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RESEARCH ARTICLE

Conservation of northern bobwhite on private lands in Georgia, USA under uncertainty about landscape-level habitat effects

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Abstract Large-scale habitat enhancement programs for birds are becoming more widespread, however, most lack monitoring to resolve uncertainties and enhance program impact over time. Georgia's Bobwhite Quail Initiative (BQI) is a competitive, proposal-based system that provides incentives to landowners to establish habitat for northern bobwhites (*Colinus virginianus*). Using data from monitoring conducted in the program's first years (1999–2001), we developed alternative hierarchical models to predict bobwhite abundance in response to program habitat modifications on local and regional scales. Effects of habitat and habitat management on bobwhite population response varied among geographical scales, but high measurement variability rendered the specific nature of these scaled effects equivocal. Under some models, BQI had positive impact at both local farm scales (1, 9 km^2), particularly when practice acres were clustered, whereas other credible models indicated that bird

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response did not depend on spatial arrangement of practices. Thus, uncertainty about landscape-level effects of management presents a challenge to program managers who must decide which proposals to accept. We demonstrate that optimal selection decisions can be made despite this uncertainty and that uncertainty can be reduced over time, with consequent improvement in management efficacy. However, such an adaptive approach to BQI program implementation would require the reestablishment of monitoring of bobwhite abundance, an effort for which funding was discontinued in 2002. For landscape-level conservation programs generally, our approach demonstrates the value in assessing multiple scales of impact of habitat modification programs, and it reveals the utility of addressing management uncertainty through multiple decision models and system monitoring.

Keywords Adaptive management · *Colinus virginianus* · Habitat · Hierarchical models · Monitoring · Northern bobwhite · Uncertainty

Introduction

Early succession and grassland landscapes provide important breeding and/or wintering habitat to many bird species. However, much of this habitat in the southeastern US has been lost to urbanization, reforestation, and to changes in agricultural practices (USDA 1995; Vesterby and Krupa 2001). In the latter half of the twentieth century, the introduction of "clean farming" methods increased farm yields, but degraded habitat for a number of bird species (Best et al. 1995; Rodenhouse et al. 1995). Concurrently, populations of a number of grassland birds declined throughout the region since the mid-1960s (Sauer et al. 2001); of these, several, including grasshopper sparrow (*Ammodramus savannarum*), eastern meadowlark (*Sturnella magna*), and prairie warbler (*Dendroica discolor*), have been identified as species of management concern (Hunter et al. 1992; Trapp 1995). Establishment and management of eastern shrub communities is a recommended priority management action as part of the North American Landbird Conservation Plan (Rich et al. 2004).

Of particular interest throughout the southeastern US, and especially in Georgia, is the plight of the northern bobwhite (*Colinus virginianus*). The species is recognized and valued by many Georgians, and sport hunting for the bird generates much interest and revenue. However, the Georgia bobwhite population has decreased by 4.3% annually over the period 1966–2000 and by 5.3% annually within the period 1980–2000 (Sauer et al. 2001).

To reverse the northern bobwhite population trend, in 1999 the Wildlife Resources Division (WRD) of the Georgia Department of Natural Resources launched a conservation incentive program for rural private landowners. The initial target of the Bobwhite Quail Initiative (BQI) (Thackston et al. 2008) was 17 Georgia counties of the Upper Coastal Plain physiographic province. The goal of the program is to improve habitat quality for the northern bobwhite and for associated early succession-habitat songbirds for the ultimate objective of increasing the distribution and abundance of these species. Implicit assumptions in this goal are that (1) northern bobwhites respond to habitat modifications, and (2) habitat modifications beneficial to northern bobwhite populations are also beneficial to sympatric species, that is, the northern bobwhite serves as a suitable "umbrella" species for a suite of grassland and shrub-scrub birds.

Under BQI, habitat restoration across the landscape is effected principally through landowner financial incentives. Landowners, through consultation with WRD biologists, propose specific habitat modifications and activities to be pursued on each parcel nominated for enrollment in the program. All proposals are scored by the WRD on a set of measureable, local field-scale attributes thought to reflect quality of bobwhite habitat. Those meeting a minimum score are competitively ranked, and the top scoring proposals are enrolled in the program. Most of the BQI practices incorporate field margin management around and across annual crop fields and prescribed fire management in pine stands. Additionally, BQI biologists provide technical assistance to landowners regardless of their enrollment status, or their desire to enroll for financial incentives.

In addition to site visits to evaluate cooperator compliance, monitoring programs for bobwhite and winter songbirds were an important component of the program during the first few years. The University of Georgia Warnell School of Forestry and Natural Resources (WSFNR) cooperated with the WRD to conduct these surveys for both enrolled (treatment) and non-enrolled (control) sites; however, monitoring ceased in 2002 when state funding for monitoring was terminated.

In its first 2 years of existence, the BQI demonstrated increases in northern bobwhite calling activity on treated sites relative to control sites (Hamrick 2002). Despite the apparent early success of the program, fundamental questions about management remain. For example, do the effects of management depend on the scale at which they are applied? What evidence is there that bobwhite response is due to effects beyond management control?

Landscape-scale management, uncertainty, and adaptive management

Several implications stem from the fact that the BQI program involves the management of a large, agricultural landscape, involving numerous ownerships and complex ecological relationships. First, management decisions potentially operate at numerous spatial scales, from (at the broadest scale) statewide incentive programs, to (at the local scale) the decision of landowners to participate, and if so, specifically how. Second, the ecological processes that drive bobwhite and other bird populations are controlled by many factors, themselves operating at multiple scales, and only partially responsive to management actions. This sets up a situation where the predicted relationship between management actions and bird response is both complex, and subject to great uncertainty, a theme in common with other complex systems (e.g., Conroy et al. 2003).

Adaptive resource management (ARM) explicitly recognizes uncertainty in resource decision making; seeks an optimal resource decision given the available decision alternatives; and seeks to reduce uncertainty via prediction-based monitoring (Walters 1986; Johnson et al. 1997; Johnson and Williams 1999; Conroy et al. 2003). We approached the problem of selecting lands for enrollment in the BQI within the framework of ARM, and we developed a decision model based on hierarchical modeling of available data as the first step in an adaptive landscape approach to bobwhite/early succession bird restoration.

In this study, we develop the modeling tools needed to bring a more adaptive focus to the BQI that would deliver consequent conservation benefits in terms of increasing northern bobwhite abundance to this region of Georgia. Although the program now has certain adaptive elements in place, it lacks mechanisms to explore the effect of alternative decision options, to exploit information feedback from the system to better guide future decision making, and to make optimal decisions under scientific uncertainty (Walters and Hilborn 1978; Walters 1986; Williams 1996). In particular, we demonstrate that the absence of a monitoring program makes gains by the BQI difficult to assess and management performance a challenge to improve.

Methods

Study area

The BQI program was initiated with three focus areas that included 17 counties in the Upper Coastal Plain of Georgia (Fig. 1). The focus areas were East (Bulloch, Burke, Jenkins, and Screven Counties), Central (Bleckley, Dodge, Emanuel, Houston, Laurens, and Treutlen Counties), and Southwest regions (Colquitt, Crisp, Dougherty, Lee, Mitchell, Sumter, and Terrell Counties). This research was conducted on sites in all counties except Colquitt, Crisp, Houston, and Mitchell Counties.

Major land uses in all three regions consisted of intensive row crop agriculture and timber/fiber production. Agricultural row crop production was dominated by cotton, peanuts, soybeans, corn, and winter wheat. Center-pivot irrigation was commonly used to irrigate crops in the Southwest and Central regions, and was used less frequently to irrigate crops in the East region. The agricultural fields in the study area tended to be much larger than northern bobwhite home ranges, but <50 ha, with little or inadequate transition zones capable of providing suitable bobwhite habitat. Historically, fencerows or hedgerows that were composed mainly of scattered trees and shrubs with abundant grassy and weedy understory separated two or more fields. Today, these important transition zones have either undergone changes in their vegetative structure that make them unsuitable bobwhite habitat or been eliminated to create one contiguous crop field out of two or more smaller fields. Forest production in the study area was dominated by plantations of loblolly (*Pinus taeda*)

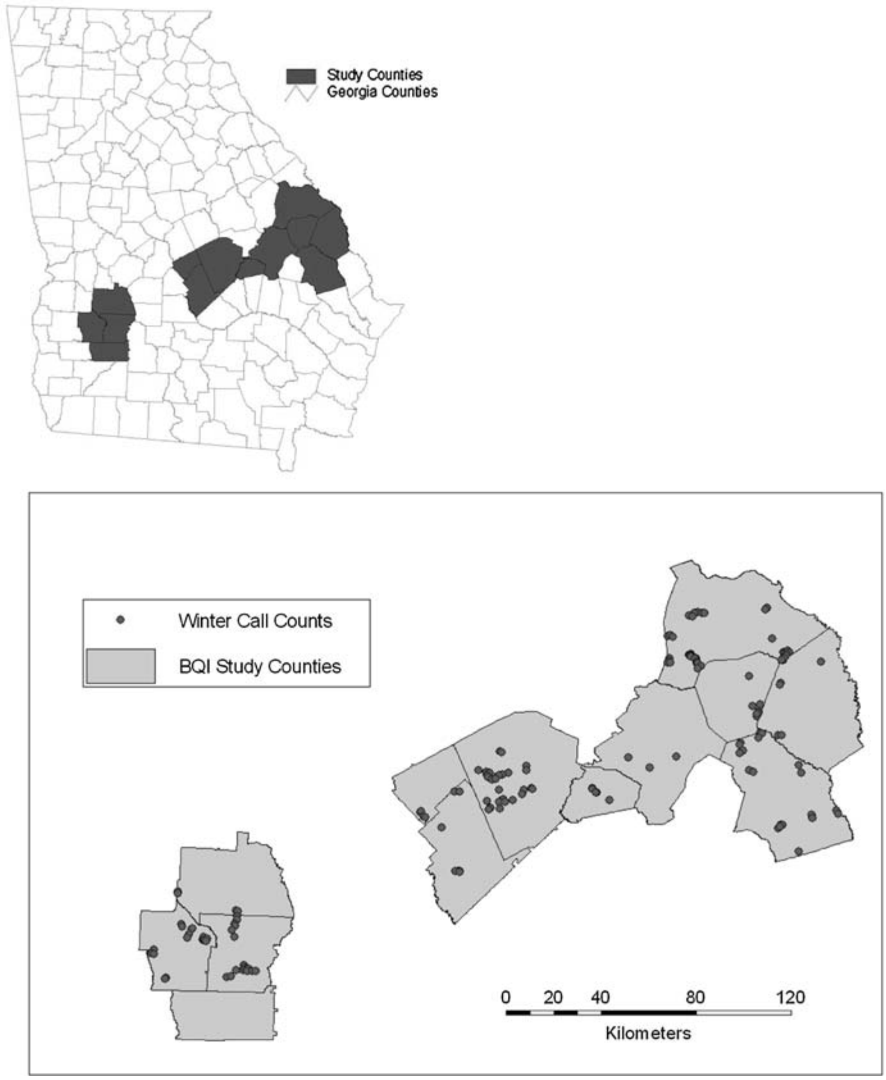


Fig. 1 Georgia counties enrolled in the Bobwhite Quail Initiative (BQI) and locations of winter call counts on BQI counties in Georgia surveyed from 1999 to 2001

and slash pine (*P. elliotti*), although longleaf pine (*P. palustris*) plantings were increasing in all regions. In the first 3–5 years after pine plantations are established, good bobwhite habitat often exists. Thereafter, pine plantations become too dense to allow adequate understory vegetation growth, and bobwhite habitat is lost until thinning and prescribed fire or other soil disturbance can be applied to increase herbaceous understory (Rosene 1969). The majority of pine stands in the study area had basal area and understory vegetation characteristics that did not constitute suitable bobwhite habitat.

Previous research in this physiographic region suggested that northern bobwhites are distributed widely, but generally at low densities (Hamrick 2002). Although not evenly distributed over this landscape, we are assuming that when habitat is improved in a location then bobwhites potentially respond by occupying more of the landscape.

Field methods, data collection, and spatial data organization

Covey-call-count indices were used to evaluate bobwhite populations on sample BQI and non-BQI sites over a broad regional scale (13 of 17 potential counties). During covey-call-counts, observers listen for the "koi-lee" covey-calls (Stoddard 1931) given by bobwhite (almost always before sunrise) during autumn. Before conducting call-count surveys, observers were trained by listening to recorded covey-calls and by spending several mornings in the field listening to calling coveys pointed out by experienced observers.

Covey-call-count surveys were conducted from mid-October to mid-December on a sample of fields including those enrolled in the BQI program from 1999 to 2001. At least 500 m separated each survey point to minimize duplicate observations between surveys conducted in the same area. Survey points were set up at least 1 day in advance of the survey to ensure that observers could efficiently locate points the morning of the survey. Observers were instructed to minimize disturbance when traveling to survey points on the morning of the survey. Surveys were not conducted during periods of sustained rainfall. Each survey utilized one of three potential covey call techniques: quadrat surveys, point counts, or two-observer surveys. We used several techniques in order to assess modifications of the quadrat technique for monitoring bobwhite abundance over much larger geographical scales (Hamrick 2002). The response variable for abundance estimation was bobwhite covey density on the landscape.

Quadrat surveys

The quadrat technique utilizes a 0.25-km^2 (25 ha, 500 $\times$ 500 m) quadrat to survey calling coveys. Four observers are required, with one observer positioned along the midpoint of each quadrat line (in 1999, a fifth observer was positioned in the center of the quadrat). Observers were instructed to arrive at survey points at least 45 min before sunrise, and surveys officially began 40 min before sunrise. On standardized data sheets and field maps, observers recorded compass bearings, estimated distances, and approximate locations for each calling covey detected. Once the first call was detected, calling coveys were recorded for a 10-min interval in order to minimize duplicate observations (as coveys often begin to move and initiate their daily activities soon after calling) and to standardize survey methods. Once the survey period expired, observers met to compare results in order to determine individual covey locations. Each unique covey location was plotted on a final field map. For each covey that was detected by more than one observer, the intersection of compass bearings to the covey was used to plot the approximate location. If only one observer detected a particular covey, the estimated distance to the covey along the compass bearing was used to plot the approximate location. Surveys were ended at the official time of sunrise if no calls were detected by this time.

Point count surveys

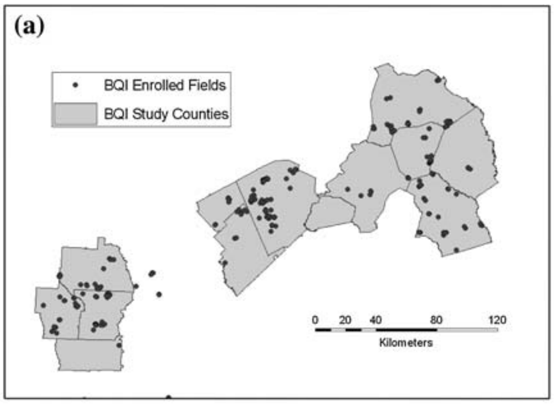
Point counts (single-observer call-counts) were used to survey bobwhite populations on remaining sample sites in 1999 and 2000, and all sample sites in 2001. It was assumed that an observer could hear a calling covey at a distance of up to 500 m (W. E. Palmer, Tall Timbers Research Station, personal communication). A single observer was positioned where as much of the area of interest as possible was covered by the assumed maximum hearing distance. Survey protocol for point counts was the same as for quadrat surveys, and approximate locations of detected coveys were determined by estimating distance to the covey along the compass bearing.

Two-observer surveys

In 2000, two-observer call-count surveys were used on a portion (about 13%) of the total number of call-count surveys conducted. Going into the 2000 field season, it was assumed that the 350-m two-observer design would be a reasonably quantitative and less labor-intensive survey method compared to the quadrat method. Time constraints prohibited employment of many such surveys, and this technique was discontinued by 2001. Observers were spaced approximately 350 m apart. Survey protocol for two-observer surveys was the same as for quadrat surveys.

Spatial data organization

For each survey on BQI-enrolled and non-BQI sites, we determined a centroid which would represent the location of the survey in a geographic information system (GIS; Fig. 1). A centroid was also determined for all surveyed and unsurveyed fields which had contracts with BQI during the study period (Fig. 2a). We then created a nested grid of hierarchical landscape levels based on biological and management factors (Fig. 2b). The finest level consisted of a



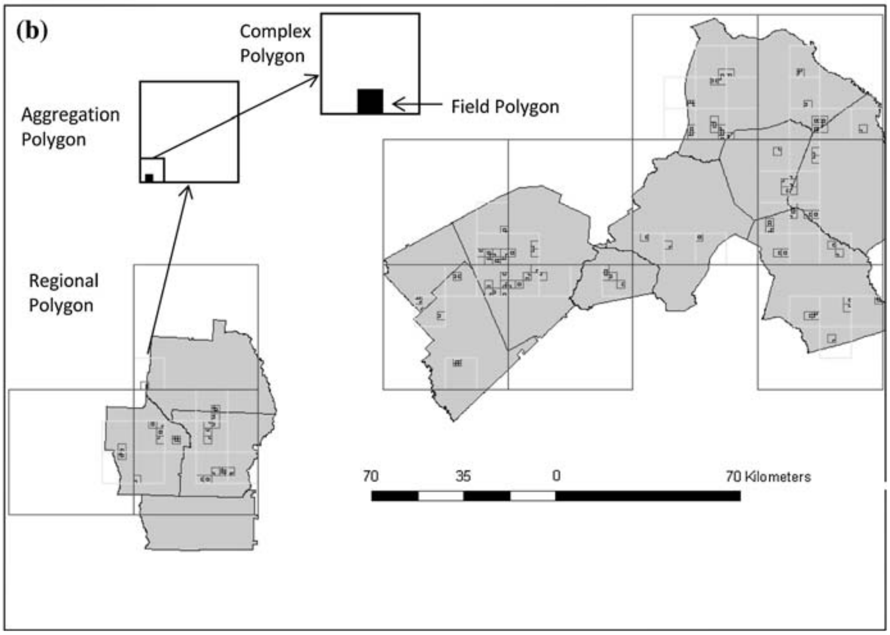


Fig. 2 **a** Centroids for fields enrolled in BQI from 1999 to 2001 in the study counties. **b** Hierarchy of spatially nested units used for modeling responses of northern bobwhite coveys to habitat and BQI management from 1999 to 2001

1-km^2 grid considered to be the field level units ("Field", L1). This level represents the individual BQI fields and the attendant factors. This field level was then nested within a grid of 9-km^2 polygons ("Complex", L2). We believe that this field complex level encompasses the likely scale at which northern bobwhite population dynamics are occurring. These field complexes were then nested within a grid of 144-km^2 cells ("Aggregation", L3). This scale represents a grouping of BQI management practices and their impacts. These management aggregates were finally nested within a grid of 2,304-km^2 cells ("Region", L4). These cells represented a management region and are roughly the size of a BQI Georgia county.

Model development

Each of our models integrated two components which share a common parameter, λ (covey density): a component which modeled the response of birds to habitat and management covariates, and a component that accounted for imperfect detection of birds through call-counts. Letting λ_i represent the true density of bobwhite coveys in field i, we assumed that the mean number detected by an observer is $E(c_i) = p\lambda_i$, where p is an estimated detection rate (discussed below). We also assumed that the actual number detected, c_i, was a Poisson random variable centered on this mean. Through these assumptions, our models used variation in call counts to make inferences about habitat and management effects at multiple scales while simultaneously accounting for uncertainty in the estimation of detection rate and stochasticity in the count itself.

Detection modeling

Data from the multi-observer quadrat surveys conducted in 1999–2000 were used to estimate covey detection rate. We assumed that the detection of coveys by k of n total observers ($n = 4$ or 5, depending on survey year) followed a binomial distribution with outcome probabilities proportional to $p^k(1-p)^{(n-k)}$.

Landscape modeling

The landscape modeling has three inputs: field-level counts of coveys (c_i), the absence (control) or presence (BQI contract) of management, and the habitat information derived from the 1998 Georgia GAP landcover map. Density and management practice inputs may vary by location and year, while habitat value inputs vary only by location. Thus, management is modeled against a background of fixed habitat conditions, as reflected through the landcover map.

Habitat and management relationships

In order to model the effect of habitat and management at each spatial hierarchical level, we used a hierarchical linear model (Wong and Mason 1985; Snijders and Bosker 1999; Howell et al. 2008). Hierarchical modeling has become increasingly common for dealing with ecological processes that occur, and are observed, at multiple scales of resolution (Royle and Dorazio 2008). Recent examples of hierarchical modeling in ecology include estimation of population parameters (Conroy et al. 2008; Kéry 2008; Royle 2008; Royle and Young 2008), spatial modeling and resource selection (Harper et al. 2008; Howell et al. 2008; Rivot et al. 2008; Wibster et al. 2008), and species richness and community structure (Kéry and Royle 2008).

The model may be described by first considering a single-level linear model:

$$\log(\lambda_i) = \alpha_0 + \alpha_1 X_{1i} + \cdots + \alpha_P X_{Pi} + r_i, \tag{1}$$

where λ_i is the density of coveys and $X_{1i} \ldots X_{Pi}$ are the P habitat and management variables measured in field unit i, α_0 is the intercept, $\alpha_1 \ldots \alpha_P$ are the corresponding coefficients, and r_i is the error assumed to be normally distributed with a mean of zero and variance σ_1^2. Thus, λ_i follows a lognormal distribution. Next we assumed that observations that occur within the same complex (3 × 3 grid of field units) are more similar to each other than to observations which occur outside of that complex. We modeled this by assuming that the intercept in Eq. 1 varies between field complex units based on a set of S habitat and management variables $W_{1j} \ldots W_{Sj}$ measured for each field complex j. The influence of these variables was modeled by expressing the level-one intercept (α_0) as a linear function of these habitat and management measures:

$$\alpha_{0j} = \beta_0 + \beta_1 W_{1j} + \cdots + \beta_S W_{Sj} + \mu_{2j}, \tag{2}$$

where $\beta_0 \ldots \beta_S$ are coefficients for the level-two habitat and management effects, and μ_{2j} is the random effect of complex j. The random effect μ_{2j} represents the spatial random group effect associated with each level-two unit that is not explained by the model, and we assumed it to be normally distributed with mean zero and variance σ_2^2. The complete two-level linear model can be expressed by substituting Eq. 2 for α_{0j} in Eq. 1:

$$\log(\lambda_{ij}) = \beta_0 + \beta_1 W_{1j} + \cdots + \beta_S W_{Sj} + \mu_{2j} + \alpha_1 X_{1ij} + \cdots + \alpha_{\mathrm{P}} X_{\mathrm{P}ij} + r_{ij}. \tag{3}$$

We performed similar substitutions for each additional hierarchical level, i.e.,

$$\beta_{0k} = \chi_0 + \chi_1 V_{1k} + \cdots + \chi_R V_{Rk} + \mu_{3k}, \text{ and} \tag{4a}$$

$$\chi_{0l} = \delta_0 + \delta_1 U_{1l} + \cdots + \delta_C U_{Cl} + \mu_{4l}, \tag{4b}$$

with corresponding random effect terms μ_{3k} and μ_{4l} distributed normally with zero mean and variances σ_3^2 and σ_4^2, respectively. In the first of these cases (Eq. 4a), the level-two intercept (β_{0k}) was modeled as a linear function of habitat and management effects occurring at the third, or aggregation, hierarchical level. In the second case (Eq. 4b), the level-three intercepts (χ_{0l}) were similarly modeled as a linear function of habitat and management effects at the fourth, or region, level.

When all algebraic substitutions are completed, the full form of the model becomes

$$\log(\lambda_{ijkl}) = \delta_0 + \delta_1 U_{1l} + \cdots + \delta_C U_{Cl} + \mu_{4l} + \chi_1 V_{1kl} + \cdots + \chi_R V_{Rkl} + \mu_{3kl} + \beta_1 W_{1jkl} + \cdots + \beta_S W_{Sjkl} + \mu_{2jkl} + \alpha_1 X_{1ijkl} + \cdots + \alpha_P X_{Pijkl} + r_{ijkl}, \quad (5)$$

where λ_{ijkl} is the density of coveys in field i of complex j of aggregation k of region l. We assumed that the relationship between density and habitat or management variables did not vary among spatial units within a hierarchy, leading to a model in which there were no interactions between variables at different spatial scales.

Temporal action of management

In order to relate our management variables, which varied over time, to densities of coveys, we developed two alternative model forms that used different degrees of lag between management and the subsequent population response. The first form of the model related covey numbers in a given year as a function of the management performed that year and the habitat values. Expressed as

$$\lambda_{ijklt} = f(\underline{D}_{ijklt}, \underline{Z}_{ijkl}),$$

where in field i of complex j of aggregation k of region l, λ_{ijklt} is the density of coveys in year t, $\underline{D}_{ijklt}$ is a vector of the management practices in year t, and $\underline{Z}_{ijkl}$ is a vector of habitat attributes. The second form of the model related numbers of coveys in a given year as a function of management in the previous year and the habitat values. Expressed as

$$\lambda_{ijkl,t+1} = f(\underline{D}_{ijklt}, \underline{Z}_{ijkl}),$$

where in field i of complex j of aggregation k of region l, $\lambda_{ijkl,t+1}$ is the density of coveys in year $t + 1$, $\underline{D}_{ijklt}$ is a vector of the management practices in year t, and $\underline{Z}_{ijkl}$ is a vector of habitat attributes. We did not undertake longer time-lag models because we expected that management and other parameters impact bobwhite density over short time periods.

Global model selection and construction of model set

Within each hierarchical level we measured habitat attributes from the Georgia GAP landcover map and aggregated BQI management practices. The landcover map designates portions of the landscape into 44 classes based on land cover type. From these classes, we selected specific variables for each hierarchical level (land classes provided in Table 1). With increasing spatial grain, we combined certain classes to create a more general landcover type. We then measured the total area at the appropriate hierarchical level of each landcover type per cell.

Management variables were based on BQI practices on contract fields during the study period (management variables and units of measurement provided in Table 1). We assigned each field to one of the Field-scale (1 km^2) cells and to that cell's corresponding parent cells. We then summed the extent (area or length) of each practice type over the fields in each cell of each hierarchical level. In order to test the impact of prolonged management, at the field complex level (L2) we created an average number of years under management weighted by the total area of the member fields.

Based on combinations of these variables, we developed a set of 36 models that considered bird outcomes as a response to combinations of (a) contemporary (M_1), time-lagged (M_T), or no (M_0) management inputs; (b) presence (H_1) or absence (H_0) of habitat variables; and (c) random effects (RE) occurring at one or more landscape scales (L_1, L_2, L_3, L_4, L_{12}, L_{1234}). The specific management or habitat variables appearing in a model depended on the landscape scale(s) represented in the model. For example, the $L_3M_1H_1$ model contained random effects occurring at the third (144-km^2) scale and the three management and three habitat variables measured at that scale (Table 1). The $L_{1234}M_1H_1$ model contained random effects occurring at all four scales and management and habitat variables measured at all scales.

Statistical analysis

Each candidate model (and the integrated detection submodel) was fit using Markov chain Monte Carlo (MCMC) methods as implemented in WinBUGS software, version 1.3 (Lunn 2003; Spiegelhalter et al. 2003). Program WinBUGS uses a "Metropolis-within-Gibbs" algorithm to efficiently sample from the posterior distributions of model parameters, under mild assumptions of convergence to stationary Markov chains (Gelman et al. 2004). The program contains built in diagnostics for evaluating

Table 1 Management and habitat variables at four landscape scales related to northern bobwhite abundance derived from the 1998 Georgia GAP landcover map and Georgia Bobwhite Quail Initiative practices

Scale	Management variables	Habitat variables (GAP landcover class index)
1. Field (1 km^2)	**Field borders**[a]	**Row crop** (83)
	Hedgerows[b]	**Pasture** (80)
		Utility (20)
		Clearcut (31)
		Open pine[d]
2. Complex (9 km^2) (including nine fields)	**Years enrolled**	**Hardwood**[e]
	Field borders[a]	**Wetland**[f]
	Hedgerows[b]	Evergreen[g]
	Pivot + fallow[c]	**Transportation** (18)
3. Aggregation (144 km^2) (including 16 complexes and 144 fields)	**Number of fields**	Evergreen[g]
	Field borders[a]	**Urban**[h]
	Hedgerows[b]	**Agriculture**[i]
4. Region (2,304 km^2) (including 16 aggregations, 256 complexes, and 2,304 fields)	**Practice acres**	**Urban**[h]
		Agriculture[i]

Variables used in restricted-variable model set appear in **bold**

[a] Dry and irrigated field borders (km): total length of field borders (field scale) or cumulative length of borders (higher scales)

[b] Dry and irrigated hedgerows (km): total length of hedgerows (field scale) or cumulative length of hedgerows (higher scales)

[c] Total area (hectares) in pivot corners and fallow patches

[d] All open or sparse pine classes: Open Loblolly-Shortleaf (422), Sandhill (512), Longleaf Pine (620)

[e] All hardwood classes (excluding montane): Hardwood Forest (412), Xeric Hardwood (413), Liveoak (420), Mixed Pine Hardwood (434), Bottomland Hardwood (900)

[f] All wetland classes: Cypress-Gum Swamp (890), Freshwater Marsh (930), Shrub Wetland (980), Evergreen Forested Wetland (990)

[g] All evergreen classes (excluding montane): Open Loblolly-Shortleaf (422), Loblolly-Shortleaf Pine (440), Loblolly-Slash Pine (441), Sandhill (512), Longleaf Pine (620)

[h] All urban classes: Low Intensity Urban—Nonforested (22), High Intensity Urban (24), Parks Recreation (72), Golf Course (73), Forested Urban—Deciduous (201), Forested Urban—Evergreen (202), Forested Urban—Mixed (203)

[i] All agricultural classes: Pasture, Hay (80) and Row Crop (83)

convergence, and permits users to export model output to other programs (e.g., the R statistical package) for further evaluation. Spiegelhalter et al. (2003) provide details for the use of WinBUGS, Congdon (2001) provides numerous examples using WinBUGS, and Link et al. (2002) provide an excellent introduction to the use of MCMC and WinBUGS in ecological modeling.

For the habitat and management relationship variables, we assigned diffuse normal prior distributions (mean 0, variance 100) to reflect a lack of prior knowledge about model parameters. Random effects at each scale were assumed to arise from a zero-centered normal distribution with a scale-specific precision "hyperparameter" τ_s. In turn, the τ_s were sampled from diffuse gamma distributions (mean 1, variance 1,000). We assigned a diffuse beta prior distribution (mean 0.5, variance 0.0833) for the detection rate parameter. Each model was run in three chains of 55,000 iterations each, with the first 4,000 iterations discarded as burn-in. To affirm convergence of the sampler, we inspected plots of the modified Gelman–Rubin statistic (Brooks and Gelman 1998) for each model. We then ranked the candidate models based on Akaike Information Criterion (AIC; Burnham and Anderson 2002). We did not use the Deviance Information Criterion (DIC) proposed by Spiegelhalter et al. (2002) because of well-known problems with proper estimation of the "effective number" of parameters under complex, nonlinear models such as ours. We interpret our AIC scores and corresponding model weights as relative, rather than absolute, measures of model fit and parsimony (Burnham and Anderson 2002).

Out of a concern that the models were all either very small (those containing only random effects) or very large (those also containing habitat and/or management effects), we tried a strategy of conditioning model selection on a subset of habitat and management variables. We fit the global model $L_{1234}M_1H_1$ and noted which variables had sizeable distribution mass to one side or the other of zero. We then restricted the total set of available habitat and management variables down to a smaller set (henceforth, the *restricted-variable set*) containing those variables not centered at or near 0 (Table 1, boldface type), and re-fit the 36 models as above.

Simulation of management under uncertainty

Because the models consider habitat and management effects at various landscape scales, the efficacy of management on any given field may be dependent on circumstances in the larger landscape matrix. Therefore, a proposal's strength may lie not only in the locally applied suite of treatments but also in the forms of habitat and management that already surround the focal field. However, different models attribute different degrees of importance to these landscape effects. Therefore, the problem for managers is to rank competing proposals for BQI enrollment while taking into account uncertainty in choosing a single model.

To evaluate decision making under various sources of uncertainty, including that induced by model selection uncertainty, we simulated a process that could be used to evaluate proposals from a landscape matrix of candidate fields. We developed a scenario based on a representative sample of 36 candidate fields in four complexes. We chose complexes that offered contrasting values in levels of management already in place within the complex (more vs. fewer practices) and types of existing habitat (more vs. less amount of suitable habitat). In our simulation exercise, we assumed that a manager was confronted with choosing two fields for BQI enrollment from the slate of 36 candidate fields, with the objective of achieving greatest bobwhite response. Therefore, our alternative decisions consisted of all possible combinations of two fields selected from among the 36. For each random draw of a pair of fields, we used the following process to simulate the response (predicted number of bobwhites) on each field in the pair:

1. Assign new management predictor variables in each chosen field by augmenting the current level of management by a fixed increment of additional practice.
2. Next, from the set of best predictive models identified by AIC (see above), select one model at random, depending on a prior model probability (ranging from 0 to 1).
3. For the given model, draw parameter values from a normal distribution with the mean and standard deviation estimated from the corresponding statistics of the posterior distribution for the parameter from the indicated model.
4. Conditioned on the selected model, randomly drawn parameter values, and predictor variables for the selected field, generate a predicted mean value for number of bobwhites.
5. Lastly, generate a random integer outcome from a Poisson distribution with mean equal to the above predicted value.

The total for two random outcomes was returned as a sample objective value for the pair under the indicated model.

We encoded the above steps in a Python program (Python Software Foundation 2008), which randomly took 315,000 samples from among the unordered field combinations, sampling each of the $\binom{36}{2}$ combinations approximately 500 times. We investigated simulation outcomes under each of five model weighting scenarios: model-averaged (weighted average over the AIC weights for all models in the model set), and probability 1.0 weight on each alternative model (i.e., certainty assumed for each model in turn).

Results and discussion

On control and treated fields during 1999–2002, we conducted 410 covey counts under the point count design (339), the quadrat design (55), and the two-

Table 2 Top ten predictive models of northern bobwhite abundance and model weights for model sets including all management and habitat variables in global model and restricted set of management and habitat variables

All variables in global model					Restricted variable set				
Model[a]	Including RE-only		Excluding RE-only[b]		Model[a]	Including RE-only		Excluding RE-only[b]	
	ΔAIC	Weight	ΔAIC	Weight		ΔAIC	Weight	ΔAIC	Weight
$L_2M_0H_0$	0	0.765363	–	–	$L_2M_0H_0$	0	0.496859	–	–
$L_{1234}M_0H_0$	3.70	0.120343	–	–	$L_{12}M_1H_0$	1.69	0.213429	0	0.502168
$L_2M_0H_1$	5.36	0.052476	0	0.459129	$L_2M_1H_0$	3.28	0.096381	1.59	0.226769
$L_2M_1H_0$	5.44	0.050418	0.08	0.441126	$L_{1234}M_0H_0$	3.70	0.078125	–	–
$L_{12}M_1H_0$	10.10	0.004905	4.74	0.042920	$L_2M_0H_1$	3.77	0.075438	2.08	0.177493
$L_2M_1H_1$	10.55	0.003917	5.19	0.034272	$L_2M_1H_1$	6.01	0.024614	4.32	0.057913
$L_2M_TH_0$	11.68	0.002226	6.32	0.019479	$L_{12}M_TH_0$	8.61	0.006708	6.92	0.015783
$L_{12}M_TH_0$	16.77	0.000175	11.41	0.001529	$L_2M_TH_0$	8.87	0.005890	7.18	0.013859
$L_2M_TH_1$	17.81	0.000104	12.45	0.000909	$L_2M_TH_1$	12.03	0.001213	10.34	0.002855
$L_{12}M_0H_1$	19.15	5.31E–05	13.79	0.000465	$L_{1234}M_1H_0$	12.61	0.000908	10.92	0.002136

[a] Model key: $L_{\{x\}}$—landscape-level random effects at scale(s) $\{x\}$; M_m—management effects at scale(s) $\{x\}$ either absent ($m = 0$), contemporaneous ($m = 1$), or lagged ($m = \mathrm{T}$); H_h—habitat effects at scale(s) $\{x\}$ either absent ($h = 0$) or present ($h = 1$)

[b] Model weights determined by excluding models containing only landscape scale random effects (RE-only models)

observer design (16). Using data from the quadrat surveys, the estimated average per observer detection probability was $P = 0.33$ (95% CI 0.23–0.45).

Posterior estimates for parameters associated with the unrestricted set of habitat and management variables varied by model, but were generally in line with our expectations when an effect was present. All BQI management variable associations were either positive or centered about zero. These effects were found at all of the spatial scales we investigated, offering evidence of local as well as region-wide positive effects from BQI on northern bobwhite abundance. Under our models, even fields not enrolled in BQI would experience positive effects so long as they were within the BQI regions.

For both the restricted and unrestricted-variable sets, the Complex-level, RE-only model ($L_2M_0H_0$) was the top-ranked model, taking ≥50% of the share of model weight from the set (Table 2) and suggesting that larger scale demographic processes may be dominating habitat and management factors at this scale. But more weight was distributed to the remaining models (i.e., smaller values of ΔAIC) in the restricted-variable model set than in the unrestricted-variable model set. This was expected, as the pre-screening process excluded variables that were unlikely to have appeared in any parsimonious model.

Models were similarly ranked between the two approaches, except for model $L_{12}M_1H_0$ (Table 2). In the unrestricted-variable model set, this model received 1/150 of the weight for the top model and about 1/10 of the weight for the $L_2M_1H_0$ and $L_2M_0H_1$ models. However, in the restricted-variable model set, it received almost half the weight of the top model and approximately 2.5 times the weight of the $L_2M_1H_0$ and $L_2M_0H_1$ models. The increase in parsimony for this model perhaps resulted from the exclusion of two management variables at the two smallest scales.

Two models containing only landscape-scale random effects ($L_2M_0H_0$ and $L_{1234}M_0H_0$) received substantial weight (≥50 and ≥8%, respectively) and low rank (1 and ≤4, respectively) under either approach (Table 2). These models propose that quail response is insensitive to both management and habitat, suggesting that the flip of a (biased) coin predicts bird occurrence on a field about as well as any more sophisticated method. These models are of management interest only for the reason that, if true, they indicate that management practices are ineffective in increasing or decreasing quail abundance. Better (more realistic) null models of management are those that contain habitat effects, but no management effects. When all RE-only models are excluded from the set of unrestricted-variable models, five

Table 3 Results of simulations (mean number of coveys in field pair) to rank combinations of fields drawn two at a time from four complexes of fields (nine fields/complex), taking into account complex- and field-level predictors and stochastic uncertainty in responses

Rank	Model									
	1. Model-averaged[a]		2. $L_2M_1H_1$		3. $L_2M_1H_0$		4. $L_2M_0H_1$		5. $L_{12}M_1H_0$	
	Pair	Mean	Pair	Mean	Pair	Mean	Pair	Mean	Pair	Mean
1	(06, 19)	18.60	(00, 08)	26.48	(08, 25)	21.77	(01, 07)	9.97	(01, 26)	19.08
2	(03, 05)	18.49	(01, 08)	26.45	(19, 21)	21.76	(00, 07)	9.92	(06, 07)	19.02
3	(01, 03)	18.29	(06, 08)	25.71	(01, 08)	21.65	(03, 05)	9.87	(19, 24)	18.99
4	(01, 21)	18.19	(05, 08)	25.58	(19, 24)	21.59	(09, 11)	9.82	(01, 24)	18.96
5	(00, 01)	18.05	(01, 06)	25.46	(02, 06)	21.58	(01, 09)	9.82	(04, 22)	18.91
6	(05, 06)	18.03	(02, 08)	25.41	(22, 23)	21.50	(01, 08)	9.82	(20, 25)	18.91
7	(02, 05)	18.01	(01, 03)	25.36	(01, 23)	21.41	(15, 16)	9.81	(03, 06)	18.87
8	(00, 06)	18.01	(01, 07)	25.35	(02, 18)	21.41	(01, 02)	9.80	(24, 25)	18.86
9	(03, 21)	18.00	(03, 06)	25.17	(00, 20)	21.39	(05, 15)	9.77	(06, 24)	18.86
10	(00, 03)	17.95	(06, 07)	25.13	(08, 19)	21.38	(04, 10)	9.76	(20, 24)	18.84
11	(07, 08)	17.94	(02, 03)	25.11	(00, 24)	21.31	(01, 16)	9.75	(24, 26)	18.82
12	(01, 06)	17.88	(03, 08)	25.04	(05, 23)	21.27	(11, 17)	9.72	(06, 08)	18.76
13	(01, 07)	17.88	(05, 06)	25.02	(04, 21)	21.26	(10, 17)	9.71	(08, 19)	18.75
14	(04, 24)	17.88	(01, 02)	25.01	(00, 19)	21.26	(02, 07)	9.71	(01, 23)	18.75
15	(04, 21)	17.83	(00, 01)	24.97	(04, 25)	21.24	(07, 11)	9.71	(06, 21)	18.67
16	(18, 24)	17.78	(03, 05)	24.97	(00, 08)	21.23	(06, 13)	9.70	(01, 06)	18.65
17	(05, 08)	17.78	(01, 04)	24.89	(02, 24)	21.20	(09, 14)	9.68	(04, 26)	18.64
18	(01, 23)	17.75	(04, 07)	24.86	(02, 26)	21.20	(06, 09)	9.68	(06, 26)	18.62
19	(02, 19)	17.74	(02, 04)	24.82	(21, 26)	21.19	(01, 14)	9.67	(07, 20)	18.60
20	(05, 24)	17.65	(00, 04)	24.80	(20, 24)	21.19	(14, 16)	9.66	(01, 21)	18.60

Complex characteristics: better habitat/more management (fields 0–8), better habitat/less management (fields 9–17), poorer habitat/more management (fields 18–26), poorer habitat/less management (fields 27–35)

[a] Model-averaged results reflect optimal selection decisions for the case of uncertainty among prediction models

models receive AIC weight of $\geq$1%: $L_2M_0H_1$ (46%), $L_2M_1H_0$ (44%), $L_{12}M_1H_0$ (4%), $L_2M_1H_1$ (3%), and $L_2M_TH_0$ (2%). For the restricted-variable set, six models receive weight $\geq$1% when RE-only models are excluded: $L_{12}M_1H_0$ (50%), $L_2M_1H_0$ (23%), $L_2M_0H_1$ (18%), $L_2M_1H_1$ (6%), $L_{12}M_TH_0$ (2%), and $L_2M_TH_0$ (1%). Models that proposed a 1-year lag effect of management were consistently ranked behind corresponding contemporary-effects models.

For our simulation exercise, we retained models $L_{12}M_1H_0$, $L_2M_1H_0$, $L_2M_0H_1$, and $L_2M_1H_1$ from the restricted-variable set, that is, we excluded RE-only and lag effect models from consideration. The simulation exercise (Table 3) illustrates how it is possible to use these models to rank candidate fields for selection. However, the closeness of the mean objective values, and the high sensitivity of the ranking to the underlying model (for example the combination [19, 24] ranked third or fourth under two models, and not in the top 20 under the other two), both suggest that the manifest uncertainty in this system could strongly influence decision making. Therefore, reduction of this uncertainty, through improved monitoring and adaptive management, potentially has management value.

Conclusions and recommendations

We have successfully built, parameterized, and evaluated alternative models that express the relationship between field and complex habitat characteristics and management practices, and predicted number of bobwhite coveys. These models can be used to evaluate alternative management practices, and to rank candidate fields for inclusion in incentive programs based on their predicted contribution to covey production. These predictions, however, are subject to a great deal of uncertainty, which degrades the ability to make optimal choices for candidate fields. Some of this uncertainty is largely beyond the control of managers: for example, random fluctuations in covey numbers because of weather conditions. However, additional uncertainty was manifested in the parameter estimates of the different models from at least three sources: (1) inadequate spatial and temporal replication of covey count and habitat data used to build the alternative models, (2) incomplete covey detection and spatial and temporal heterogeneity in observer detection rates, (3) uncertainty in discriminating between possible biological processes as represented by the alternative models. The first of these must be remedied by the collection of additional spatial and temporal replicates over the scope of the study area, to allow for better estimation of parameters, and we recommend that these additional data be collected in designed studies. The second requires further work on the calibration and testing of covey call-count indices and we likewise recommend further studies directed at this problem.

The last source of uncertainty, that due to the lack of discrimination among alternative models, would be helped by addressing (1) and (2), because more precise predictions could then be made under each alternative model. However, there are limits to how much this source of uncertainty could be reduced by this approach, and it likely could not be eliminated; we would anticipate that even given very precise models, there would still remain a great deal of structural uncertainty. The remedy to this source of uncertainty is to move forward with a limited set of models under adaptive management. Adaptive management requires, however, that a monitoring program be in place, so that predictions under the alternative models can be compared to monitored state of the bobwhite system. Monitoring is also needed, of course, to evaluate the actual (vs. assumed) success of any management decisions (i.e., choices of fields to be included in the program). Restoration and continuance of a monitoring program for BQI should be a top priority to resolve uncertainties and increase program efficacy over time.

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