhite

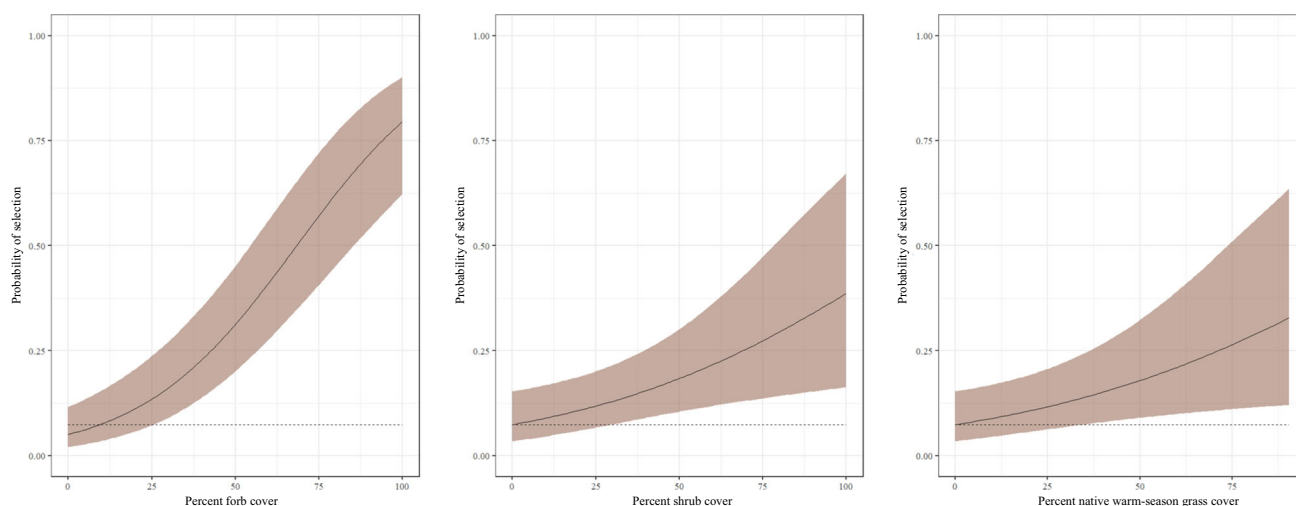


Figure 1. Predicted probability of northern bobwhite nest-site selection in relation to proportion of forb, shrub, and native warm-season grass cover on a working farm implementing bobwhite habitat management practices in Bladen County, North Carolina, USA (2014–2015).

nesting in 75% of areas consisting of little bluestem, big bluestem, and indiangrass, which were seeded at lower densities than the switchgrass. Our observations were consistent with those from previous studies that documented bobwhites avoided areas with densely planted native warm-season grasses, which did not provide proper nesting structure and impeded movement (Barnes et al. 1995, Unger et al. 2015).

Our results support those of Puckett et al. (1995), who showed greater nest initiation rates of bobwhite on farms with field borders. However, Puckett et al. (1995) observed low early season nest survival increasing as the nesting season progressed, which was attributed to an increase in nesting cover provided by maturing soybeans. Conversely, we observed very little use of row crops as nesting cover (1.6%) and greater nest survival rates than Puckett et al. (1995), with no significant seasonal variation. It is possible that individuals in our study did not experience similar variation in nest survival because of a low reliance on row crops for nest cover; instead, bobwhites commonly nested in the persistent shrubland patches (e.g., longleaf pine plantings) along the interface between woody winter cover and crop fields early in the nesting season before moving into perennial grasses and forbs in field borders (i.e., prior to 15 Jun, 29% of nests were in field borders and 71% were in nonlinear shrub patches along forest edges).

Concurrent to our study, we monitored bobwhite on 2 farms without habitat management (Richardson 2016). Individuals on the 2 unmanaged farms either made no known attempt to nest or nested in notably poorer sites (i.e., a cornfield void of ground cover, a densely forested pine stand, logging slash within a clear-cut pine stand, hay fields). Additionally, when individuals on the unmanaged farms did nest, they experienced low nest success. The recurring positive relationships between forb cover and nest-site selection on the farm in this study suggest that low bobwhite nest-initiation rates, low nest survival, and overall low population density across agricultural landscapes of the southeastern United States result from the lack of adequate herbaceous vegetation needed as nesting cover. However, we recognize the need for additional research to directly test the hypothesis that low forb cover is the factor most limiting bobwhite on many working farms.

MANAGEMENT IMPLICATIONS

If bobwhite conservation is an objective on working farms, sufficient herbaceous and shrub cover should be retained in addition to grass cover at cropland edges along ditches, roads, adjacent woodlands, and areas of low crop production to create a mosaic of escape and nesting cover. Field borders and other areas of naturally occurring early successional vegetation provide opportunities to increase bobwhite nesting potential on working farms and could be a link to maintaining high densities of bobwhites on private farmland in regions where high-quality early successional vegetation, especially native forbs, has been removed. We do not recommend planting warm-season grasses to create bobwhite nesting cover where forbs can be established as volunteer

vegetation; the volunteer vegetation provides as good or better nesting cover and is much less expensive to establish and maintain (Moorman et al. 2013, GeFellers 2019). Increasing fallow herbaceous vegetation on working farms should increase nesting cover for bobwhite in landscapes where adequate nesting cover otherwise is not available. However, managers should ensure herbaceous cover is juxtaposed with adequate shrubs and grasses to provide the complexity of cover necessary to increase nesting potential.

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LITERATURE CITED

- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management* 74: 1175–1178.
- Barnes, T. G., L. A. Madison, J. D. Sole, and M. J. Lacki. 1995. An assessment of habitat quality for northern bobwhite in tall fescue-dominated fields. *Wildlife Society Bulletin* 23:231–237.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Berger, D. J., J. N. Piispanen, T. F. Ginnett, and J. D. Riddle. 2017. Northern bobwhite nest site selection in field borders. *Proceedings of the National Quail Symposium* 8:225–231.
- Best, L. B., H. Campa III, K. E. Kemp, R. J. Robel, M. R. Ryan, J. A. Savidge, H. P. Weeks, Jr., and S. R. Winterstein. 1997. Bird abundance and nesting in CRP fields and cropland in the Midwest: a regional approach. *Wildlife Society Bulletin* 25:864–877.
- Bowling, S. A., C. E. Moorman, C. S. Deperno, and B. Gardner. 2014. Influence of landscape composition on northern bobwhite population response to field border establishment. *Journal of Wildlife Management* 78:93–100.
- Brennan, L. A. 1991. How can we reverse that northern bobwhite population decline? *Wildlife Society Bulletin* 19:544–555.
- Brennan, L. A., and G. A. Hurst. 1995. Summer diet of northern bobwhite in eastern Mississippi: implications for habitat management. *Proceedings of the Southeastern Association of Fish and Wildlife Agencies* 49:516–524.
- Burger, L. W., Jr. 2001. Quail management: issues, concerns, and solutions for public and private lands—a southeastern perspective. *Proceedings of the National Quail Symposium* 5:20–34.
- Burger, L. W., Jr., E. W. Kurzejeski, T. V. Dailey, and M. R. Ryan. 1990. Structural characteristics of vegetation in CRP fields in northern Missouri and their suitability as bobwhite habitat. *Transactions of the North American Wildlife and Natural Resources Conference* 55:74–83.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer, New York, New York, USA.
- Collins, B. M., C. K. Williams, and P. M. Castelli. 2009. Reproduction and microhabitat selection in a sharply declining northern bobwhite population. *Wilson Journal of Ornithology* 121:688–695.
- DeVos, T. A., Jr., and B. S. Mueller. 1993. Reproductive ecology of northern bobwhite in north Florida. *Proceedings of the National Quail Symposium* 3:83–90.

- Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83:3476–3488.
- Engstrom, R. T., R. L. Crawford, and W. W. Baker. 1984. Breeding bird populations in relation to changing forest structure following fire exclusion: a 15-year study. *Wilson Bulletin* 96:437–450.
- Evans, K. O., L. W. Burger, C. S. Oedekoven, M. D. Smith, S. K. Riffell, J. A. Martin, and S. T. Buckland. 2013. Multi-region response to conservation buffers targeted for northern bobwhite. *Journal of Wildlife Management* 77:716–725.
- Fox, J. 2011. *An R companion to applied regression*. SAGE, Thousand Oaks, California, USA.
- GeFellers, J. W. 2019. An evaluation of early seral plant communities following tall fescue eradication and crop field abandonment. Thesis, University of Tennessee, Knoxville, USA.
- Gill, D. E., P. Blank, J. Parks, J. B. Guerard, B. Lohr, E. Schwartzman, J. G. Gruber, G. Dodge, C. A. Rewa, and H. F. Sears. 2006. Plants and breeding bird response on a managed Conservation Reserve Program grassland in Maryland. *Wildlife Society Bulletin* 34:944–956.
- Greenfield, K. C., M. J. Chamberlain, L. W. Burger, Jr., and E. W. Kurzejeski. 2003. Effects of burning and discing Conservation Reserve Program fields to improve habitat quality for northern bobwhite (*Colinus virginianus*). *American Midland Naturalist* 149:344–353.
- Harper, C. A., G. E. Bates, M. P. Hansbrough, M. J. Gudlin, J. P. Gruchy, and P. D. Keyser. 2007. Native warm-season grasses: identification establishment and management for wildlife and forage production in the mid-south: a manual for natural resource professionals and other land managers. University of Tennessee Extension, Publication 1752, Knoxville, USA.
- Hernandez, F., L. A. Brennan, D. J. Demaso, J. P. Sands, and D. B. Wester. 2013. On reversing the northern bobwhite population decline: 20 years later. *Wildlife Society Bulletin* 37:177–188.
- Hughes, D. W., T. M. Terhune, D. C. Sisson, and H. L. Stribling. 2005. Demographics of northern bobwhite on agricultural and intensively managed bobwhite plantation landscapes. *Proceedings of the Southeastern Association of Fish and Wildlife Agencies* 59:30–42.
- King, J. W., and J. A. Savidge. 1995. Effects of the Conservation Reserve Program on wildlife in southeast Nebraska. *Wildlife Society Bulletin* 23:377–385.
- Klimstra, W. D., and J. L. Roseberry. 1975. Nesting ecology of the bobwhite quail in southern Illinois. *Wildlife Monographs* 41.
- Lohr, M., B. M. Collins, P. M. Castelli, and C. K. Williams. 2011. Life on the edge: northern bobwhite ecology at the northern periphery of their range. *Journal of Wildlife Management* 75:52–60.
- Moorman, C. E., and D. C. Gwynn, Jr. 2001. Effects of group-selection opening size on breeding bird habitat use in a bottomland forest. *Ecological Applications* 11:1680–1691.
- Moorman, C. E., C. J. Plush, D. B. Orr, and C. Reberg-Horton. 2013. Beneficial insect borders provide northern bobwhite brood habitat. *PLoS ONE* 8:e83815.
- Nickerson, C., R. Ebel, A. Borchers, and F. Carriazo. 2011. Major uses of land in the United States, 2007. U.S. Department of Agriculture, Economic Research Service Publication 89, Washington D.C., USA.
- Palmer, W. E., T. M. Terhune, and D. F. McKenzie. 2011. The national bobwhite conservation initiative: a range-wide plan for recovering bobwhite. National Bobwhite Technical Committee Technical Publication, version 2.0, Knoxville, Tennessee, USA.
- Palmer, W. E., S. D. Wellendorf, J. R. Gillis, and P. T. Bromley. 2005. Effect of field borders and nest-predator reduction on abundance of northern bobwhites. *Wildlife Society Bulletin* 33:1398–1405.
- Potter, L. M., D. L. Otis, and T. R. Bogenschutz. 2011. Nest success of northern bobwhite on managed and unmanaged landscapes in southeast Iowa. *Journal of Wildlife Management* 75:46–51.
- Puckett, K. M., W. E. Palmer, P. T. Bromley, J. R. Anderson, Jr., and T. L. Sharpe. 1995. Bobwhite nesting ecology and modern agriculture: a management experiment. *Proceedings of the Southeastern Association of Fish and Wildlife Agencies* 49:503–517.
- Richardson, A. 2016. Summer vital rates and movement of northern bobwhite in response to habitat management on working farms. Thesis, North Carolina State University, Raleigh, North Carolina, USA.
- Riddle, J. D., C. E. Moorman, and K. H. Pollock. 2008. The importance of habitat shape and landscape context to northern bobwhite populations. *Journal of Wildlife Management* 72:1376–1382.
- Riffell, S., D. Scognamiglio, and L. W. Burger. 2008. Effects of the Conservation Reserve Program on northern bobwhite and grassland birds. *Environmental Monitoring and Assessment* 146:309–323.
- Samson, F., and F. Knopf. 1994. Prairie conservation in North America. *BioScience* 44:418–421.
- Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski, Jr., and W. A. Link. 2014. The North American Breeding Bird Survey, results and analysis 1966–2013. Version 01.30.2015. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland, USA.
- Smith, M. D., P. J. Barbour, L. W. Burger, Jr., and S. J. Dinsmore. 2005. Density and diversity of overwintering birds in managed field borders in Mississippi. *Wilson Bulletin* 117:258–269.
- Stoddard, H. L. 1931. *The bobwhite quail: its habits, preservation and increase*. Charles Scribner's Sons, New York, New York, USA.
- Taylor, J. S., K. E. Church, and D. H. Rusch. 1999. Microhabitat selection by nesting and brood-rearing northern bobwhite in Kansas. *Journal of Wildlife Management* 63:686–694.
- Terhune, T. M., D. C. Sisson, and H. L. Stribling. 2006. The efficacy of relocating wild northern bobwhites prior to breeding season. *Journal of Wildlife Management* 70:914–921.
- Unger, A. M., E. P. Tanner, C. A. Harper, P. D. Keyser, F. T. Van Manen, J. J. Morgan, and D. L. Baxley. 2015. Northern bobwhite season habitat selection on a reclaimed surface coal mine in Kentucky. *Journal of Wildlife Management* 2:235–246.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:S120–S139.
- White, G. C., and R. A. Garrott. 1990. *Analysis of wildlife radio-tracking data*. Academic Press, San Diego, California, USA.
- Zuur, A. F., G. M. Smith, and E. N. Ieno. 2007. *Analyzing ecological data*. Springer, New York, New York, USA.

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