Research Article

Spatial Models of Northern Bobwhite Populations for Conservation Planning

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ABSTRACT Since 1980, northern bobwhite (*Colinus virginianus*) range-wide populations declined 3.9% annually. Within the West Gulf Coastal Plain Bird Conservation Region in the south-central United States, populations of this quail species have declined 6.8% annually. These declines sparked calls for land use change and prompted implementation of various conservation practices. However, to effectively reverse these declines and restore northern bobwhite to their former population levels, habitat conservation and management efforts must target establishment and maintenance of sustainable populations. To provide guidance for conservation and restoration of habitat capable of supporting sustainable northern bobwhite populations in the West Gulf Coastal Plain, we modeled their spatial distribution using landscape characteristics derived from 1992 National Land Cover Data and bird detections, from 1990 to 1994, along 10-stop Breeding Bird Survey route segments. Four landscape metrics influenced detections of northern bobwhite: detections were greater in areas with more grassland and increased aggregation of agricultural lands, but detections were reduced in areas with increased density of land cover edge and grassland edge. Using these landscape metrics, we projected the abundance and spatial distribution of northern bobwhite populations across the entire West Gulf Coastal Plain. Predicted populations closely approximated abundance estimates from a different cadre of concurrently collected data but model predictions did not accurately reflect bobwhite detections along species-specific call-count routes in Arkansas and Louisiana. Using similar methods, we also projected northern bobwhite population distribution circa 1980 based on Land Use Land Cover data and bird survey data from 1976 to 1984. We compared our 1980 spatial projections with our spatial estimate of 1992 populations to identify areas of population change. Additionally, we used our projection of the spatial distribution and abundance of bobwhite to predict areas of population sustainability. Our projections of population change and sustainability provide guidance for targeting habitat conservation and rehabilitation efforts for restoration of northern bobwhite populations in the West Gulf Coastal Plain. (JOURNAL OF WILDLIFE MANAGEMENT 71(6):1808–1818; 2007)

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Widespread population decline of northern bobwhite (*Colinus virginianus*) throughout its range (Brennan 1994, 1999) has been documented from analyses of national databases such as the Breeding Bird Survey (Robbins et al. 1986) and Christmas Bird Counts (Sauer et al. 1996). This quail species has averaged a 3.9% range-wide annual rate of decline since 1980 (Sauer et al. 2005). Local populations of northern bobwhite have also declined (Ward et al. 2001) with 8.2% annual declines of northern bobwhite within the West Gulf Coastal Plain Bird Conservation Region (http://www.nabci-us.org/map.html) from 1982 to 1999 (Dimmick et al. 2002). From 1980 to 2005, annual statewide declines within the 4 states that comprise the West Gulf Coastal Plain were 4.7% in Arkansas, 6.0% in Louisiana, 1.8% in Oklahoma, and 3.8% in Texas, USA (Sauer et al. 2005).

Many factors have contributed to population declines of northern bobwhite at broad landscape scales (Burger 2002). However, the primary factor has been a range-wide reduction in useable landscape space (Guthery 1997, Veech 2006). This reduction in usable space is attributed to changing agricultural (Peterson et al. 2002) and silvicultural (Brennan 1991) land use, as well as increasing suburbanization. Generally, clean farming practices and conversion of native pine forests to high-density pine plantations, with concomitant reduction in the use of prescribed fire, has diminished the suitability of these lands as quail habitat.

The Northern Bobwhite Conservation Initiative (NBCI) was implemented to assess the population status and provide a plan to recover the species (Dimmick et al. 2002). The NBCI recommended restoration of northern bobwhite to 1980 population levels via widespread changes in management practices within 6 improvable land use classes. Land use classes within which alternative management would improve habitat suitability for northern bobwhite were cropland, pasture and hay, rangeland, pine forest, mixed forest, and lands enrolled in the United States Department of Agriculture's Conservation Reserve Program. The NBCI did not establish spatially explicit population targets within the West Gulf Coastal Plain but did provide region-wide density estimates and population goals based on the area of these 6 improvable land cover classes.

Although the NBCI has been praised for its regionally based approach targeting bobwhite restoration, Burger (2002) and Williams et al. (2004) recommended more highly focused and targeted restoration. Historically, diffuse, fine-scale management practices have been largely ineffec-

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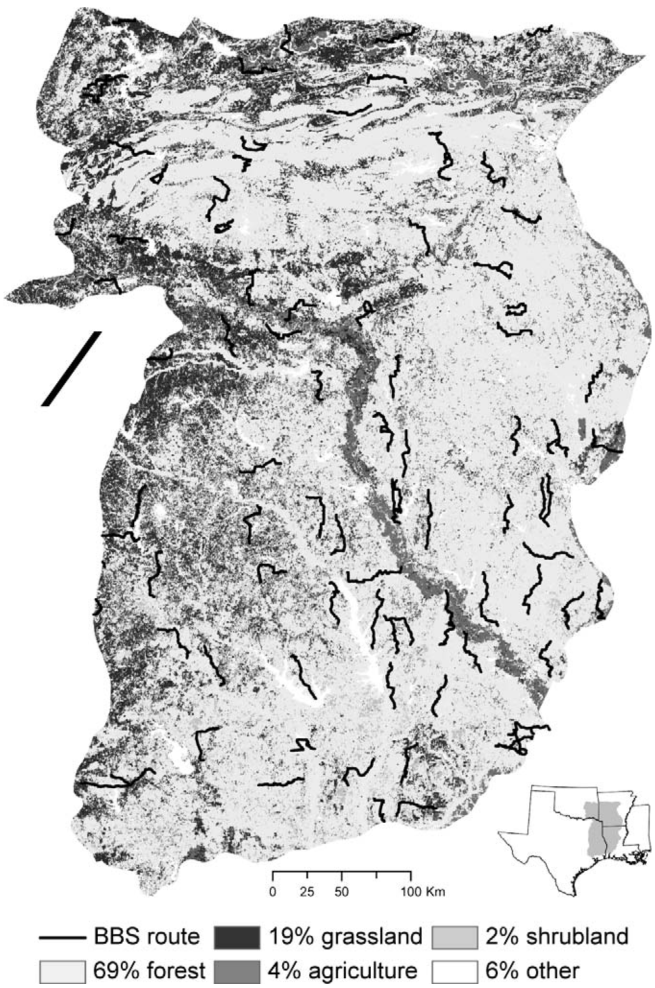

Figure 1. National Land Cover Data (1992) within the West Gulf Coastal Plain Bird Conservation Area, USA, including portions of Arkansas, Louisiana, Oklahoma, and Texas, aggregated into 5 habitat classes that we used to model the abundance of northern bobwhite determined from Breeding Bird Surveys conducted from 1990 to 1994.

tive at restoring sustainable quail populations. To be effective, conservation efforts must concentrate on large tracts of usable space, targeting focal areas within regional landscapes that support northern bobwhite populations that are immune to local extirpation (Williams et al. 2004).

Williams et al. (2004) suggested 3 priority categories to guide restoration: 1) areas of low priority for conservation actions because they are beyond redemption as suitable quail habitat, 2) high priority areas within which to focus rehabilitation efforts so as to restore suitable quail habitat, and 3) areas that continue to harbor sustainable populations of quail in suitable habitat where management actions should be directed at maintaining large areas of usable space. The question for managers is, which geographic areas fall into each category, and where on the landscape should restoration efforts be focused?

To aid in conservation decision making regarding restoration of northern bobwhite, we combined data on northern bobwhite detections that were obtained from Breeding Bird Surveys (http://www.pwrc.usgs.gov/bbs/) with habitat data derived from National Land Cover Data (NLCD; Vogelmann et al. 2001) and Land Use Land Cover data (LULC; U.S. Geological Survey 1986) to identify landscape characteristics that are correlated with the distribution and abundance of northern bobwhite within the West Gulf Coastal Plain. We used these data to develop spatially explicit models of northern bobwhite that were representative of their 1980 and 1992 populations. We used these spatial models of bobwhite to evaluate NBCI population targets and identify priority geographic foci for conservation efforts that target rehabilitation of habitat for this species.

Our objectives were to identify landscape characteristics that influence the distribution and abundance of northern bobwhite and to translate these landscape characteristics into spatially explicit models of northern bobwhite populations. Using a spatially explicit model of 1992 bobwhite populations, we identified within the West Gulf Coastal Plain: 1) areas that likely harbor sustainable populations of bobwhite, 2) high priority areas where habitat rehabilitation efforts will likely restore sustainable populations of bobwhite, and 3) low priority areas where sustainable quail populations are not likely to be achieved without intensive conservation and restoration efforts.

STUDY AREA

The West Gulf Coastal Plain Bird Conservation Region including the Ouachita Mountains (http://www.nabci-us.org/map.html) encompassed >21 million ha within the south-central United States (Fig. 1). This region had rolling to relatively flat topography, with deep, typically well-drained soils. The southern portion of this region, in Louisiana and Texas, was historically dominated by longleaf pine (*Pinus palustris*) savanna. Longleaf savannas are highly suitable habitat for northern bobwhite but most have been converted to industrial plantations of other pine species that usually harbor poor habitat for bobwhite. Similarly, the Ouachita Mountains of Arkansas and Oklahoma were historically forested. Mixed pine and hardwood forests remained on ridges and slopes within the Ouachita Mountains but many of the fertile valleys within this ecosystem have been converted to pasture and hayland. Overall, the West Gulf Coastal Plain remains dominated by forests but changes in forest management, such as conversion of native forests to industrial plantations and reduced occurrence of fire within pine savannas, have contributed to the decline of northern bobwhite populations.

METHODS

Data Sources

To characterize habitat within the West Gulf Coastal Plain, we obtained from the United States Geological Survey 30-m resolution NLCD derived from 1992 satellite imagery (http://landcover.usgs.gov/natllandcover.php) and vector representation of LULC data derived from circa 1980 high-altitude photographs (http://edc.usgs.gov/products/landcover/lulc.html). To facilitate our modeling process,

Table 1. Landscape metrics obtained from FragStats analysis within 7,300-ha areas of the West Gulf Coastal Plain Bird Conservation Region, USA, using Land Use Land Cover data (1980) and National Land Cover Data (1992) after aggregation to 5 land cover classes: forest, shrub, grass, agriculture, and unsuitable habitat. We used these metrics to model northern bobwhite distribution circa 1980 and 1992.

Metric	Description of metric
%Grass	% of grassland class in the landscape
Total_Edge	(Amt of edge in the landscape)/(total area)
Forest_Edge	(Amt of edge of the forest class)/(total area)
Grass_Edge	(Amt of edge of the grassland class)/(total area)
Ag_Clump	A continuous measure of the distribution of agriculture: −1 (when maximally disaggregated) through 1 (when maximally clumped).
Grass_Clump	A continuous measure of the distribution of grassland: −1 (when maximally disaggregated) through 1 (when maximally clumped).
Contagion	Reflects both the dispersion and intermixing of patch types: approaches zero when the patches are maximally disaggregated (i.e., every cell is a different patch type) and interspersed and equals 100 when all patch types are maximally aggregated (i.e., a single patch)

we converted the LULC vectors to 30-m resolution raster data. We separately aggregated the 20 NLCD and 29 LULC classes represented within these data into 5 habitat classes that likely influence population status of northern bobwhite (Veech 2006): 1) forest (deciduous, evergreen, mixed, or woody wetlands); 2) grassland (grass, herbaceous, pasture, hay, or fallow); 3) shrubland (shrubland or recently harvested forest); 4) agriculture (row crop or small grain); and 5) unfavorable quail habitat (water, marsh, developed areas, or barren areas). Because agriculture and grassland cover classes were not separate in LULC data, we assumed that lands within this combined agriculture–grassland class were grasslands if their NLCD cover class was grassland.

The North American Breeding Bird Survey (BBS) annually enumerates birds across the continent through use of standardized 3-minute counts at 50 consecutive stops located 0.8 km apart along 40-km routes. We obtained tabular and spatial data for 33 BBS routes surveyed from 1976 to 1984 and 51 routes surveyed from 1990 to 1994 within the West Gulf Coastal Plain (ftp://ftpext.usgs.gov/pub/er/md/laurel/BBS/DataFiles/). The BBS divided each route into 5 segments with each segment comprising 10 stop locations in their sequential order of completion (e.g., first 10 stops = segment 1). We used only route segments that fell within the West Gulf Coastal Plain for analysis. Because BBS did not survey all routes during all years, we calculated the number of detections of northern bobwhite along each 10-stop segment as the mean for each of the years BBS surveyed a route during the years that bracketed the dates of land cover imagery: 1976 to 1984 and 1990 to 1994, respectively. However, not all northern bobwhite present are detected during surveys: their calling rates being influenced by time of day, season, wind speed, cloud cover, barometric pressure change, and the number of adjacent coveys (Wellendorf et al. 2004). The BBS does not account for detection probability (Somershoe et al. 2006), thus these data should be viewed as an index of bobwhite populations and likely underestimate actual populations.

Model Development

We calculated landscape metrics separately for 1980 and 1992 land cover based on aggregated cover classes within 3,000-m buffers surrounding BBS route segments using FragStats software (http://www.umass.edu/landeco/research/fragstats/fragstats.html) and ArcGIS (ArcMap, Version 9.1). We used a 3,000-m buffer because it approximates the maximum seasonal dispersal distance of northern bobwhite (Dimmick 1992; L.W. Burger, Mississippi State University, personal communication). Breeding Bird Survey routes, however, were not uniformly linear features, such that the average area surrounding 10-stop route segments was 7,344 ± 27 ha ($\bar{x}$ ± SE).

Based on the assumption that northern bobwhite require permanent usable space (Guthery et al. 1997) and because populations appear to be positively associated with higher proportions of grassland, cropland, and rangeland within the landscape (Veech 2006), we identified 7 metrics generated from FragStats that we considered potentially relevant to quail ecology (Table 1). Because agriculture and shrublands were minor components of the landscape in most of the West Gulf Coastal Plain (Fig. 1), we assumed the proportion of grassland (%Grass) was the primary habitat consideration influencing bobwhite abundance. We also assumed that the placement, size, and distribution of habitat patches within landscapes, as defined by landscape metrics Ag_Clump, Grass_Clump, and Contagion, were important determinants of northern bobwhite distributions. Finally, we assumed some level of connectivity among habitats, as revealed by different edge densities (Total_, Grass_, and Forest_Edge), influenced bobwhite dispersal and thereby their distribution and abundance.

We calculated these 7 landscape metrics for landscapes surrounding all BBS route segments and used them to created 18 a priori candidate models (Table 2) to relate mean northern bobwhite detections (adjusted for time of survey) to their respective landscape conditions. We used only data from BBS route segments 1, 3, and 5 for model development. Because data distributions differed markedly between survey periods, we used Poisson regression to model 1992 population data but we employed Gaussian regression to model square root transformed (i.e., normalized) 1980 population data. In both cases, model adequacy was evaluated using the principles of information theory (Akaike 1973, Burnham and Anderson 1998) wherein we

Table 2. Akaike's Information Criterion adjusted for small sample size and overdispersion of data ($QAIC_c$), model parameterization (K), deviations from maximum $QAIC_c$ (Δ_i), model weight (w_i), and model likelihood (w_i/w_{max}) for 18 candidate models relating northern bobwhite detections on 10-stop Breeding Bird Survey route segments surveyed from 1990 to 1994 ($n = 147$) and 7 landscape metrics obtained from FragStats analysis of 5-class aggregated 1992 National Land Cover Data within the West Gulf Coastal Plain Bird Conservation Region, USA.

Candidate model	$QAIC_c$	K	Δ_i	w_i	w_i/w_{max}
%Grass, Ag_Clump, Total_Edge	14.93	5	0.00	0.242	1.000
%Grass, Ag_Clump, Grass_Edge	15.94	5	1.01	0.146	0.603
%Grass, Grass_Edge	15.95	4	1.02	0.146	0.601
%Grass, Total_Edge	16.68	4	1.74	0.101	0.418
%Grass, Grass_Clump, Grass_Edge	17.88	5	2.95	0.055	0.229
%Grass, Forest_Edge	17.95	4	3.02	0.053	0.221
%Grass, Contagion, Grass_Edge	18.07	5	3.18	0.050	0.208
%Grass, Ag_Clump, Forest_Edge	18.08	5	3.15	0.050	0.208
%Grass, Grass_Clump, Total_Edge	18.40	5	3.47	0.042	0.176
%Grass, Contagion, Total_Edge	18.61	5	3.68	0.038	0.159
%Grass, Contagion, Forest_Edge	19.20	5	4.27	0.029	0.118
%Grass, Contagion	20.00	4	5.06	0.019	0.080
%Grass, Grass_Clump, Forest_Edge	20.02	5	5.09	0.019	0.079
Global (7 variable model)	23.57	9	8.64	0.003	0.013
%Grass	24.54	3	9.61	0.002	0.008
%Grass, Ag_Clump	24.67	4	9.74	0.002	0.008
Grass_Edge, Grass_Clump	26.65	4	11.71	0.001	0.003
Null	80.48	2	65.55	0.000	0.000

compared candidate models based on Akaike's Information Criterion (AIC) adjusted for small sample size (AIC_c) and corrected for overdispersion of 1992 sample data ($QAIC_c$; Hurvich and Tsai 1989, Anderson and Burnham 2002).

We adjusted the mean number of detections to account for temporal declines because independent regressions (see Results) indicated the mean number of northern bobwhite detections decreased on successive BBS route segments. However, BBS route segments on which no quail were detected were not adjusted but were maintained at no detections. We corrected for time bias prior to and independent of modeling the relationship between landscape and bobwhite detections because our objective was to generate a model that could be uniformly applied to the entire West Gulf Coastal Plain, not to just the areas covered by BBS routes.

Model Application

To generate spatially explicit predictions of northern bobwhite populations, we used Geographic Information System software (TNT-MIPS, Version 6.8 or IMAGINE, ERDAS, Version 9.0) to create separate raster data layers for each landscape parameter we evaluated. For some landscape parameters (e.g., %Grass and Grass_Edge) we used a 7,361-ha square (286 × 286 pixel), roving window that approximated the area of buffered BBS route segments. This roving window resulted in a landscape parameter value for each 30-m pixel within the West Gulf Coastal Plain. For a few model parameters (e.g., Ag_Clump) computational constraints limited our ability to use a roving window and we instead employed a pseudo roving window approach wherein we created 9,052 equally spaced overlapping squares, each of 7,361 ha, that completely covered this ecoregion. We calculated landscape metrics within each overlapping area and associated them with each square's centroid. We then interpolated among these values by kriging (Isaaks and Srivastava 1989), using a linear semivariogram model and a variable search radius of 30 m to estimate landscape metrics for every 30-m pixel within this bird conservation region.

We combined separate data layers for each landscape parameter based on model-averaged parameter estimates from the best-fit statistical models (see Results). The resultant rasters represented the predicted mean number of northern bobwhite detections along hypothetical 10-stop survey route segments centered on each 30-m pixel in the West Gulf Coastal Plain.

We extended the predicted number of detections to project presumed population abundance of northern bobwhite contingent on several assumptions. First, we assumed that BBS detected bobwhite at each survey point within 400 m (approx. 50 ha). Thus, BBS surveyed bobwhites on approximately 500 ha during the 10 stops on each BBS route segment. Additionally, we assumed BBS data represented only singing (calling) males, BBS detected all calling birds, and that each male detected represented one fall covey of 12 birds (Dimmick et al. 2002). However, as previously stated, we have no knowledge regarding what proportion of the northern bobwhite present BBS actually detected. Thus, our projections of population abundance likely underestimate the true population.

Model Assessment

After model development, we used BBS data from route segments 2 and 4 (segments we did not use for model development) to assess the predictive ability of our models. To accomplish this, we applied model-averaged parameter estimates from the best-fit statistical models (see Results) to the landscape parameters derived from within 3,000-m buffers surrounding each of these route segments and thereby predicted the number of bobwhite detections along each route segment. We compared these predicted bobwhite detections with the mean number of bobwhite detections (adjusted for time) observed during BBSs (1976 to 1984 or 1990 to 1994, respectively) using index of agreement (IA) criteria (Willmott 1981) and correlation analysis.

For comparison with our projected population estimates, we generated random predictions from bootstrapped data sets (Efron and Tibshirani 1994) and calculated these same measures of model adequacy. That is, for each of 200 random models generated from 1980 and 1992 data, we assigned a number of bobwhite detections to route segments 2 and 4 by randomly selecting (with replacement) from among mean observed bobwhite detections on all route segments surveyed circa 1980 ($n = 160$) or 1992 ($n = 247$), respectively.

We also compared our 1992 model predictions to independent data sets obtained from spatially defined quail call-count surveys (F. D. Ward and R. Fowler, Arkansas Game and Fish Commission, unpublished report; B. J. Carner, Arkansas Game and Fish Commission, unpublished data; F. G. Kimmel, Louisiana Department of Wildlife and Fisheries, unpublished data). Louisiana personnel conducted surveys during autumn from 1983 through 2003 along 20-stop survey routes with stops at 1.6-km intervals and detections recorded at each stop. Arkansas personnel collected data during spring from 2003 through 2004 along 15-stop survey routes with stops at 1.6-km intervals but reported detections were summed for each route. Quail call-count surveys differ markedly in methodology from the BBS, but we again assumed that maximum detection distance was 400 m and translated observed bobwhite detections to number of detections per 500 ha (i.e., 10 stops) along each surveyed route.

Following the methodology used for BBS route segments, we established a 3,000-m buffer around each quail call-count survey route and used FragStats to generate landscape metrics from 1992 NLCD based quail cover classes within each of these polygons. In Louisiana we calculated mean landscape metrics for 4 call-count survey route segments (approx. 8 km) along each 32-km survey route. Using these landscape metrics, we applied our model-averaged parameter estimates from the best-fit statistical model to predict the number of bobwhite detections along each quail call-count survey route.

We compared model predictions of 1992 bobwhite abundance (detections/500 ha) with observed quail detections along call-count routes in Louisiana during the same time period (1990 to 1994) as the BBS data used for model development. Additionally, we compared mean detections along quail call-count routes from the most recent survey years, 2000 to 2003 in Louisiana or 2003 to 2004 in Arkansas, with our model predictions after we adjusted model predictions for respective statewide population declines derived from BBS data (Sauer et al. 2005). We again used index of agreement and correlation analysis to evaluate the ability of our model to predict bobwhite detections observed along quail call-count survey routes.

Decision Support for Northern Bobwhite Conservation

Assuming northern bobwhite populations in the West Gulf Coastal plain are subject to catastrophic events during summer but not during winter, Guthery et al. (2000) suggested that sustainable populations of northern bobwhite require a minimum of 700 individuals. At the NBCI target density for this region (0.14 birds/ha), the area required to support 700 individuals is approximately 5,000 ha. We assessed the distribution of local landscapes that harbored sustainable populations by calculating the predicted mean quail abundance (birds/500 ha) within 5,000 ha through use of a 236×236 pixel moving window and extending this to 5,000 ha (i.e., $\times 10$).

We used these estimates to spatially identify areas where northern bobwhite populations were considered sustainable under 1980 and 1992 habitat conditions. We also identified areas where quail can likely be restored to sustainable populations through focused habitat enhancement and rehabilitation. Finally, we delineated areas where quail management will not likely yield sustainable bobwhite populations without expansive and far-reaching habitat restoration.

We compared 1980 and 1992 spatial projections of northern bobwhite populations to assess geographic areas of population change. For comparison with the northern bobwhite population projection derived from our model based on 1980 LULC landscape metrics, we estimated the 1980 northern bobwhite population by simple extrapolation of the 1980 average bobwhite density assumed by the NBCI (0.1408 birds/ha; Dimmick et al. 2002) to all improvable quail habitat within the West Gulf Coastal Plain. We also estimated the 1980 bobwhite population via reverse projection of our 1992 bobwhite abundance estimates using region-wide and state-specific estimates of population decline from 1980 through 1992. Similarly, we estimated current northern bobwhite populations by projection of our 1992 abundance estimates based on presumed population declines from 1992 through 2005 (Sauer et al. 2005).

RESULTS

Model Development

A Poisson regression using 1992 data indicated the mean number of northern bobwhite detections decreased on successive BBS route segments by 0.122 ± 0.031 detections ($\chi^2 = 15.8$, df $= 245$, $P < 0.01$). Similarly, a Gaussian regression using 1980 data indicated detections declined by 0.078 ± 0.045 ($\chi^2 = 3.01$, df $= 158$, $P = 0.08$) on successive route segments.

After aggregation of 1992 NLCD classes, the West Gulf Coastal Plain was characterized as 69% forest, 19% grassland, 2% shrubland, 4% agriculture, and 6% unfavorable habitat (Fig. 1). Evaluation of 18 candidate models relating northern bobwhite detections along BBS route segments to 7 landscape metrics based on 5 class NLCD data yielded 4 models with $\Delta QAIC_c < 2.0$ (Table 2). These 4 models had Akaike model weights between 0.10 and 0.24 with model likelihoods >0.41. Because any of these 4 models

Table 3. Model-averaged parameter estimates and their associated odds ratios, obtained from the 4 best (model wt > 0.1) models[a] derived from 1992 National Land Cover Data and the 2 best models[b] derived from 1980 Land Use Land Cover data that related northern bobwhite detections along 10-stop Breeding Bird Survey route segments to landscape metrics generated from FragStats analysis of 5-class aggregated land cover data.

Landscape parameter		Model-averaged estimate	SE	Odds ratio	95% CI on odds ratio
1992	Intercept	0.4052	0.1744	1.499	1.260–1.785
	%Grass	0.0351	0.0040	1.036	1.032–1.040
	Ag_Clump	0.3303	0.3283	1.391	1.002–1.932
	Total_Edge	−0.0054	0.0052	0.955	0.989–0.999
	Grass_Edge	−0.0058	0.0066	0.994	0.988–1.001
1980	Intercept	1.8892	0.2107	6.614	5.357–8.166
	%Grass	0.0100	0.0068	1.010	1.003–1.0170
	Forest_Edge	0.0230	0.0240	1.023	0.999–1.048

[a] Best models from 1992 data were 1) %Grass, Ag_Clump, Total_Edge; 2) %Grass, Ag_Clump, Grass_Edge; 3) %Grass, Grass_Edge; and 4) %Grass, Total_Edge.

[b] Best models from 1980 data were: 1) %Grass, Forest_Edge; and 2) %Grass.

had a high likelihood of being the best model, we derived model-averaged parameter estimates for the 4 landscape metrics that comprised these 4 models (Table 3). The resultant predictive model is

$$\mathrm{Pred}_{1992} = \exp[0.4052 + 0.0351(\%\mathrm{Grass}) + 0.3303(\mathrm{Ag\_Clump}) - 0.0054(\mathrm{Total\_Edge}) - 0.0058(\mathrm{Grass\_Edge})] \quad (1)$$

where Pred_{1992} is predicted number of bobwhite detections during 1992 at 10 point counts (i.e., within 500 ha), %Grass is the proportion of grassland, Ag_Clump is the extent of spatial aggregation of agriculture, Total_Edge is the total amount of cover class edge, and Grass_Edge is the amount of grassland cover class edge derived from a 5 class, 30-m NLCD raster within 7,300-ha landscapes (Table 1).

At this scale, detection of northern bobwhite along survey routes was positively associated with the proportion of grassland and more aggregated agriculture. Conversely, increased density of edge among our 5 cover classes and increased grassland edge were associated with decreased quail abundance. The 95% confidence interval on the odds ratio for 3 of these landscape metrics (Table 3) did not include 1.0 which suggests that they are import model parameters (Peak et al. 2004).

Evaluation of these same 18 candidate models relative to reclassified LULC and BBS data from 1980 yielded 5 models with $\Delta\mathrm{AIC}_c < 2.0$ (Table 4). Although any of these 5 models could be the best model, 3 of these models had Akaike model weights of <0.10 with model likelihoods <0.47. We derived model-averaged parameter estimates for the landscape metrics comprising these top 5 models as well as from the top 2 models that had models likelihoods ≥0.60 (Table 4). Because the predictive abilities of these two model-averaged parameter estimates were similar, we elected to project the simpler 2 parameter model to the West Gulf Coastal Plain. The resultant predictive model is

$$\mathrm{Pred}_{1980} = [1.8892 + 0.0100(\%\mathrm{Grass}) + 0.0230(\mathrm{Forest\_Edge})]^2 \quad (2)$$

where Pred_{1980} is predicted number of bobwhite detections during 1980 at 10 point counts (i.e., within 500 ha), %Grass is the proportion of grassland, and Forest_Edge is the amount of forest cover class edge derived from a 5 class, 30-m LULC raster within 7,300-ha landscapes (Table 1).

At this scale, detection of northern bobwhite along survey routes was positively associated with the proportion of grassland and the density of forest edge. Only the proportion of grassland, however, had a 95% confidence interval on its odds ratio that did not include1.0 (Table 3).

Model Assessment

Mean northern bobwhite abundance (2.15 ± 1.45 [SD] detections/500 ha) within the WGCP predicted by our 1992 NLCD derived population model (Fig. 2a) was markedly less than mean abundance (5.11 ± 1.12 [SD] detections/500 ha) derived from our 1980 LULC derived population model (Fig. 2b). Both models, however, accurately reflected abundances and spatial distribution of

Table 4. Akaike's Information Criterion adjusted for small sample size (AIC_c), model parameterization (K), deviations from maximum AIC_c (Δ_i), model weight (w_i), and model likelihood ($w_i/w_{\max}$) for the 6 models with greatest likelihood from among 18 candidate models relating northern bobwhite detections on 10-stop Breeding Bird Survey route segments surveyed from 1976 to 1984 ($n = 95$) and landscape metrics obtained through application of FragStats to 5-class aggregated 1980 Land Use Land Cover data within the West Gulf Coastal Plain Bird Conservation Region, USA.

Candidate model	AIC_c	K	Δ_i	w_i	$w_i/w_{\max}$
%Grass, Forest_Edge	219.4	3	0.00	0.189	1.000
%Grass	220.4	2	1.02	0.114	0.599
%Grass, Contagion	220.9	3	1.54	0.088	0.464
%Grass, Grass_Clump, Forest_Edge	221.0	4	1.60	0.085	0.449
%Grass, Contagion, Grass_Edge	221.1	4	1.68	0.082	0.431
%Grass, Ag_Clump, Forest_Edge	221.4	4	2.01	0.069	0.366

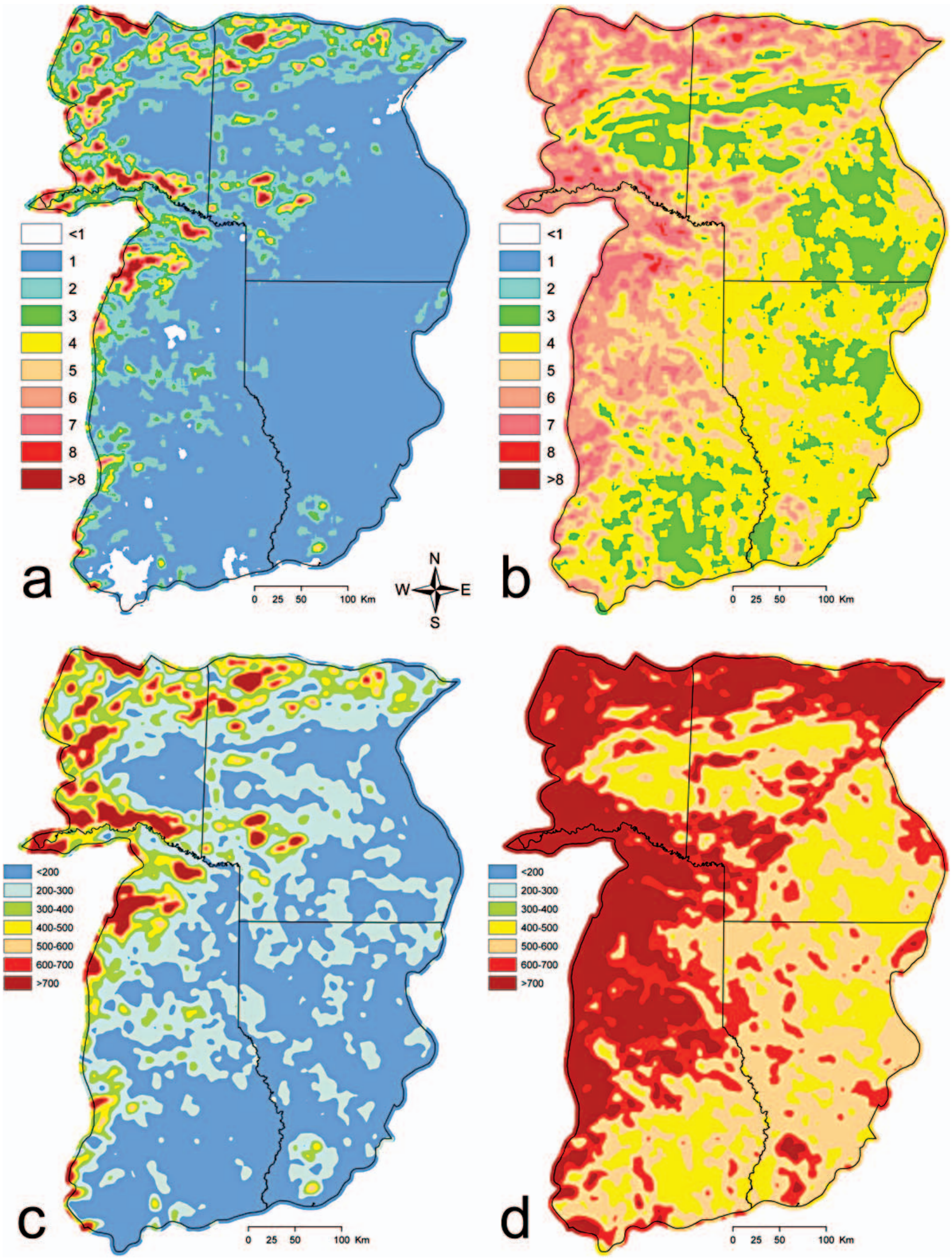

Figure 2. Predicted number of northern bobwhite detections per 10-stop Breeding Bird Survey (BBS) route segment in the West Gulf Coastal Plain, USA, circa 1992 (a) and 1980 (b), based on regression models relating 5-class aggregated National Land Cover Data (1992) or Land Use Land Cover data (1980) to mean northern bobwhite detections along BBS route segments surveyed from 1990 to 1994 or from 1976 to 1984, respectively. These predictions were used to model the spatial distribution, circa 1992 (c) and 1980 (d), of local populations of northern bobwhite (birds/5,000 ha) within the West Gulf Coastal Plain. We presume population sustainability within these local landscapes (5,000 ha) is dependent upon existing population abundance: likely sustainable (>700 birds), potentially sustainable (400–700 birds), sustainability dependent upon habitat improvement via conservation actions (200–399 birds), or unsustainable (<200 birds). Digital data are available online at http://www.lmvjv.org.

Table 5. State-specific area (ha × 1,000) and northern bobwhite population (covey) estimates within the West Gulf Coastal Plain (WGCP) Bird Conservation Region, USA. Each covey is assumed to represent 12 individuals.

State	Area[a]	1992 NLCD based model population[b]	1980 NBCI population target[c]	1980 population from recession of 1992 NLCD model[d]	1980 population from LULC based model[e]	1999 NBCI population estimate[f]	2005 population from projection of 1992 NLCD model[g]
AR	6,472	27,802	49,127	49,666–64,727	64,987	15,520	11,130–21,437
LA	4,596	15,102	31,891	26,012–35,160	42,546	10,075	4,258–6,046
OK	2,960	20,028	32,771	22,108–46,628	34,101	10,353	8,018–10,682
TX	7,128	28,797	77,123	46,882–67,043	76,433	24,364	11,528–16,374
WGCP	21,156	91,729	190,913	144,668–213,558	218,069	60,311	36,721–52,751

[a] Area of improvable quail habitat within the West Gulf Coastal Plain identified by the Northern Bobwhite Conservation Initiative (Dimmick et al. 2002) was 16,270 (ha × 1,000) within AR (4,187), LA (2,718), OK (2,792), and TX (6,573).

[b] Population estimate based on Poisson model generated from 1992 National Land Cover Data (NLCD)–based landscape metrics and 10-stop Breeding Bird Survey route segments surveyed from 1990 to 1994.

[c] Population target based on a density of 0.1408 birds/ha of improvable quail habitat (Dimmick et al. 2002). NBCI = Northern Bobwhite Conservation Initiative.

[d] Upper bound on population estimated from backward projection of 1992 model-based population estimates using 6.8% region-wide decline and lower bound based on statewide declines from 1980 to 1992 of 4.72% in AR, 4.43% in LA, 0.82% in OK, and 3.98% in TX (Sauer et al. 2005). Statewide declines include change in areas outside the West Gulf Coastal Plain but may better represent disproportional population change among states.

[e] Population estimate based Gaussian model generated from 1980 Land Use Land Cover (LULC) landscape metrics and 10-stop Breeding Bird Survey route segments surveyed from 1976 to 1984.

[f] Population estimate based on 1999 population density of 0.0444 birds/ha of improvable quail habitat (Dimmick 2002).

[g] Population based on forward projection of 1992 population estimates using 6.8% region-wide decline and statewide declines from 1992 to 2005 of 1.98% in AR, 9.28% in LA, 6.52% in OK, and 4.25% in TX (Sauer et al. 2005). Because statewide declines reflect areas outside the West Gulf Coastal Plain, state projections do not sum to regional totals.

northern bobwhite within validation BBS data sets for route segments we did not use for model development.

When compared with observed abundances of northern bobwhite along 100 BBS route segments from 1990 to1994, abundance predicted by our 1992 NLCD derived population model (2.34 ± 0.17 detections/500 ha) had an index of agreement (IA = 0.778) that was over twice that obtained from the average of 200 random bootstrap predictions (IA = 0.329 ± 0.005). Moreover we found a high correlation between predicted and observed bobwhite abundances (r = 0.700), whereas the correlation between observed abundance and random predictions was essentially nonexistent (r = −0.001 ± 0.007).

Similarly, when compared with observed abundances of northern bobwhite along 65 BBS route segments from 1976 to 1984, abundances predicted by our 1980 LULC derived population model (5.22 ± 0.15 detections/500 ha) had an index of agreement (IA = 0.683) that far exceeded that obtained from bootstrapped predictions (IA = 0.398 ± 0.005). The correlation between 1980 predicted and observed bobwhite abundances (r = 0.449) was less that our 1992 model but again far exceeded random predictions (r = −0.007 ± 0.009).

Prediction of current (circa 2004) bobwhite populations by correcting our 1992 NLCD model predictions to account for region-wide population declines also appears to have merit. Comparison of northern bobwhite abundance observed on 114 BBS route segments during 2000–2005 (1.11 ± 0.15 detections/500 ha) with predicted 2004 abundance (0.93 ± 0.06) resulted in a high index of agreement (IA = 0.60) and correlation (r = 0.54) when contrasted with random bootstrap predictions (IA = 0.331 ± 0.005, r = −0.005 ± 0.007).

Although our ability to predict bobwhite detections along BBS route segments was good, our ability to predict quail abundance (detections/500 ha) along quail call-count survey routes was poor. In Louisiana, 29 quail call-count routes surveyed during fall from 1990 to 1994 yielded 1.44 ± 0.16 detections/500 ha, which was similar to our predicted bobwhite abundance along these routes (1.61 ± 0.02) but their spatial agreement was poor (IA = 0.234, r = −0.067). Similarly, 1992 NLCD based model predictions (after adjustment for population decline) poorly predicted detections along recently conducted quail call-count survey routes. We found only a slight positive correlation between 2004 abundances predicted by our model and abundances observed during 2003 to 2004 along quail call-count routes in Arkansas (n = 83, r = 0.073) and during 2000–2003 along call-count routes in Louisiana (n = 29, r = 0.140). Moreover, these relationships had poor indices of agreement (IA_{AR} = 0.373, IA_{LA} = 0.162).

Model Application

Application of the model derived from 1992 NLCD-based habitat conditions (Equation 1) to the entire West Gulf Coastal Plain provides a spatially explicit projection of northern bobwhite populations (Fig. 2a). Extending the regional mean of 2.15 ± 1.45 [SD] detections/500 ha, we estimated the 1992 bobwhite population at 91,729 coveys or approximately 1.1 million birds (Table 5). Reverse projection of these 1992 population estimates to approximate the 1980 northern bobwhite population, based on population trends derived from BBS data over this same interval, resulted in population estimates that ranged from 144,668 to 213,558 coveys or 1.7–2.6 million birds (Table 5). This projection was slightly lower than our estimate of 218,069 coveys or >2.6 million birds (Table 5) that was derived from

Table 6. Area (ha × 1,000) supporting local populations of northern bobwhite within the 4 states that comprise the West Gulf Coastal Plain (WGCP) Bird Conservation Region, USA.

		Local population (birds/5,000 ha)			
State	Yr	<200	200–399	400–699	≥700
AR	1992	2,685	3,236	502	102
	1980	0	0	5,131	1,395
LA	1992	3,371	1,325	15	0
	1980	0	0	4,661	49
OK	1992	609	1,222	785	342
	1980	0	0	1,387	1,572
TX	1992	3,805	2,644	493	187
	1980	0	0	4,624	2,504
WGCP	1992	10,470	8,427	1,796	632
	1980	0	0	15,803	5,520

the regional mean of 5.11 ± 1.12 [SD] detections/500 ha of our 1980 LULC-based population model (Fig. 2b).

DISCUSSION

The NBCI has an objective of restoring northern bobwhite to their 1980 population levels. Based on the Initiative's estimated 1980 density of 0.14 birds per improvable hectare, this population within the West Gulf Coastal Plain was 190,913 coveys or approximately 2.3 million birds (Table 5). Although the populations target established by the NBCI was similar to our estimated 1980 region-wide population, state-specific estimates differed markedly between these 2 methods (Table 5). Northern Bobwhite Conservation Initiative–based estimates placed greater burden for recovery on populations in Texas whereas our model projections indicated populations in Arkansas were farther from recovery. Moreover, to achieve NBCI target populations, approximately 16 million ha must support quail at or above their target density of 0.14 birds/ha. Our model of 1992 northern bobwhite populations suggests that only 3% of this region (<1 million ha) support quail densities ≥0.14 birds/ha.

Assessment of the sustainability of local (5,000 ha) landscapes to support quail populations in 1992 indicated landscapes would support 65–1,989 northern bobwhite (Fig. 2c). Of these local populations, merely 3% (632,000 ha) are likely sustainable with ≥700 birds/5,000 ha (Table 6). However, Guthrey et al. (2000) surmised that when quail populations were only subject to winter catastrophes, populations of 400 birds were resistant to extirpation. Furthermore, as our population estimates likely underestimate actual populations, we believe that landscapes within the WGCP that support local populations of between 400 birds/5,000 ha and 700 birds/5,000 ha are potentially sustainable but would benefit from additional habitat rehabilitation. Even so, based on 1992 population projections, only 8% of this ecoregion harbored local populations between 400 birds and 700 birds (Table 6). Moreover, projected sustainable populations varied widely among states. Less than 1% of the area in Louisiana supported sustainable populations, whereas in Oklahoma

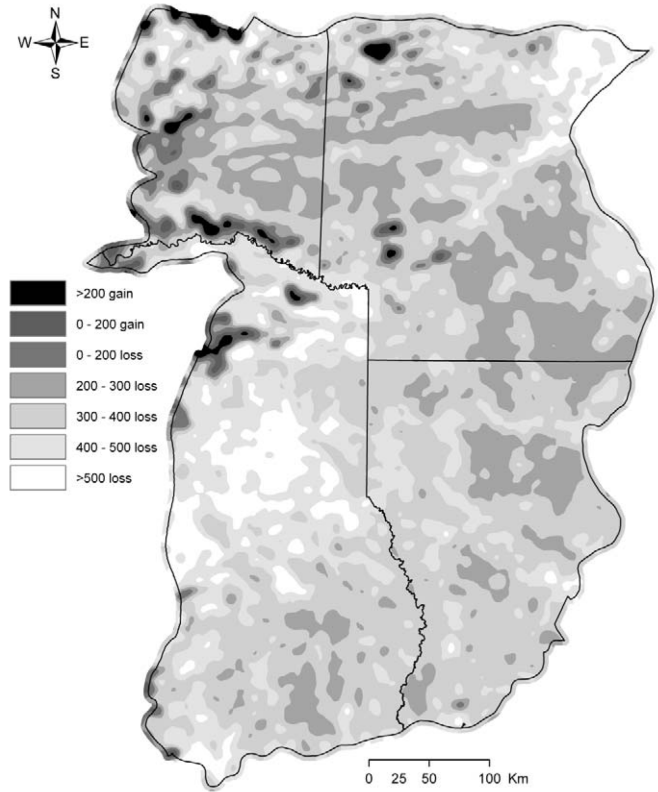

Figure 3. Magnitude and spatial distribution of northern bobwhite population change (birds/5,000 ha) within the West Gulf Coastal Plain, USA, between 1980 and 1992.

>38% of the area supported sustainable populations (Table 6).

As of 1992, over 89% of the West Gulf Coastal Plain supported local populations of <400 birds/5,000 ha—these populations are likely susceptible to local extirpation. Moreover, nearly 50% of this region had local northern bobwhite populations of <200 birds which we believe to be unsustainable without extraordinary habitat rehabilitation.

Assessment of the sustainability of local landscapes to support quail populations in 1980 indicated landscapes supported 428–991 northern bobwhite (Fig. 2d). Based on these projections, 26% of this ecoregion supported sustainable populations of >700 northern bobwhite/5,000 ha in 1980. Moreover, we postulate that in 1980 all areas of the West Gulf Coastal Plain harbored potentially sustainable quail populations of >400 birds/5,000 ha. Despite our supposition that potentially sustainable populations were present in all areas during 1980, population declines (Fig. 3) resulted in vast areas with unsustainable populations by 1992.

Predicted northern bobwhite abundance circa 1992, however, appears to accurately depict quail abundances along BBS routes during the same time period (1990 to 1994) as used for model construction. In addition, after compensation for population decline, this model adequately depicted recent northern bobwhite detections along these survey routes. Conversely, this model was a poor predictor of bobwhite detections along call-count survey routes. This discrepancy may be attributable to differences in the methodology between the BBS and quail call-count surveys, including seasonal differences as well as species-specific targeting of northern bobwhite and longer duration of quail call-counts compared to the all-species, 3-minute BBS counts.

Our projection of the population's sustainability circa 1980 suggests that at that time all areas within the West Gulf Coastal Plain harbored potentially sustainable populations of northern bobwhite. Thus, the NBCI's target of restoring this species to its 1980 population level appears to be well founded. However, population declines between 1992 and 2005 raise concern regarding this restoration target. The NBCI suggested just over 130,000 additional coveys were required to raise 1999 quail populations to their 1980 population objective (Dimmick 2002). However, projection of our 1992 population estimates to 2005, using the aforementioned statewide population declines, suggests that restoration of 140,000–150,000 coveys will be required to achieve 1980 populations of northern bobwhite. Based on our assessment that $\leq$11% of the area within the West Gulf Coastal Plain is currently capable of supporting sustainable populations of northern bobwhite, achieving this restoration goal seems a herculean task.

Our models were subject to the temporal limitations imposed by availability of land cover data. Additionally, these models were subject to the limitations and biases associated with BBS data (O'Connor et al. 2000) as well as the spatial inaccuracies of land cover data (Stehman et al. 2003). As with most spatial models, there are likely spatial autocorrelation issues that we have not adequately addressed. Possibly of greatest consequence, however, is that our models are limited to quantitative landscape characteristics expressed within land cover data (NLCD and LULC) and do not reflect habitat quality that likely influences bobwhite abundance. Indeed, most of the rehabilitation of habitat recommended by the NBCI represents improvement of habitat quality, through changes in management practice or alteration of species composition, and not a substantial increase in overall quantity of quail habitat. Thus, the landscape metrics we used for model construction are unlikely to reflect future improvements in habitat quality, such as returning high-density pine plantations to low-density, frequently burned pine savannas or conversion of exotic sod-grass pastures to native warm-season bunchgrasses.

Spatial data reflecting forest condition, in addition to land cover class, may provide insight into how northern bobwhite populations are influenced by habitat quality. Determinations of these qualitative forest conditions are being undertaken through innovative approaches that assess percent forest canopy cover within the 2001 NLCD classification (Homer et al. 2004) and model applications that incorporate spatial projections of Forest Inventory and Analysis data (Farrand et al. 2006; Tirpak et al., in press). We look forward to future population models for northern bobwhite in the West Gulf Coastal Plain that are able to incorporate these and other qualitative measures of habitat condition.

MANAGEMENT IMPLICATIONS

Because we modeled the abundance and spatial distribution of northern bobwhite, we provide spatially explicit population estimates within local landscapes. These estimates provide guidance for decisions on where to implement conservation and management actions through identification of geographic variation in northern bobwhite population viability. Specifically, we assert that local landscapes of 5,000 ha supporting populations of >400 northern bobwhite are potentially sustainable, landscapes supporting populations of 400–600 birds likely require habitat enhancement to ensure sustainable populations, whereas landscapes supporting <400 birds are likely unsustainable. Wildlife managers and conservation planners may further refine their restoration foci by combining our geographic projections of sustainable northern bobwhite populations (Fig. 2c) with locations of historical population decline (Fig. 3). Moreover, we discourage expending resources for habitat rehabilitation in areas with unsustainable populations of northern bobwhite if it is at the expense of restoration efforts in landscapes that support higher quail populations. However, if habitat restoration and rehabilitation are implemented within areas that currently harbor unsustainable populations, we recommend preference be given to landscapes that support larger populations (e.g., >200 birds) and that conservation and management actions planned for areas supporting populations of <200 birds be redirected towards more hospitable landscapes.

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