EVALUATION OF THE LANDSCAPE SURROUNDING NORTHERN BOBWHITE NEST SITES: A MULTISCALE ANALYSIS

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Abstract: Implementation of the Conservation Reserve Program (CRP) altered the interspersion and abundance of patches of different land-cover types in landscapes of the southeastern United States. Because northern bobwhites (*Colinus virginianus*) are experiencing significant population declines throughout most of their range, including the Southeast, it is critical to understand the impacts of landscape-scale changes in habitat on their reproductive rates. Our objective was to identify components of landscape structure important in predicting nest site selection by bobwhites at different spatial scales in the Upper Coastal Plain of Georgia. We used a Geographic Information System (GIS) and spatial analysis software to calculate metrics of landscape structure near bobwhite nest sites. Logistic regression was used to model the relationship of nest sites to structure within the surrounding landscape at 4 spatial scales. We found that patch density and open-canopy planted pine were consistently important predictor variables at multiple scales, and other variables were important at various scales. The density of different patch types could be increased by thinning rows of pines in large monotypic stands of closed-canopy planted pine stands. Thinning and creating openings in CRP pine plantations should provide increased nesting opportunities for bobwhites. We interpret the support for other variables in our analysis as an indication that various patch configuration lead to different combinations of landscape structure that provide an acceptable range of habitat conditions for bobwhites.

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Northern bobwhite (hereafter, bobwhite) abundance has declined over much of the species' range (Brennan 1991, Church et al. 1993, Brady et al. 1998). Many factors have been considered potential causes of these declines (Brennan 1991, Burger 2002). Recently, numerous studies have used long-term and region-wide data sets to evaluate the influence of several of these factors on bobwhite numbers, including weather (Guthery et al. 2000, Bridges et al. 2001, Guthery et al. 2002, Lusk et al. 2002), harvest (Guthery et al. 2000, Peterson 2001), and land-use and land-cover changes (Brady et al. 1998, Bridges et al. 2002, Lusk et al. 2002, Peterson et al. 2002). While it is probable that no single factor is responsible for the bobwhite's decline, habitat change clearly is a primary cause (Brennan 1991, Guthery et al. 2000, Burger 2002).

Historically, the interspersion of fallow fields, hardwood forest, pine plantations, and croplands found in the southeastern United States created a landscape mosaic of land-cover patches amenable to bobwhites and their selection of early-successional habitats and edges (Stoddard 1931, Rosene 1969, Burger 2002). This patchy landscape mosaic has been changed by intensification of agriculture and silviculture, resulting in increased field sizes, planted monocultures, and loss of diversity within landscapes dominated by agriculture (Langner 1985) and silviculture (Helinski 2000). Moreover, since the inception of the CRP in 1985, >830,202 ha of farmland have been converted to tree plantations (mostly pine) in the Southeast (Farm Service Agency 1997). The CRP was designed to be a large-scale cropland retirement program and the primary purposes were to control commodity supply and long-term soil erosion. It has evolved into a multipurpose conservation program with wildlife conservation being added as a priority (McKenzie 1997, Helinski 2000). The establishment of pine plantations (primarily loblolly [*Pinus taeda*]) was the most commonly selected conservation practice under the CRP in the Southeast, rendering

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CRP's potential benefits for bobwhites there quite different than its effects in other regions of the United States (Burger 2002). In fact, Burger (2002) predicted that conversion of agricultural lands to CRP pine plantations probably would result in a long-term loss of bobwhite habitat in the southeastern United States.

The CRP potentially could benefit bobwhites if its implementation resulted in a landscape of diverse land-cover patches. The suitability of pine plantations and other land cover for use by bobwhites in the Southeast is questionable, however (Hays and Farmer 1990, Stauffer et al. 1990, Ryan et al. 1998). In Illinois, the contribution of CRP fields to bobwhite habitat depended not only on the quantity and quality of CRP fields, but also on the juxtaposition of CRP fields with other habitat components (Roseberry et al. 1994, Weber et al. 2002). Allen et al. (1996) suggested that southeastern pine plantations could contribute to landscape-level habitat if their location, placement, and management objectives were favorable.

Although Roseberry and Klimstra (1984) noted that habitat management for bobwhites should consider the juxtaposition and interspersion of habitat types (Burger et al. 1990, Stauffer et al. 1990), these factors have not been adequately quantified in most regions of the United States. Roseberry and Sudkamp (1998) assessed the suitability of landscapes for bobwhites in Illinois by comparing landscape structure with indexes of bobwhite abundance. Guthery et al. (2001) assessed the relationship between abundance of bobwhites and land-cover classes on Oklahoma farms and ranches using landscape metrics. Little work, however, has been completed to evaluate the relationship between bobwhite populations and the components of landscape structure associated with agricultural and silvicultural practices in the Southeast, particularly in areas influenced by the CRP. Such analyses are critical because bobwhite numbers are declining significantly in this region, except on a few intensively managed quail plantations.

Our objectives were to determine (1) the component(s) of landscape structure important in predicting nest-site selection by bobwhites and (2) the scale(s) at which each operated that best predicted nest-site selection by bobwhites. Our study sites included CRP pine plantings typical of the Upper Coastal Plain of Georgia and much of the Southeast. We used Geographic Information Systems (GIS) and spatial analysis software to classify land use and calculate metrics of landscape type around bobwhite nest sites. We used logistic regression to model (Manly et al. 1993) the location of bobwhite nest sites in relation to structure (i.e., composition and configuration) of the surrounding landscape at different 4 spatial scales.

STUDY AREA

Our study was conducted on Alexander and Di-Lane Plantation Wildlife Management Areas (WMAs) and surrounding lands in Burke County, Georgia, USA. These areas were representative of the Upper Coastal Plain physiographic region. Alexander WMA is a 555-ha tract which, until 1988, was privately owned and planted primarily in row crops or used as pasture. In 1988, 380 ha of cropland were planted in loblolly pines following CRP planting guidelines (1,793 trees/ha). The property was unmanaged after 1988 and was acquired by the Georgia Department of Natural Resources (DNR) in November 1997. As of 1999, Alexander WMA included hardwoods (166 ha), fallow fields (9 ha), and planted pines (380 ha). Movements of radiomarked bobwhites beyond the Alexander WMA boundary increased the study area to 3,898 ha.

Di-Lane Plantation WMA was a 3,278-ha tract on which 286 ha were enrolled in the CRP in 1986 by the private landowner and planted in loblolly pine at 1,793 trees/ha. The U.S. Army Corps of Engineers purchased the land in 1992 as mitigation for lands flooded by Lake Russell and contracted the Georgia DNR to manage the property. Land cover on Di-Lane Plantation WMA included mixed pine–hardwoods (1,666 ha), fallow fields (849 ha), and planted pines (497 ha). Movement of radiomarked bobwhites beyond the Di-Lane Plantation WMA boundary increased the study area to 11,918 ha.

Alexander and Di-Lane Plantation WMAs were 16 km apart and situated within a landscape of fallow fields, agricultural fields, residential areas, commercial hardwood operations (pecan [*Carya illinoensis*] orchards), and pine plantations, all interspersed throughout an upland and bottomland hardwood matrix. Radiomarked bobwhites moved on and off the WMAs, but not between them. We delineated study area boundaries around the WMAs arbitrarily, based on features such as roads and rights-of-way that were ≥800 m outside any recorded bobwhite location. When an unbroken land-cover patch extended ≥1,000 m beyond a recorded bobwhite location, but no feature was present to serve as an arbitrary delineation, we designated a logical cut-off point with-

Table 1. Land-cover types and their composition delineated for classification of the study area in Burke County, Georgia, USA.

Land-cover types	Composition
Agricultural fields	Cultivated fields, pecan orchards, <1 year old clearcuts, pasture, hay fields, mowed areas, exposed soils
Closed-canopy pine	Managed planted pine stands at canopy closure (typically >5 years old), and natural stand composed of >50% pines >20 years old, and patches ≥0.8 ha in size in large forested hardwood tracts (>12 ha)
Fallow fields	Fallow and idle areas (typically ≤5 years), 1-4 year old clearcuts, rights-of way
Hardwoods	Stand composed of 50% bottomland and/or upland hardwoods >5 years old, clearcuts ≥5 years old
Hedgerow	Linear or curvilinear cover type that is 8–15 m in width and longer than it is wide, and forms an edge with or runs through another land-cover type(s)
Open-canopy planted pine	Thinned, managed pine plantations, and young planted pine (typically ≤5 years)
Unavailable	Residential areas (houses or large buildings), roads (major paved or unpaved road with ≥2 lanes, and water (permanent or semi-permanent open ponds >0.2 ha)

in the land-cover patch, such as a narrow area. We considered the WMAs and surrounding area as 1 study area for data analysis because the WMA boundaries did not limit movement of bobwhites, the areas delineated around the WMAs were relatively close together (<6 km), and the WMAs were surrounded by similar cover types.

METHODS

Land Cover

We digitized land-cover types at a scale ≥1:3,000 m, referencing U.S. Geological Survey 1993 Digital Orthophoto Quarter Quadrangles with a root mean square error of ≤1.6 m in ArcView™ (ESRI 1999*b*). We used our knowledge of the area, remote imagery, and inspection of unfamiliar areas to classify, modify, and update 1993 landscape polygons to represent 1997–2000 landscapes. The final GIS database included >15,816 ha of delineated land cover.

Seven land-cover types were delineated: agricultural fields, closed-canopy pine, fallow fields, hardwoods, hedge rows, open-canopy planted pine, and unavailable areas (Table 1). Cultivated crops within the agricultural field land-cover type consisted mostly of row crops (primarily cotton, soybean, and peanuts; Morgan 2000). We included recent (1–4 yr old) clearcuts in the fallow fields category because they mimicked the vegetative succession or structure of fallow and idle fields in the vicinity. We defined rights-of-way (gas and power lines) as fallow field, except portions that intersected an agricultural field, where they were defined as agricultural field. Most hardwoods were located along river bottoms and floodplains. Oak (*Quercus* spp.) and hickory (*Carya* spp.) dominated hardwood forests in the study area (Morgan 2000). Managed planted pine stands in our study area were primarily loblolly pine. The distinction between open-canopy and closed-canopy pine is a gradient, but our GIS and field efforts (including ground verification) captured this distinction and all other land-cover distinctions precisely. In all land-cover categories the smallest mapping unit was 0.2 ha, except residential areas within the unavailable area category that were digitized in mapping units <0.2 ha.

Nests and Random Points

We captured, banded, and radiomarked bobwhites from January to April, 1997–2000. Bobwhites were captured using wire funnel traps (Stoddard 1931) baited with cracked and whole kernel corn. We checked traps at mid-morning and late afternoon daily. Each bobwhite was fitted with a size 3 aluminum leg band and 6.1-g necklace-style radio transmitter (Holohil Systems, Ontario, Canada). We located marked bobwhites at least every other day in an opportunistic manner, and we ensured that we located each individual at various times of the day between January and September. We used homing (Mech 1983) and occasionally flushing to determine locations of bobwhites. We identified nesting bobwhites by inactive signals during normally active periods or by the repetition of daily locations. Locations of nests and radiomarked birds were recorded as Universal Transverse Mercator (UTM) coordinates using a GeoExplorer II hand-held Global Positioning System (GPS) receiver (Trimble Navigation Ltd., Sunnyvale, California, USA). Research was conducted under the University of Georgia IACUC Protocol No. A960216C2.

We located 39 nest attempts by bobwhites and recorded their geographical coordinates. A nesting attempt ranged from construction of a nest bowl to the successful hatching of a brood. Ten of

39 nesting attempts were renesting or double-clutching attempts (hereafter referred to as renests). Twenty-nine nests were considered first nest attempts. To avoid pseudoreplication (Hurlbert 1984) and lack of independence between nests belonging to the same radiomarked bird, and with no a priori justification to select >1 nest from the same hen, we randomly selected 1 nest from any bobwhite that had 2 or more nest attempts in 1 season. In one instance, the geographic coordinates of a renesting attempt for a bobwhite were lost and the first nest attempt was selected as the nest representing this bobwhite. Hence, 29 nest sites were used in modeling.

We selected random points ($n = 29$) within the digitized study area, in proportion to the number of nests associated with each WMA, using a uniform random distribution in the Animal Movement extension (Hooge and Eichenlaub 1999) of ArcView. Locations of the 39 known nest sites were excluded from selection as random points.

Table 2. Description of landscape metrics[a] used as predictor variables in the development of logistic regression models for northern bobwhite nest site selection in Burke County (1997–2000), Georgia, USA.

Abbreviation	Units	Description
PD	no./100 ha	Patch density.
PSCV	%	Patch size coefficient of variation.
TECI	%	Total edge contrast index. Quantified edge contrast for the landscape as a whole, ignoring patch average.
SHEI	0 ≤ SHEI ≤ 1	Shannon's evenness index.
IJI	%	Interspersion and juxtaposition index.
CCP	%	Percentage of landscape composed of closed-canopy pine.
Fld	%	Percentage of landscape composed of fallow field.
Hwd	%	Percentage of landscape composed of hardwoods.
OCPP	%	Percentage of landscape composed of open-canopy planted pine.

[a] See McGarigal and Marks (1995) for formulas and more detailed descriptions of habitat measures; table adapted in part from Penhollow and Stauffer (2000:364).

Calculation and Selection of Landscape Metrics

Around each nest site and random point, we designated buffer zones with radii of 250, 500, 750, and 1,000 m (hereafter referred to as 19.6-, 78.5-, 176.7-, or 314.1-ha areas, respectively). These radii were selected because the resulting buffered areas corresponded well to bobwhite home-range sizes detected for our study area (38–171 ha; Parnell et al. 2001). We intersected each buffered nest site and random point with the study area map using the ArcView Geoprocessing Wizard. Polygons from the intersection were converted from shape files to coverages with ArcInfo 8 GIS (ESRI 1999*a*). We calculated patch, class, and landscape level metrics (McGarigal and Marks 1995) from landscapes using FRAGSTATS*ARC (Pacific Meridian Resources 2000).

We selected 9 metrics (out of a set of >40 produced for the landscape coverages) as predictor variables for our models. These metrics were chosen a priori to avoid redundancy among measurements as evaluated by correlation diagnostics (PROC CORR; SAS Institute 1990), and they were excluded if correlated ($r \geq 0.75$) with ≥1 other metric. Selection of metrics was also based on their perceived biological relevance to the dependent variable and their relevance to the objectives of this study (Penhollow and Stauffer 2000).

The 9 variables chosen for inclusion were patch density (PD), patch size coefficient of variation (PSCV), total edge contrast index (TECI), Shannon's evenness index (SHEI), interspersion and juxtaposition index (IJI), and the percentage of the landscape composed of closed-canopy pine (CCP), fallow fields (Fld), hardwoods (Hwd), and open-canopy planted pine (OCPP; Table 2). To calculate the variable TECI, we defined edge contrast values between each potential pair of edge types based on our knowledge and field experience of structural differences and degree of gradient between land-cover types. We did not include the variable IJI in the analysis of the 19.6-ha landscapes because there were too few patches to calculate this index around several random nest sites (McGarigal and Marks 1995).

Modeling

We used logistic regression (Afifi and Clark 1990) to develop predictive models of nest site selection at 4 landscape scales (19.6-, 78.5-, 176.7-, and 314.1-ha areas), based on class and landscape metrics. We estimated resource selection functions based on samples of used (bobwhite nests) and available (random points) resource units as outlined by Manly (1993:26, 129–130). Thus we modeled the probability of use relative to availability, conditional on the samples drawn. Our models could not be used to predict, for example, the absolute probability of resource use given a set of predictor metrics. Because no model we examined contained >5 variables, we avoided considering models that were too detailed to be reasonably supported by the available data. Further, we maintained a >10:1 ratio between the number of samples and number of independent variables (Williams and Titus 1988).

Our objective was to determine which variable(s) correctly predicted nest use/non-use status in 70% or more cases, suggesting the biological relevance of these variables to bobwhite management. For each spatial scale, we first conducted a model search using a macro (All Possible Logistic Regressions [APLR]; available from C. T. Moore) written in SAS programming language (SAS Institute 1999). This procedure used the corrected Akaike's Information Criterion (AIC_c) score to evaluate models based on a joint assessment of model bias and precision (Akaike 1973, Burnham and Anderson 1998). The program fit all possible logistic regression models up to size k, where k was user-specified, and it provided a set of estimated coefficients for a global prediction model, accounting for model-selection uncertainty (Burnham and Anderson 1998). We entered all 9 landscape variables into the procedure for the binary nest use outcome and selected $k = 5$ as the maximum size of any model.

For each landscape scale, we evaluated the predictive accuracy of the model with the smallest AIC_c using the following procedure. We performed a Monte Carlo cross-validation (Shao 1993) using the Monte Carlo Cross-Validation for Logistic Regression (CVLR) SAS macro (available from C. T. Moore). The Monte Carlo cross-validation procedure iteratively split a set of data into random model-fitting and prediction subsets, fit the specified model to the first subset, and tested the model against data in the second subset. Over many iterations, statistics on frequency of correct classification provided an estimate of model classification accuracy for data not used to fit the model. The number of cross-validation iterations was set at ≥1,000. The proportion of data withheld for validation was based on the number of variables in the model being cross-validated. Of these data, 50, 40, 35, 30, and 30% were withheld to validate the 1-, 2-, 3-, 4-, or 5-variable models, respectively.

To examine the importance of each variable after accounting for uncertainty due to model selection, we estimated parameters of a global prediction model using model averaging (Burnham and Anderson 1998). Before doing this, we standardized variables so patterns of variable importance could be evaluated within each scale and across scales. We obtained standardized, model-averaged coefficients and 95% CIs for each variable at each landscape scale. We used these quantities to make qualitative judgments about the strength and direction of association of each variable with site use at each scale: estimated coefficients with 95% CIs that did not overlap zero were strongly associated with site use; coefficients with CIs that included zero had less support.

RESULTS

Land Cover and Nest Statistics

The average composition of our study area from 1997 through 2000 was 34.5% hardwood (SD = 0.4%), 27.0% agricultural fields (SD = 1.1%), 19.0% closed-canopy pine (SD = 1.5%), 11.9% fallow field (SD = 0.8%), 5.2% open-canopy planted pine (SD = 0.6%), 2.2% unavailable (SD = 0.1%), and 0.4% hedgerow (SD = 0.02%). Land-cover types selected by bobwhites for nest sites included agricultural fields ($n = 1$), closed-canopy pine ($n = 13$), fallow fields ($n = 17$), hardwoods ($n = 1$), and open-canopy planted pine ($n = 7$). We found at least 1 successful nest in each land-cover type except hardwood. In the fallow field cover type, 5 nests were successful and 9 failed. We did not monitor 2 nests to the end of incubation due to field constraints, and 1 bobwhite abandoned its nest shortly after being flushed. In the open-canopy planted pine cover, 5 nests were successful while 2 failed. Nesting occurred both in young pine plantations (<7 yr old) and in row-thinned older plantations (>7 yr old). In the closed-canopy pine cover, 9 nests were successful and 1 nest failed. Two nests were abandoned for unknown reasons. In all field seasons, 9 of 12 nests located in closed-canopy pine were <25 m from the edge.

There was overlap within nest site and random point buffers, and between nest sites and random point buffers. Random points overlapped nest sites by a total of 5.8, 16.3, 18.4, and 21% at the 19.6-, 78.5-, 176.7-, and 314.1-ha area scales, respectively. Overlap of all buffers (both within and between those around nest sites and random points) was 15.5, 40.0, 51.8, and 62.4% at the 19.6-, 78.5-, 176.7-, and 314.1-ha area scales, respectively.

Models

Models with minimum AIC_c for the 19.6-, 78.5-, 176.7-, and 314.1-ha area scales contained 1, 2, 5, and 4 variables, respectively (Table 3). After cross-validation, the mean percent of correctly classified nest and random site locations ranged from 60.0 to 69.5%. The variable OCPP occurred in each minimum-AIC_c model, and the variable's coefficient was positively related to the occurrence of a bobwhite nest for each model. The variable PD was also positively related to the occurrence of a bobwhite nest and was present in minimum-AIC_c models at 3 spatial scales (78.5-, 176.7-, 314.1-ha). Variables IJI and Fld occurred in minimum-AIC_c models at 2 spatial scales (176.7-, 314.1-ha) and were negatively related to the occurrence of a nest. The variable CCP occurred at 1 scale (176.7-ha area) and was positively related to the occurrence of a nest.

Table 3. Best[a] model coefficients and standard errors (SE), corrected Akaike's Information Criteria (AIC_c), and cross-validation results from logistic regression analysis of bobwhite nest selection at 4 landscape scales, 1997–2000, Burke County, Georgia, USA (n = 58).

Landscape area (ha)	Variable[c,d]	Estimate	SE	AIC_c	Correctly classified (%)[b] $\bar{x}$	SE
19.6	Intercept	0.562	0.330	74.467	69.29	0.25
	OCPP	0.088	0.034			
78.5	Intercept	–1.857	0.885	80.281	60.00	0.24
	OCPP	0.050	0.028			
	PD	0.060	0.032			
176.7	Intercept	3.971	2.728	73.984	66.36	0.30
	OCPP	0.129	0.048			
	PD	0.185	0.087			
	CCP	0.061	0.033			
	IJI	–0.129	0.051			
	Fld	–0.063	0.033			
314.1	Intercept	5.560	3.323	71.379	69.46	0.29
	OCPP	0.231	0.072			
	PD	0.288	0.120			
	IJI	–0.150	0.059			
	Fld	–0.099	0.044			

[a] The model at each landscape scale with the minimum-AIC_c score.
[b] Cross-validation based on ≥1,000 iterations and withholding 50, 40, 35, 30, and 30% of data to validate the 1-, 2-, 3-, 4-, or 5-variable models, respectively.
[c] See Table 2 for descriptions of predictor variables.
[d] There were too few patches around several random nest sites at the 19.6-ha scale to calculate the IJI index (McGarigal and Marks 1995).

We observed several relationships between predictor variables and nest sites (Fig. 1). Two variables (PD and OCPP) had a moderately to strongly positive association with nest site use at each landscape scale evaluated. We found a moderately positive association for the variable CCP at all landscape scales, a negative association for the variable TECI at 3 scales (78.5, 176.7, 314.1 ha), and a negative association for the variable Fld at 2 scales (176.7, 314.1 ha). The variable IJI could not be included in the 19.6-ha scale analyses, but was negatively associated with nest site selection at 2 landscape scales (176.7, 314.1 ha). For both IJI and Fld, the association became more negative as landscape area increased.

DISCUSSION

We found that bobwhites responded to the composition of landscape (i.e., percent of land-cover types) and to the configuration of landscape (i.e., patch diversity). Other studies (Brady et al. 1998, Roseberry and Sudkamp 1998, Guthery et al. 2002) that examined bobwhites' response to landscape features focused on variability of bobwhite abundance indices relative to landscape features, whereas we focused on nest locations. In general, these studies found that the index of bobwhite abundance responded to composition of the landscape (percentage of land-cover types) and its configuration (patch diversity; Guthery et al. 2001:846), as did bobwhite selection of nest sites.

Open-canopy planted pine was a predictor variable in the best models at all 4 landscape scales, indicating strong selection for this landscape cover type by bobwhites for nest sites. Because bobwhites feed on seeds, invertebrates, and succulent leafy material, seek cover overhead, and they are small (≤170 g), they require bare ground amongst stems and clumps of herbaceous vegetation for movement and feeding, as well as residual herbaceous vegetation for nests. Such structure and cover are found in early-successional habitat at edges of ecotones, old fields, and open-canopy pine plantations. Guthery et al. (2001) also noted that bobwhites responded strongly to cover type composition.

At the 78.5-, 176.7-, and 314.1-ha scales, we found that bobwhite nest sites were associated with PD, an index of spatial heterogeneity (McGarigal and Marks 1995). At the 2 largest landscape scales (176.7, 314.1 ha), the IJI metric was included as a predictor variable of nest site selection. Higher values of this index represented more complete interspersion of patch types

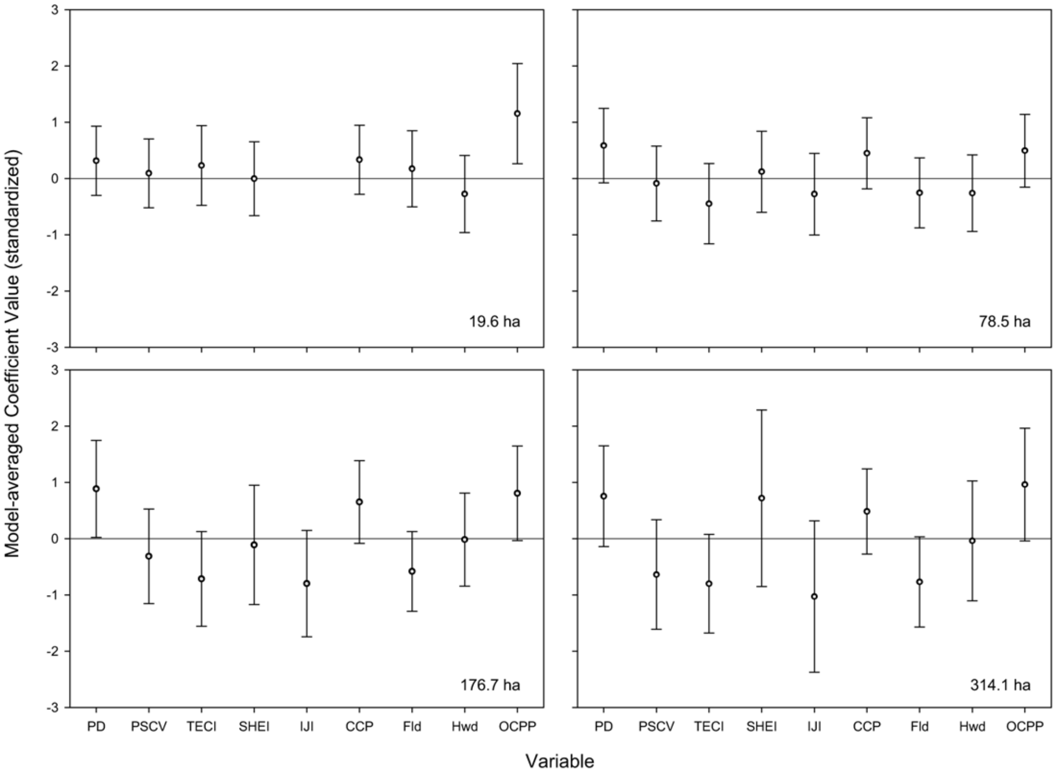

Fig. 1. Model-averaged standardized coefficients and 95% CIs for predictor variables (Table 2) used in logistic regression to predict northern bobwhite nest selection at 4 landscape scales (19.6-, 78.5-, 176.7-, 314.1-ha). Variables with 95% CIs that did not include zero were considered to be strongly associated with relative probability of nest site selection. Variable IJI was not included as a potential predictor variable in models based on the 19.6-ha landscape scale because there were too few patches to calculate this index around several randomly selected points (McGarigal and Marks 1995).

(McGarigal and Marks 1995:53). We interpret the presence of PD and IJI in our models as an indication that bobwhites used nesting areas that contained many cover patches, probably representing an uneven mix of 2 or 3 patch types rather than a diversity of patch types. Guthery et al. (2001) also found that bobwhite abundance declined as diversity and patch richness increased, whereas Roseberry and Sudkamp (1998) found that bobwhites occurred primarily in diverse and patchy landscapes.

Based on the results of other local studies, we expected to find a preference for nest site selection in fallow fields (Lewis 1999, Parnell et al. 2001). Our models, however, did not detect this relationship. It is possible that we were unable to detect it because nests in such habitats typically are found near transitions from one land-cover type to another (Stoddard 1931, Rosene 1969, Lewis 1999). Perhaps our analysis could not detect selection at such a fine spatial scale or could not measure the association sufficiently. At any rate, the importance of fallow field cover should not be discounted because 17 of 39 nests (43.6%) were located in this cover type, yet fallow fields accounted for only 11.9% of the total land cover in the study.

The consistent occurrence of just a few variables in our models, and some support for inclusion or interchange of other variables—as indicated by model averaging—lends support to the contention that various patch configurations lead to different combinations of landscape structure that provide an acceptable range of habitat conditions for bobwhites.

Guthery (1997, 1999) hypothesized that managers are more likely to increase bobwhite abundance by increasing the quantity of habitat that can support all requisites of life for bobwhites throughout the year than by increasing the quality of areas already inhabited by bobwhites (Peterson 2001). If the configuration of habitat contains slack (different patch configurations that result in landscapes of equal and optimal value to bobwhites), then bobwhite production is possible over a broad spectrum of land uses and land-cover types (Guthery 1999, Peterson 2001). Guthery (1999) suggested that slack occurs because multiple patch types have interchangeable functions.

Our approach for modeling nest site selection has potential weaknesses. The overlap within nest site and random point buffers, and between nest sites and random point buffers, could lead to underestimation of variance due to autocorrelation and difficulty in distinguishing predictive characteristics of used and available sites. The possibility also exists that some of the random sites (presumed unused) were in fact used. Further, our inferences were limited by small sample size; caution should be used when interpreting any model until validations with data from other study areas can be completed. Although the mean percent correct classification rates of the top logistic regression models (60.0–69.5%) were similar to the percentage reported in many field studies (65%; C. T. Moore, USGS Patuxent Wildlife Research Center, unpublished summary data), they were lower than we expected.

By using the AICc scores to determine the best model at each scale, however, we attempted to select for parsimonious models that achieved a good balance between precision and freedom from bias (Burnham and Anderson 1998). We maintain that by using only 1 nest per bird per year, selecting variables a priori, limiting the size of models, cross-validating, and using AIC_c scores, we evaluated these data appropriately and conservatively at each spatial scale. Further, by accounting for uncertainty in model selection using model averages, we were able to assess appropriately the evidence for each variable's association with nest site selection, and the use of standardized data permitted these assessments within and across scales.

Our models indicated that associations between nest site selection and landscape components varied by the scale at which the component was measured (Table 3; Fig. 1). Our objective was not to determine relative importance of the 4 measurement scales on nest site selection, and we conducted no formal analysis to assess this. However, the model providing greatest overall predictive performance (as measured by AIC_c and cross-validation) was that using 4 landscape components measured at the largest (314.1 ha) scale. An almost equal level of predictive performance (by cross-validation) was provided by the open-canopy planted pine component measured at the smallest (19.6 ha) scale.

Two variables, open-canopy planted pine and patch density, were relatively strong predictors in models at all scales, suggesting scale independence in these variables, at least over the range of scales we investigated.

MANAGEMENT IMPLICATIONS

Land managers should consider the entire range of cover types and their associations within landscapes when deciding how to benefit bobwhite populations. Conservation programs supported by federal or state agencies should strive to enhance bobwhite habitat on a large scale through landowner cooperation and landscape-scale planning. Most landscapes in the Upper Coastal Plain region are composed of the cover types delineated during our study; hence, bobwhite populations would benefit from landscape-scale management plans that ensure juxtaposition of fallow fields and young, open-canopy pine stands with cover types such as closed-canopy pine stands and cropland. Our results suggest that landscapes could be structured in several ways and still be functionally equivalent for bobwhite use (Guthery 1999). We recommend that patch density be increased in large monotypic agricultural fields and closed-canopy planted pine stands by interspersing these land-use types with fallow areas and areas of thinned pines, respectively. The benefit of open-canopy planted pine for bobwhites will vary by patch and over a short time frame (a few years) because early successional habitat in thinned pine stands is ephemeral. Follow-up management will be necessary to impede succession. Future research on modifications to CRP pine plantations should evaluate the intensity and duration of their use by bobwhites for nesting and rearing broods.

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