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Northern Bobwhite Demographic and Population Response Following an Intensive Habitat Modification to an Agricultural Landscape

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Northern Bobwhite (*Colinus virginianus*) populations have been declining throughout most of their endemic range due to numerous factors (e.g., increased urbanization, predators); however, changing land-use practices have proved most detrimental to bobwhites. In parts of the southeastern USA, small-scale farming has been replaced by large-scale center-pivot irrigated fields and this has exacerbated habitat loss. Despite these trends, bobwhite populations in the Southeast have remained stable or increased on many areas employing intensive habitat management regimes, substantiating the importance of appropriate habitat management for long-term bobwhite persistence. In effort to reverse one such decline, we intensively modified a center-pivot, agriculture dominated landscape to benefit bobwhites by creating new habitat and improving existing habitat. Techniques utilized to modify this landscape were: establishment of linear habitats (field borders and buffer strips); planting longleaf pines; and management of existing habitat via prescribed burning and timber management. During 1998-2001, we monitored bobwhite ($n = 498$) demographics and population response following annual habitat restoration and management using radio-telemetry and fall abundance estimation (i.e., covey call-counts). Average survival during over-winter (0.4698, SE = 0.0721), breeding (0.3561, SE = 0.0667) and annual (0.1673, SE = 0.0411) time-periods were higher than those reported for other agriculture studies and similar to those of intensively managed, "plantation" habitats. Bobwhite coveys and broods used newly developed longleaf pine, linear habitats (e.g. field borders/hedgerows), and managed woodlands. Further, nest site selection was commonly associated with these novel habitat types. As a result of the positive demographic response to habitat modification, bobwhite abundance also improved during the study. Consequently, we surmised that modification of agricultural landscapes may improve habitat quality and quantity for bobwhites and subsequently help to increase demographic rates and bobwhite abundance.

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Key words: agriculture, buffer strips, field borders, habitat use, home range, northern bobwhite, PROC NLMIXED, Program MARK, reproduction, SAS, survival

Introduction

Despite being the most studied upland gamebird in North America, northern bobwhite (*Colinus virginianus*) populations have continued to decline throughout most of their endemic range. Whereas declining populations have been associated with various factors (e.g., increased urbanization, changing predator dynamics), changing land-use practices have proved most detrimental to bobwhites (Bren-

nan 1991, 1999, Church et al. 1993, Rollins and Carroll 2001). Recent changes among agriculture landscapes have dramatically affected bobwhites by reducing habitat quantity and quality (Brennan 1999). Clean farming, larger fields, center-pivot irrigation systems and increased herbicide and pesticide use (Capel et al. 1993, Sotherton et al. 1993) have become a common rubric among these landscapes-an ecosystem which once supported high densities of bobwhites. As these habitats, which once benefited

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bobwhites, have diminished, bobwhite populations have also waned. Further, more intensive or lack of management among remaining forested habitats (e.g. silviculture) surrounding agriculture fields has also contributed to habitat loss (Burger 2002). Notably, the declining status of bobwhite populations are not unique to bobwhites, but have also affected numerous species of songbirds (Conover 2005). Contrary to these trends, bobwhite populations in the Southeast have not declined on many areas that have employed intensive habitat management regimes (Brennan et al. 2000, Palmer et al. 2002, Stribling and Sisson 2009); this substantiates the importance of appropriate habitat management to maintaining long-term bobwhite populations.

During the past decade, in an attempt to mitigate habitat loss among agricultural landscapes, federal Farm Bill programs (e.g., CRP, WHIP, EQIP) have been implemented to provide landowners monetary incentive to restore or set aside portions of their cropland to promote early-succession vegetation (Burger 2002). Numerous management practices qualify for enrollment in these programs benefiting bobwhites and other species: cool- and warm-season grass plantings; conservation tillage; exotic grass control; wildlife habitat improvement or development; pine tree management; and linear habitats (LH) including filter or buffer strips, field borders and riparian buffers. However, the utility of these linear habitats, pine plantings, and other habitats, when applied to agricultural ecosystems, to bobwhite demographics and population growth is poorly understood.

Previous research has demonstrated that bobwhites used, and in some cases preferred, LHs for normal daily activities, brood-rearing and nesting (Puckett et al. 2000, Cook 2004). Likewise, previous research has documented increases in bobwhite and songbird abundance when combined with mesomammal reduction (Bromley et al. 2000) and without mesomammal reduction (Hamrick 2002, Cook 2004, Conover 2005). Additionally, Cook (2004) found that bobwhites on areas with LHs exhibited higher survival and lower dispersal proclivities compared to

areas without LHs.

However, despite the wide-spread habitat implementation gained from Farm Bill programs and the purported population increase associated with LHs and agricultural ecosystems as mentioned above, the utility of LHs relative to bobwhite demographic parameters at both the local and regional scale remains uncertain. Similarly, few studies have examined the utility of planting longleaf pines (PPs) among agriculture landscapes to improve bobwhite habitat. Whereas previous studies revealed that bobwhite abundance increased on areas with LHs compared to areas without them (Bromley et al. 2000, Hamrick 2002), their methods employed could not provide the means to adequately ascribe whether the observed population increase was a consequence of higher survival, increased reproductive success, or due to immigration. Furthermore, although Puckett et al. (2000) suggested that linear habitats were preferred among bobwhites, they reported that nest survival was low, particularly during the early nesting season. Moreover, Cook (2004) suggested that more research was needed to examine the utility of linear habitats to bobwhite broods. Thus, more research has been warranted to ascertain whether novel habitats improve demographic parameters and provide a practical utility to facilitate reversal of population declines observed among agricultural landscapes.

The primary objective of this study was to examine the utility of augmenting an agricultural dominated landscape with novel habitat types and examine bobwhite habitat-use, demographics, and population response following an intensive modification. We intensively modified the center-pivot, agriculture dominated landscape to benefit bobwhites by creating new habitat and improving existing habitat. Techniques utilized to modify this landscape were: establishment of linear habitats, field borders and buffer strips; planting longleaf pines at a conservative spacing; and management of existing habitats via prescribed burning and timber management. Finally, we compared our results, when applicable, from this study to intensively managed sites and an unmanaged agriculture site in southwest Georgia

since we did not have pre-treatment demographic data.

Study Area

The study was conducted on a privately-owned property, Whitehall Plantation (3734 ha), in Laurens and Bleckley counties, Georgia, USA. This study site was located in the Upper Coastal Plain physiographic region near the fall line. Prior to intensive habitat modification during 1998-1999, the study site was comprised of dry and irrigated agriculture fields (55%), unmanaged woodlands (40%) comprised of mixed hardwoods and pines (*Pinus* spp.), and 5% other, miscellaneous-type habitats (e.g., pastures, ponds). During this time, the primary land-use objective was agriculture (i.e., row-crop farming) and the estimated bobwhite population was <1 bird/4 ha. However, during 1997, the primary land-use objective changed to management that benefited northern bobwhites, but farming remained an objective-albeit secondary.

During 1998-1999, intensive habitat management was undertaken converting the agriculture predominated landscape to a landscape more conducive to bobwhites. We employed numerous habitat techniques to improve habitat for bobwhites: dry-land agriculture fields were planted in longleaf pines (*Pinus palustris*); 15 m field borders, buffer strips, and hedgerows were created in all irrigated, agriculture fields; no-tillage farming practices was implemented; annual autumn disking and fallow field management was employed to stimulate annual weed production and arthropods for bobwhite broods; and both chemical and mechanical silvicultural treatments to decrease basal area (timber density) among upland and lowland timberland areas was applied as needed. As such, the new landscape matrix was comprised of agriculture (22%), managed woodlands (21%), and planted longleaf (21%) with interspersed linear habitats (LH [12%]; hedgerows, terraces and field borders), hardwoods (10%), other (ponds, pastures, etc; 8%) and fallow fields (6%).

Methods

Trapping and Monitoring

We trapped bobwhites during October-November and March-April 1998 - 2002 using standard funnel traps (Stoddard 1931) baited with grain sorghum and cracked corn. We covered traps with brush (e.g., fresh-cut pine limbs) to minimize stress on captured birds and to conceal traps from predators. We classified bobwhites by age and gender, and we weighed, leg-banded and released them at the capture sites. We outfitted birds weighing ≥ 132 g with pendant-style (Mueller et al. 1988) transmitters (6.0 g) equipped with an activity switch (Holohil Systems Ltd., Ontario, Canada). Trapping, handling, and marking procedures were consistent with the guidelines in the American Ornithologists' Union Report of Committee on the Use of Wild Birds in Research (American Ornithologists' Union 1988) and the protocol was approved by the Auburn University Institutional Animal Care and Use Committee, IACUC (Protocol Review Numbers: 2002-0364).

Survival - We monitored bobwhites ≥ 3 times weekly using the homing method (White and Garrett 1990, pg. 42). We approached birds within 25-50 m to minimize location and classification errors; and entered the locations into a geo-database using Geographic Information Systems (GIS) and ArcView® software (Environmental Systems Research Institute, Inc.). We determined specific causes of mortality when possible, by evidence at the kill site and condition of the radio-transmitter (Curtis et al. 1988). When radio contact was lost, we systematically searched on and off the study area within approximately 5 km of the bird's last known location.

Reproduction - During nesting season, we assumed inactive birds, determined via an activity switch, observed in the same location on 2 consecutive days to be nesting. We approached inactive hens and marked their location with flagging tape at a distance of 5-10 m and recorded the location in our geo-database. We monitored nests ≥ 5 times weekly and determined exact nest location and number of eggs when the incubating hen left the nest to feed.

Table 1: Models explaining northern bobwhite survival derived via Program MARK (known-fate model; $\hat{c} = 1.78$) relative to gender- and time-dependent factors for Whitehall Plantation located in Laurens and Bleckley County, Georgia, 1999 - 2002.

Model	K	$QAIC_c$	$\Delta QAIC_c$	QDeviance	W_i
S(season-constant)	2	1605.8567	0.0000	1601.8554	0.4700
S(season + gender)	3	1607.4971	1.6404	1601.4942	0.2070
S(.)	1	1608.2812	2.4245	1606.2806	0.1398
S(season+gender*season interaction)	4	1608.9472	3.0905	1600.9428	0.1002
S(. + gender)	2	1609.7107	3.8540	1605.7095	0.0684
S(annual-constant)	4	1613.6336	7.7769	1605.6295	0.0096
S(season-time)	7	1614.9662	9.1095	1600.9549	0.0049
S(t)	26	1636.7524	30.8957	1584.6097	0.0000

We monitored nests daily from distances of >10 m and we determined fate of the nest as abandoned, successful, or unsuccessful. We defined a depredated nest as any nest in which ≥ 1 eggs was destroyed and the adult bird did not return to incubate the remaining clutch. A nest was deemed abandoned when the hen did not complete incubation and all eggs were still intact. We defined a nest successful when ≥ 1 egg hatched.

Statistical Analysis

Survival And Cause-specific Mortality - We used the known-fate model in program MARK (version 5.2; White and Burnham 1999) to explain variation in survival, estimate daily survival rates and estimate the probability of surviving explicit time-periods (e.g., season, year) for male and female bobwhites. The known-fate model employs a binomial likelihood (weekly in our case) and permits incorporation of individual covariates (e.g., gender) delineated by groups (e.g., years in our case) to evaluate their affect on survival. When the fate (alive, dead or censored) of every radio-marked animal is known for each survival interval, the known fates model generates Kaplan-Meier survival estimates (Kaplan and Meier 1958, Pollock et al. 1989). However, because we had missing data for some intervals (e.g.,

when radio-contact was lost or bobwhites were not checked during a given interval due to stochastic events [i.e., inclement weather]), the variance components of the survival estimates generated from the known-fate model in program MARK are more suitable than those calculated by traditional Kaplan-Meier methods.

We used an information-theoretic approach (Burnham and Anderson 2002, Anderson et al. 2000) to evaluate the set of candidate models. The models were developed *a priori* based on biological insight to avoid superfluous model building (i.e. data dredging). The best approximating model in the set of candidate models was determined by Akaike's Information Criteria (AIC); adjusted for small sample bias and over-dispersion ($QAIC_c$; Burnham and Anderson 2002). We used the median \hat{c} method as implemented in Program MARK to assess and correct for over-dispersion ($\hat{c} = 1.78$) among our data. $QAIC_c$ is a valid model selection method for both nested and non-nested sets of models (Burnham and Anderson 2002). $QAIC_c$ was used to compare each candidate model, and the model with the lowest $QAIC_c$ value was considered to be the best approximating model given the data.

Nest Survival - We estimated daily survival rate

Table 2: Predicted probability of surviving (mean survival and 95% confidence intervals) during overwinter (OW), breeding (Breed) and annual time-periods derived via Program MARK for northern bobwhites located on Whitehall Plantation in Laurens and Bleckley County, Georgia, 1999 - 2002.

Season	DSR ^a	SE ^b	LCI ^c	UCI ^d	Survival	SE	LCI	UCI
OW 1998 - 1999	0.9757	0.0054	0.9625	0.9843	0.5272	0.0748	0.3806	0.6737
Breed 1999	0.9627	0.0073	0.9454	0.9746	0.3717	0.0713	0.2319	0.5116
ANNUAL	0.9697	0.0044	0.9597	0.9773	0.2024	0.0474	0.1094	0.2953
OW 1999 - 2000	0.9693	0.0056	0.9563	0.9786	0.4448	0.0655	0.3164	0.5732
Breed 2000	0.9605	0.0067	0.9449	0.9717	0.3503	0.0625	0.2277	0.4729
ANNUAL	0.9652	0.0043	0.9556	0.9727	0.1583	0.0365	0.0867	0.2299
OW 2000 - 2001	0.9710	0.0054	0.9582	0.9800	0.4656	0.0667	0.3348	0.5963
Breed 2001	0.9600	0.0072	0.9431	0.9720	0.3463	0.0664	0.2162	0.4764
ANNUAL	0.9662	0.0044	0.9565	0.9739	0.1677	0.0392	0.0908	0.2446
OW 2001 - 2002	0.9690	0.0071	0.9517	0.9803	0.4415	0.0815	0.2817	0.6013

^aDSR is the interval survival 7-days for this study, ^bSE = standard error, ^cLCI = lower 95% confidence interval, ^dUCI = upper 95% confidence interval

(DSR) for bobwhite nests and evaluated competing models explaining variation in nest survival using a general linear mixed model approach (Dinsmore et al. 2002, Stephens 2003, Rotella et al. 2004). We fit models using PROC NLMIXED in SAS because it provided the framework needed to model our binomially distributed data (nest fate = 0 if failed and 1 if successful) and provided a user defined link option (i.e., logit link) while concurrently considering the affects of habitat (PP [planted pines], LH [linear habitats], and other) and gender covariates and, the random effect of year on nest survival (PROC NLMIXED; Institute 1999). We considered year a random effect because we assumed that year was a random level sample and to avoid confounding fixed effects of other variables of interest (e.g., LH, PP).

We used an information-theoretic approach (Burnham and Anderson 2002, Anderson et al. 2000) to evaluate the set of candidate models. The models were developed *a priori* based on biological insight to avoid superfluous model building (i.e., data dredging). The best approximating model in the set

of candidate models was determined by Akaike's Information Criteria (AIC); adjusted for small sample bias (AIC_c; Burnham and Anderson 2002). AIC_c is a valid model selection method for both nested and non-nested sets of models (Burnham and Anderson 2002). AIC_c was used to compare each candidate model, and the model with the lowest AIC_c value was considered to be the best approximating model given the data. The relative plausibility of each model in the set of candidate models was assessed by Akaike weights (w_i , Burnham and Anderson 2002, Anderson et al. 2000), where the best approximating model in the candidate set has the greatest Akaike weight (Burnham and Anderson 2002, pg. 447). We used model averaging (Burnham and Anderson 2002, pg. 448) to calculate model averaged coefficients (LH, gender); and we report these coefficients, their standard errors and 95% confidence intervals, and odds ratios.

Habitat Use and Selection - We examined habitat use for bobwhite coveys (1 Oct - 31 Mar) and broods (breeding season) with 2nd and 3rd order habitat selection (Johnson 1980) for individual cov-

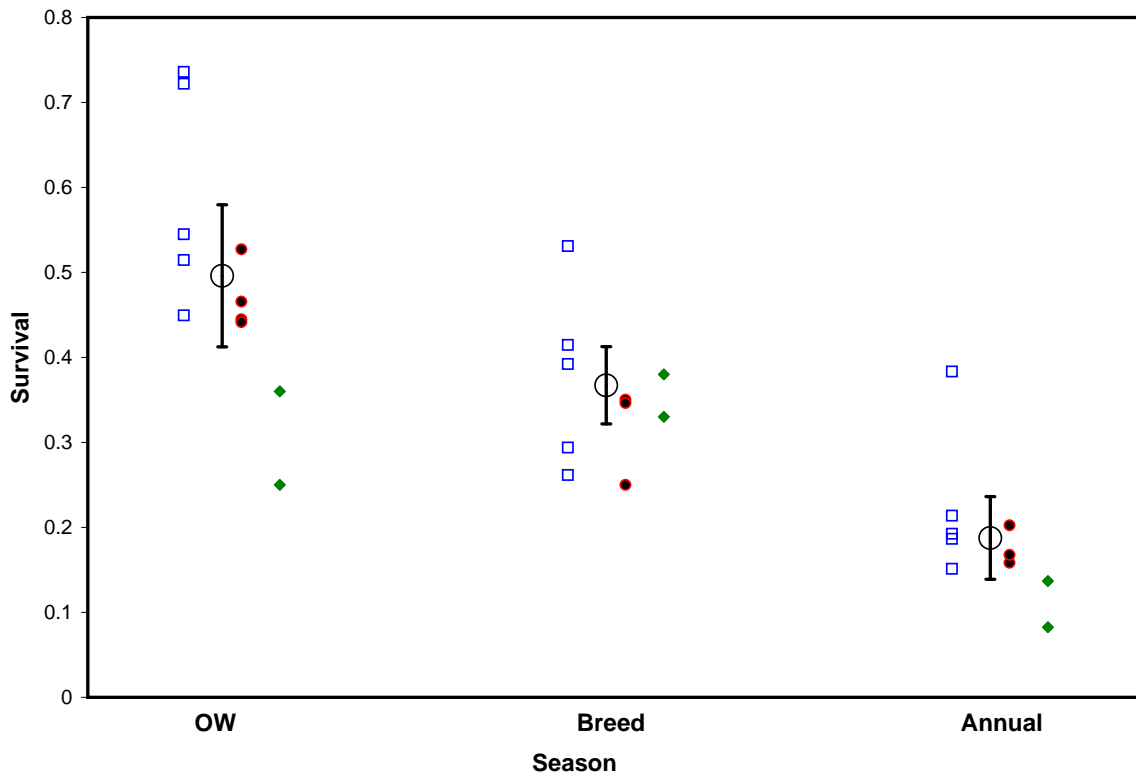


Figure 1: Predicted probability of surviving (mean survival and 95% confidence intervals) during overwinter (OW), breeding (Breed) and annual time-periods obtained via Program MARK (black circles with red outline data points), for our data compared to long-term plantation survival estimates (hollow square-shaped points) and an unmanaged agriculture site (green diamond-shaped points) in southwestern Georgia derived via Kaplan-Meier during 1998 - 2002.

eys and broods, respectively, using compositional analysis (CA; Aebischer et al. 1993, Manley et al. 2000). We defined second order availability for individual coveys and broods (only when $n > 3$ radio-tagged bobwhites/covey). The average habitat proportions within these polygons was calculated and considered to be second order availability. Second-order use was defined as the proportions of each habitat type within home ranges. We defined 3rd order availability as the proportion of each habitat type within home ranges and habitat use as the proportion of individual radio-locations within each habitat type. Prior to analysis, we replaced zero values for use with the value 0.001—an order of magnitude less than the smallest nonzero value (Aebischer et al. 1993). When a habitat was not available

for use, we replaced missing values in each log-ratio with the mean of all non-missing values for the respective log-ratio (Aebischer et al. 1993). All habitat selection analyses were conducted using Compos Analysis (version 6.2; Smith 2005). We used a multivariate analysis of variance (MANOVA) test to examine habitat selection (Aebischer et al. 1993). Habitats were ranked using a matrix that indicated the difference of log ratios between habitat types, and log ratio differences were determined with paired t-tests (Aebischer et al. 1993).

We used GIS to assess metrics of habitat composition and configuration using the Animal Movements Extension (AME; Hooge and Eichenlaub 1997) to calculate fixed kernel winter home ranges (Worton 1989) using a 95% isopleth. Kenward (2001, pg. 231)

Table 3: Cause-specific mortality for known-fate radio-tagged northern bobwhites ($n = 253$) on Whitehall Plantation in Laurens and Bleckley counties, Georgia, 1999 - 2002.

	Causes of Mortality				Total
	Mammal	Avian	Snake	Harvest	
1998-1999	14	47	1	2	64
1999-2000	12	67	0	2	81
2000-2001	13	63	3	2	81
2001-2002	3	22	0	2	27
Pooled	42	199	4	8	253
Percent	16.6	78.66	1.58	3.16	100

indicated that ~20 locations was needed for home range size stability when using the kernel method; thus, coveys and broods with ≤ 20 locations were excluded from analysis. We also excluded mortality locations from analysis since predators may have transported birds away from the original kill site.

Results

Survival

We monitored 498 bobwhites ($n_{\text{female}} = 279$, $n_{\text{male}} = 219$) during the 3.5-year study. The most parsimonious known-fates model for our data included time-dependency as a constant-seasonal effect (Table 1) with a model weight of 0.47. The model averaged coefficient for breeding season (1 May - 30 Sep) was -0.303 (SE = 0.151). This indicated that breeding season had a negative effect (i.e., survival was lower than over-winter season) on survival for our data. Annual variation in survival was not evident ($w = 0.0096$; Table 1) for our data. The additive effect of gender to the best model did warrant some consideration ($w = 0.2070$; Table 1). Whereas the model averaged coefficient estimate for gender (i.e., female) effect was 0.124 (SE = 0.175) indicating that females survived better than males, but the confidence limits for the effect of gender included 0. Further, the model including a season and gender

interaction had relatively little support ($\Delta\text{QAIC}_c = 3.09$, $w = 0.1002$) indicating that variation in survival relative to gender was not dependent on season (i.e., breeding or over-winter) for our data.

Generally, over-winter (OW) seasonal survival was higher than breeding (Breed) season survival (Table 2). Breeding season had a negative effect on survival ($\beta = -0.318$; 95% CI: -0.614, -0.023). The average OW and Breed season survival was 0.4698 (SE = 0.0721) and 0.3561 (SE = 0.0667), respectively. OW survival was lower than long-term bobwhite estimates from plantations but higher than unmanaged agriculture sites in southwestern Georgia (Figure 1). Breeding season and annual survival was similar among sites (Figure 1). Avian species were the most prevalent agent of mortality accounting for 78.66% of the known-fate bobwhites (Table 3). Mammals accounted for 16.60% of bobwhite mortalities, whereas snakes and harvest combined for <5%.

Reproduction

We monitored 165 nests ($n_{1999} = 45$, $n_{2000} = 72$, $n_{2001} = 48$) during the 3.5-year study. The constant-among years-model was the best supported model for our data (Table 4); however, models including individual-additive fixed effects of gender, PPs, LHs and a random year-effects model warranted consideration ($\Delta\text{AIC}_c \leq 2$, $w > 0.1000$). The model

Table 4: Mixed models (i.e., fixed and random effects models) explaining nest survival treating year as fixed and random effects; and, linear habitats (LH) and gender as fixed effects for northern bobwhites located on Whitehall Plantation in Laurens and Bleckley County, Georgia, 1999 - 2002.

Model	K	AIC	AIC_c	$\Delta Q AIC_c$	W_i
B_0	1	604.8676	604.8695	0.0000	0.3013
$B_0 + B_1^*(PP)$	2	606.7752	606.7808	1.9113	0.1159
$B_0 + B_1^*(Gender)$	2	606.8171	606.8226	1.9531	0.1135
$B_0 + B_1^*(LH)$	2	606.8453	606.8508	1.9813	0.1119
$B_0 + u$	2	606.8676	606.8732	2.0037	0.1106
$B_0 + B_1^*(Year1) + B_2^*(Year2)$	3	607.9712	607.9823	3.1128	0.0635
$B_0 + B_1^*(PP) + B_2^*(LH)$	3	608.7739	608.7849	3.9154	0.0425
$B_0 + u + B_1^*(PP)$	3	608.7752	608.7863	3.9168	0.0425
$B_0 + u + B_1^*(Gender)$	3	608.8171	608.8281	3.9587	0.0416
$B_0 + u + B_1^*(LH)$	3	608.8453	608.8563	3.9869	0.0410
$B_0 + u + B_1^*(PP) + B_2^*(LH)$	4	610.7739	610.7923	5.9228	0.0156

considering year as a fixed effect had relatively little support ($\Delta AIC_c = 3.11$, $w = 0.0731$) compared to other top-ranked models. Therefore, we primarily fit models treating years as random effects so as not to confound with other fixed effect parameters.

We used model averaging to interpret coefficients for nest survival and individual covariates (Table 5). The odds ratios for gender, PP and LH were 1.07, 1.07 and 0.95 (Table 5), respectively, indicating that females and nests located in PPs were 7% more likely to be successful than nests incubated by males and found in other habitats, respectively; however, the confidence interval for these log ratios included 1. Daily nest survival (DSR) for 1999, 2000, and 2001 was 0.9727 (SE = 0.0065), 0.9645 (SE = 0.0055), and 0.9705 (SE = 0.0065), respectively. The average DSR for years pooled was 0.9687 (SE = 0.0037). Nest survival for years pooled delineated by gender and habitat type was higher for females and nests located in PPs, although these differences were not significant (Figure 2).

Habitat Use

Coveys - We combined all coveys ($n = 67$) during the 3.5-year study for habitat selection analysis; we determined that habitat selection did not differ between years ($F_{2,66} = 1.58$, $P = 0.214$). Covey habitat selection departed from random at both the second-order ($\lambda = 0.6467$, $\chi^2_3 = 29.206$, $P < 0.001$) and third-order ($\lambda = 0.2644$, $\chi^2_3 = 89.139$, $P < 0.001$) levels. For our data, coveys preferred PP types over hardwoods and miscellaneous types (Table 6; 2nd order: $t_{66} = 3.515$, $P < 0.001$; 3rd order: $t_{66} = 5.870$, $P < 0.001$) and AG/FAL habitat types (Table 6; 2nd order: $t_{66} = 3.628$, $P < 0.001$; 3rd order: $t_{66} = 9.580$, $P < 0.001$). LH habitat types was preferred to hardwoods and miscellaneous habitats, but the difference was not significant at the 3rd order level (Table 6; 2nd order: $t_{66} = 2.921$, $P = 0.005$; 3rd order: $t_{66} = 0.220$, $P = 0.827$), and LH was preferred to AG/FAL habitat (Table 6; 2nd order: $t_{66} = 4.247$, $P < 0.001$; 3rd order: $t_{66} = 3.181$, $P = 0.002$). In order of preference at the second order level bobwhite coveys preferred: planted pines, linear habitats, managed woodlands, hardwoods and thinned hardwoods, agricultural and fallow land. And at the

Table 5: Model averaged, estimated coefficients and associated precision for parameters used to model variation in nest survival for northern bobwhites located on Whitehall Plantation in Laurens and Bleckley County, Georgia, 1999 - 2002.

Parameter	Estimate	SE	Confidence Interval		Odds Ratio
			Lower 95%	Upper 95%	
Gender (female)	0.0710	0.3136	-0.5437	0.6856	1.0736
Planted Pine (PP)	0.0764	0.2518	-0.1755	0.3282	1.0793
Linear Habitat (LH)	-0.0486	0.3234	-0.3720	0.2748	0.9525

third order level bobwhite coveys preferred: planted pines, managed woodlands, linear habitats, hardwoods and thinned hardwoods, agricultural and fallow land.

Broods - We combined all broods ($n = 73$) to examine habitat selection and preference for the 3.5 year study. Brood habitat selection was not random at both the second-order ($\lambda = 0.2631$, $\chi^2_3 = 97.470$, $P < 0.001$) and third-order ($\lambda = 0.2632$, $\chi^2_3 = 97.441$, $P < 0.001$) levels. Broods preferred LHs over all other habitat types at the second-order level and all other habitat types except PPs at the third-order levels (Table 7). At the second-order level: LHs were preferred to agriculture and fallow habitats although the difference was not significant ($t_{72} = 1.034$, $P = 0.302$), PPs ($t_{72} = 3.051$, $P = 0.003$), hardwoods and other habitats ($t_{72} = 12.906$, $P < 0.001$), and managed woodlands ($t_{72} = 2.867$, $P = 0.005$); PPs was preferred to hardwoods and other habitats ($t_{72} = 7.859$, $P < 0.001$), and managed woodlands ($t_{72} = 2.867$, $P = 0.005$); agriculture and fallow lands was preferred over hardwoods ($t_{72} = 10.132$, $P < 0.001$), managed woodlands ($t_{72} = 2.034$, $P = 0.046$), and planted pines (PPs) although the difference was not significant ($t_{72} = 1.785$, $P = 0.085$); and managed woods was preferred over hardwoods ($t_{72} = 6.583$, $P < 0.001$). At the third-order level: PPs was preferred to agriculture/fallow land ($t_{44} = 4.672$, $P < 0.001$), hardwoods and other habitats ($t_{10} = 7.709$, $P < 0.001$), man-

aged woodlands ($t_{34} = 2.876$, $P = 0.007$), and LHs, although the difference was not significant ($t_{46} = 0.371$, $P = 0.713$); and LHs was preferred to agriculture habitats ($t_{54} = 4.688$, $P < 0.001$), hardwoods and other late-succession habitats ($t_{12} = 2.154$, $P < 0.050$), and managed woodlands although the difference was not significant ($t_{72} = 1.303$, $P = 0.200$).

Population Response

We used covey call counts via the point-count method (Wellendorf et al. 2004) to determine bobwhite abundance. Using a replicated design and 14 individual, fixed points we estimated the initial bobwhite abundance at 0.86 birds/ha (~45 coveys). During fall 2001, we estimated a final bobwhite abundance of 1.48 birds/ha. Thus, we observed an estimated 75% increase in bobwhite abundance during the 3.5-year study.

Discussion

Survival

Bobwhite survival has been documented to vary both temporally and spatially (Burger et al. 1995a, 1998, Curtis et al. 1988, Sisson et al. 2009, Taylor et al. 2000, Terhune et al. 2007) and relative to gender (Pollock et al. 1989). During this study, variation in survival was best explained by models including seasonal effects. There was a negative effect of breeding season on bobwhite survival; bobwhites were 1.37 times (37%) less likely to survive during breeding

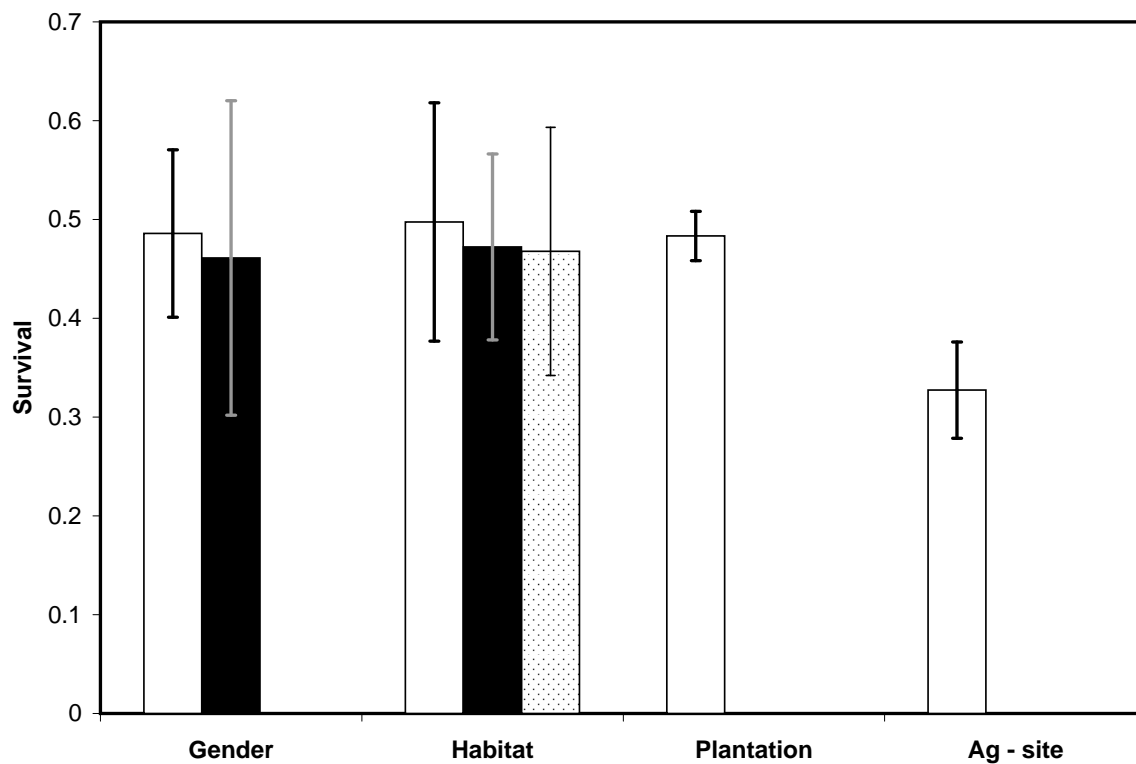


Figure 2: Predicted probability of survival (mean survival and 95% confidence intervals) of northern bobwhite nests as estimated via model averaging for gender (male [solid black bars], female [solid white bars]) and habitat (LH [black-speckled bars], other habitats [solid black bars], and PPs [solid white bars]) on Whitehall Plantation in Laurens and Bleckley County, Georgia, compared to nest survival estimates for an intensively managed plantation and an unmanaged agriculture site during 1999 - 2002.

season than OW season. Whereas the most parsimonious model including gender did warrant some consideration, the model including the interaction of gender and season was not adequately supported ($\Delta \text{QAIC}_c = 3.09$). This suggested that survival relative to gender was not dependent on season. Our survival estimates were similar to those of other reported studies (Curtis et al. 1988, Burger et al. 1998, Sisson et al. 2009, Terhune et al. 2007). Breeding season and annual survival during our study was, in general, similar to intensively managed plantation sites and an unmanaged agriculture site (Figure 1); however, OW survival was markedly disparate between sites. Interestingly, survival during OW declined relative to management strategy whereby intensively managed plantation sites, managed agriculture sites (i.e. our study site), and un-

managed agriculture sites incurred the highest, near average, and lowest survival, respectively. Similarly, Cook (2004) demonstrated that bobwhites exhibited higher survival on areas with linear habitats compared to those void of them. As such, the utility for augmenting habitat among agricultural landscapes via novel habitats (i.e. PPs and LHs) to improve survival, at least compared to unmanaged agricultural landscapes, was substantiated by our critique.

Fies et al. (2002) suggested bobwhite dispersal and movement proclivities are potentially greater among fragmented landscapes and Kabat and Thompson (1963) reported increased movements of bobwhites when landscapes typically consisted of marginal habitat. Incidentally, Cook (2004) reported that bobwhites on sites with linear habitats exhibited lower dispersal rates than sites without these

Table 6: Simplified ranking matrices for northern bobwhite coveys based on second- and third-order compositional analysis on Whitehall Plantation located in Laurens and Bleckley counties, Georgia 1999-2002.

	Ag / Fall ^a	PP ^b	LH ^c	HW / Other ^d	MW ^e	Rank
<i>2nd Order habitat selection (n = 67)^f</i>						
Ag / Fall		—	—	-	—	0
PP	+++		+	+++	+	4
LH	+++	-	+	+++		3
HW / Other	+	—	—		—	1
MW	+++	-		+++	-	2
<i>3rd Order habitat selection (n = 67)^g</i>						
Ag / Fall		—	—	-	—	0
PP	+++		+++	+++	+	4
LH	+	—	+		—	2
HW / Other	+++	—		-	—	1
MW	+++	-	+++	+++		3

^aAg / Fall denotes habitat types including agriculture and fallow fields, ^bPP represents planted pines (typically longleaf), ^cLH represents linear habitats: field buffers and borders, hedgerows, linear longleaf pines, and terraces, ^dHW denotes habitat types including hardwoods and other habitats not typically associated with early succession vegetation (e.g., drains), ^eMW represents managed woods: upland pines, early succession vegetation areas other than fallow fields, burned and unburned habitats, and thinned and managed mixed hardwood pine stand, ^f2nd order analysis was based on comparing the proportional habitat use within home ranges with the proportion of total available habitat types (i.e., study area vs. home range); a triple sign indicates a significant deviation from random at the alpha level of 0.05 and positive and negative signs indicates habitat preference and avoidance, respectively, ^g3rd order analysis was based on comparing the proportional habitat use within home ranges with the proportion of telemetry locations located within each habitat type within each bird's home range (i.e., home range vs. locations).

habitats. Additionally, Sisson et al. (2000, 2002) demonstrated that survival and home range size was dependent on resource quality and availability. Hughes et al. (2005) reported evidence to support these notions: they suggested that due to lack of resources (e.g. habitat and food availability) bobwhites were forced to utilize lower quality habitats (e.g. creek swamps, hardwoods) and traverse unsuitable habitat(s) to get to suitable habitat and/or food; however during years of abundant food resources they determined that home range size and survival improved dramatically. Although not reported herein, bobwhites on our study site generally retained high site fidelity; home range size was only marginally larger than those on intensively managed plantation sites and smaller than those on unmanaged agriculture sites (S. Mitchell, Alabama

Quail Project, unpublished report), indicating that resource availability was likely not a limiting factor during our study - although supplemental feeding did occur on our study site and thus home range size may have been low from this highly available resource (Sisson et al. 2000). Collectively, novel habitats (e.g. PPs and LHs) may decrease home range size, improve survival, and reduce dispersal rates among fragmented and/or agricultural landscapes.

Covey Habitat Use - Bobwhite coveys preferred PP habitats, managed woodlands, and LHs to all other available habitats (Table 6). These findings were not contrary to what we expected because during OW months (1 Oct - 31 Mar) a significant portion of the agriculture area was disked under and was thus bare soil. The preference of PP and LH (3rd Order selection) habitats over managed woodlands

Table 7: Simplified ranking matrices for northern bobwhite broods based on second- and third-order compositional analysis on Whitehall Plantation located in Laurens and Bleckley counties, Georgia 1999-2002.

	Ag / Fall ^a	PP ^b	LH ^c	HW / Other ^d	MW ^e	Rank
<i>2nd Order habitat selection (n = 73)^f</i>						
Ag / Fall		+	-	+++	+++	3
PP	-		—	+++	+	2
LH	+	+++		+++	+++	4
HW / Other	—	—	—		—	0
MW	—	-	—	+++		1
<i>3rd Order habitat selection (n = 73)^g</i>						
Ag / Fall		—	—	+	-	2
PP	+++		+	+++	+++	4
LH	+++	-		+	+	3
HW / Other	-	—	-		+	1
MW	+	—	-	-		1

^aAg / Fall denotes habitat types including agriculture and fallow fields, ^bPP represents planted pines (typically longleaf), ^cLH represents linear habitats: field buffers and borders, hedgerows, linear longleaf pines, and terraces, ^dHW denotes habitat types including hardwoods and other habitats not typically associated with early succession vegetation (e.g., drains), ^eMW represents managed woods: upland pines, early succession vegetation areas other than fallow fields, burned and unburned habitats, and thinned and managed mixed hardwood pine stand., ^f2nd order analysis was based on comparing the proportional habitat use within home ranges with the proportion of total available habitat types (i.e., study area vs. home range); a triple sign indicates a significant deviation from random at the alpha level of 0.05 and positive and negative signs indicates habitat preference and avoidance, respectively, ^g3rd order analysis was based on comparing the proportional habitat use within home ranges with the proportion of telemetry locations located within each habitat type within each bird's home range (i.e., home range vs. locations).

was likely a result of the timing of the study. The managed woodlands were heavily disturbed when they were logged and cleaned up therefore producing mostly weeds during the first couple of years. This made good summer habitat but had not yet developed into good winter cover. We speculated that bobwhites utilized PP habitats at a higher than expected rate because of the woody vegetation component provided via the longleaf pines and the fact that groundcover was more fully developed, thereby improving the quality of "escape" cover for coveys.

Among agriculture landscapes a paucity of suitable bobwhite habitat exists throughout the year. This was evident by the extremely low OW survival and large home range sizes observed on agricultural sites without PPs and LHs or newly created early-succession habitats (Hughes et al. 2005) when com-

pared to OW survival for our site where these habitats were available during the entire study. Furthermore, breeding season survival did not vary among sites, irrespective of management strategy, indicating that PP habitat was more critical during OW seasons, a time when habitat is likely a limiting factor among agricultural landscapes. Because bobwhites are considered an r-selected species (demonstrated by high annual mortality and high reproductive output), OW survival has been recognized as a vital demographic parameter for increasing bobwhite populations (Burger et al. 1998, Sisson et al. 2009). Under this tenet, by increasing OW survival, whether via habitat management or other means, the number of bobwhites available to reproduce is potentially augmented; and thus, improving reproductive output and subsequently increasing bobwhite abundance.

Therefore, the utility of creating novel habitats (PPs and LHs) and improving existing habitat as demonstrated in this study, under this tenet alone, may immensely improve bobwhite abundance among agricultural landscapes and other OW-habitat deficient sites.

Cause-specific Mortality - Despite numerous studies reporting agents responsible for mortalities of bobwhites, cause-specific mortality remains an enigma and is one of high observer subjectivity. Therefore, in this study, we only report assessed causes of mortality and compare our results to those studies conducted by the AQP (where protocols for ascribing causes of mortality were similar) to limit observer variability.

During this study, avian depredation was the leading cause of mortality for all years accounting for nearly 80% of all known-fate mortalities. Mammals accounted for approximately 17% and snake and harvest combined for <5%. Our results were generally similar to those reported by Sisson et al. (2009); however, avian mortality was elevated for our study site compared to their long-term results. Surprisingly, differences in causes of mortality did not vary relative to season for our data; avian species remained the leading mortality agent during both breeding and OW season. Notably, other sites exhibited variation in causes of mortality relative to season, whereas during breeding season mammals typically became a more salient cause of mortality than during OW seasons (Sisson et al. 2009). For example, Sisson et al. (2009) reported that one site in east-central Georgia experienced high OW-avian mortality (>71%) and high breeding-season mortality caused by mammals (>61%). Particularly noteworthy was the unmanaged agriculture site: avian mortality during breeding season (>61%) was much higher than mammalian mortality (<34%). Perhaps avian mortality, while ostensibly dependent on the timing and duration of raptor migration, is higher on agriculture sites whether or not PP and LH habitats are present. In such cases, habitat composition and juxtaposition may play a key role in the efficiency of avian predators to locate (and depredate)

bobwhites among these types of landscapes. Thus, more research is warranted to determine whether wider linear habitats may mitigate avian mortalities and/or whether other proximate habitats (e.g. hardwoods) decrease the utility of novel habitats on specific sites.

Reproduction

Daily survival rates for northern bobwhite nests in our study did not vary among years for our data (Table 4). Since we were interested in nest survival among PPs and LHs compared to other habitat types, we treated year as a random effect to evaluate habitat type and gender effects on nest survival. The most parsimonious model was a constant survival model with no covariate effects. Our nest survival estimates were higher than those reported for other nest studies (Burger et al. 1995b, Puckett et al. 1995, Hughes et al. 2005), and similar to long-term nest survival estimates for intensively managed plantations (Figure 2). However, mammalian nest predator management did occur on these study sites.

Hughes et al. (2005) surmised that lack of resource availability, particularly habitat availability, was a limiting factor during their study, and suggested that habitat development - such as field borders, field buffers, and hedgerows as well as other habitat practices (e.g., no-till farming) - would benefit bobwhite nest survival and production. Previous researchers have indicated that nest predators may more efficiently forage in landscapes comprised of small and/or narrow habitats (Puckett et al. 1995, 2000). Additionally, Puckett et al. (1995) reported low nest success for nests located in filter strips, particularly during the early nesting season. We did not, however, find evidence suggesting that linear habitats negatively impacted nest survival (Figure 2). Notably, when compared to our study, the effective land area and width of filter strips was different for the study conducted by Puckett et al. (1995, 2000), mean filter strip width was 9.2 m and the effective land area comprised of filter strips was <10 percent. Further, filter strips were designed to reduce soil erosion and thus oftentimes were located

along ditches (Puckett et al. 1995) - a habitat conducive to certain predators (e.g., snakes). In contrast, during our study, the effective land area created from PP (21%) and LH (12%) habitat development was >30% and the mean LH width was 15 m. Therefore, implementation of wider LHs and increased effective land area may improve nest survival, increasing the amount of habitat for nest predators to rummage. As such, recent implementation has demonstrated that when the effective land area was increased and wider LHs were constructed, bobwhite demographics and population levels increased among agricultural landscapes (D. C. Sisson, Albany Quail Project, unpublished report).

Among PP habitats, longleaf pines provided woody substrate and pine needles for nest building; nearly 42% of all nests during this 3.5-year study were located in PP habitats (S. Mitchell, Alabama Quail Project, personal communication) and nest survival among these habitat types was highest during our study. When combined with the nests located in LHs nearly 64% of all nests were constructed and incubated in these newly created habitat types. Thus, the development of these habitat types minimally improved the quantity of habitat available during nest season and, seemingly, did not render bobwhite nests more susceptible to predation.

Brood Habitat Use - Bobwhite hens preferred to raise broods in LHs, PPs and fallow areas compared to other habitat types, and they used PPs and LHs more than agriculture sites (Table 7). The higher use of LHs and PPs compared to agriculture cropland may have been attributed to later cover availability via crops in those areas combined with pesticide use (and low arthropod availability). Our results, for brood habitat use, were similar to those reported for other studies (Puckett et al. 1995, 2000, Cook 2004).

Cook (2004) and Puckett et al. (2000) reported that hens raising broods used LHs more than agriculture fields and other habitat types. Puckett et al. (2000) also reported that bobwhite chick survival was high among LHs and brood home range sizes were small. Although not reported herein, we

observed that, in general, bobwhite brood home-range size was similar to those of intensively managed plantation broods (S. Mitchell, Alabama Quail Project, personal communication). Therefore, we surmised that given the preference for LHs and PPs, and similar home range size of broods during our study when compared to other intensively managed sites that these habitat types may facilitate reduced home range size for broods in agriculture landscapes. Thus, provided herbicides and pesticides are not exploited in these habitats, LHs and PPs may render the much needed niche for bobwhite broods in agriculture ecosystems whereby weedy vegetation and arthropods are prevalent and year-round habitat is made available.

Summary

In this study, we reported data that advocated novel habitat (e.g. PPs and LHs) establishment as a practical utility to promote improved demographics when compared to intensively managed plantation sites and unmanaged agriculture sites: survival was generally similar to managed sites and higher than unmanaged sites; reproduction was similar to managed sites and higher than unmanaged sites; habitat use by broods and coveys was high among novel habitats and, while anecdotal, broods and coveys benefited from PPs and LHs by reducing their home range size and providing the much needed resource availability during germane times (i.e. OW months). And, these novel habitats effectively rendered nesting habitat during breeding season and nest survival was similar among these habitat types compared to other habitat types. The combined effect of novel habitat establishment and improvement of existing habitat provided a substantial overhaul to the landscape on this study site. We effectively managed >60% of the landscape to benefit bobwhites, while maintaining farm practices on much of the remainder. As a result, bobwhites utilized novel and improved habitats heavily for covey home ranges, nest sites, and brood habitat which resulted in increased bobwhite abundance and a renewed optimism for managing bobwhites outside

the traditional “plantation belt” located in southwest Georgia and north Florida. Bobwhite abundance increased each year following habitat modification whereby point counts conducted during the fall (Oct-Nov; Wellendorf et al. 2004) indicated an increase by >75 percent. Bobwhite abundance increased from <0.86 birds per hectare to >1.48 birds per hectare during the 3.5-year study.

Management Implications

Researchers and biologists have demonstrated that the most effective mode to restore bobwhite populations, both at local and regional scales, is to increase habitat availability (Klimstra 1972, Brennan 1991). Likewise, long-term research corroborates this notion where, despite the declining status of bobwhites throughout most of their range during the past decade, intensively managed bobwhite plantations have experienced stable-to-increasing bobwhite abundance (Brennan 1991, Stribling and Sisson 2009). The results from this study also illustrated the importance of habitat management to benefit bobwhites. Thus, for bobwhites to persist among agricultural landscapes, restoration (i.e., Farm Bill - CRP) programs should continue to focus on habitat management. Whereas implementation of novel habitats is by no means a panacea for reversing population declines, they may serve as pragmatic utility for at least improving bobwhite habitat among agricultural landscapes and perhaps extenuate bobwhite population declines among these ecosystems. Further, several other techniques (i.e. conservative bobwhite harvest, nest predator management, supplemental feeding) when used in conjunction with establishing novel habitats among agriculture ecosystems, may also increase restoration success.

When establishing linear habitats among agricultural landscapes, we recommend setting the target of land area affected at a minimum of 10-15% and linear habitat widths ≥ 15 m (and when applicable wider). We also recommend employing other habitat management techniques in conjunction with linear habitat establishment when appropriate: managing dry corners for early-succession vegetation,

timber density reduction on adjacent sites, mid- and over-story hardwood reduction, prescribed burning, supplemental feeding and nest predator management. When planting pines, we recommend planting longleaf pines at a conservative (8X8 or greater; 600 trees/acre or less) spacing, and utilizing prescribed fire and limb pruning as needed to benefit early-succession vegetation over time. Proper management of woodlands surrounding agricultural areas should also greatly improve habitat conditions among agricultural ecosystems - this type of management was a large part of the success observed during our study. Additionally, we encourage federal and state programs implementing early-succession habitat establishment to concentrate efforts to specific-focal areas, particularly areas located near existing bobwhite populations, and expand outward in order to maximize restoration efforts at both the local and regional scale. Lastly, we recommend continued research and monitoring of bobwhite populations among these types of ecosystems to continue gleaning insight about the utility of novel habitats and learn how these ecosystems function, as a whole, both locally and regionally.

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References

- Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313–1325.
- American Ornithologists' Union. 1988. Report of committee on use of wild birds in research. *Auk* 105:1–41.
- Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal Wildlife Management* 64:912–923.

- Brennan, L. A. 1991. How can we reverse the Northern Bobwhite population decline? *Wildlife Society Bulletin* 19:544–555.
- Brennan, L. A. 1999. Northern bobwhite (*Colinus virginianus*). Account 397 in A. Poole and F. Gill, editors. *The Birds of North America*. The Birds of North America, Inc., Philadelphia, PA, USA.
- Brennan, L. A., J. M. Lee, E. L. Staller, S. D. Wellendorf, and R. S. Fuller. 2000. Effects of seasonal fire applications on northern bobwhite brood habitat and hunting success. Pages 66–69 in L. Brennan, W. Palmer, L. W. Burger, Jr., and T. Pruden, editors. *Quail IV: Proceedings of the Fourth National Quail Symposium*. Tall Timbers Research Station, Tallahassee, FL, USA.
- Bromley, P. T., S. D. Wellendorf, W. E. Palmer, and J. F. Marcus. 2000. Effects of field borders and mesomammal reduction on northern bobwhite and songbird abundance on three farms in North Carolina. Page 71 in L. Brennan, W. Palmer, L. W. Burger, Jr., and T. Pruden, editors. *Quail IV: Proceedings of the Fourth National Quail Symposium*, volume 4. Tall Timbers Research Station, Tallahassee, FL, USA.
- Burger, L. W., Jr. 2002. Quail management: issues, concerns, and solutions for public and private lands - a southeastern perspective. Pages 20–34 in *Proceedings of the National Bobwhite Quail Symposium*, volume 5.
- Burger, L. W., Jr., T. V. Dailey, and E. W. Kurzejeski. 1995a. Survival and cause-specific mortality of northern bobwhite in Missouri. *Journal of Wildlife Management* 59:401–410.
- Burger, L. W., Jr., T. V. Dailey, E. W. Kurzejeski, and M. R. Ryan. 1995b. Seasonal and annual survival and cause specific mortality of northern bobwhite in Missouri. *Journal of Wildlife Management* 59:401–410.
- Burger, L. W., Jr., D. C. Sisson, H. L. Stribling, and D. W. Speake. 1998. Northern bobwhite survival and cause specific mortality on an intensively managed plantation in Georgia. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 52:174–190.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: A practical information-theoretic approach*. 2nd edition. Springer, New York, NY, USA.
- Capel, S., J. A. Crawford, R. J. Robel, L. W. Burger, Jr., and N. W. Sotherton. 1993. Strategic plan for quail management and research in the United States: issues and strategies-agricultural practices and pesticides. Pages 172–173 in K. Church and T. Dailey, editors. *Quail III: National Quail Symposium*, volume 3. Kansas Department of Wildlife and Parks, Pratt, KS, USA.
- Church, K. E., J. R. Sauer, and S. Droege. 1993. Population trends of quails in North America. Pages 44–54 in K. E. Church and T. V. Dailey, editors. *Quail III: National Quail Symposium*. Kansas Department of Wildlife and Parks, Pratt, KS, USA.
- Conover, R. R. 2005. Avian response to field borders in the Mississippi Alluvial Valley. Master's thesis, Mississippi State University, Mississippi State, MS, USA.
- Cook, M. P. 2004. Northern bobwhite breeding season dispersal, habitat use, and survival in a southeastern agricultural landscape. Master's thesis, University of Georgia, Athens, GA, USA.
- Curtis, P. E., B. S. Mueller, P. D. Doerr, and C. F. Robinette. 1988. Seasonal survival of radio-marked northern bobwhite quail from hunted and non-hunted populations. Pages 263–275 in *Proceedings of the International Biotelemetry Symposium*, volume 10.
- Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83:3476–3488.
- Fies, M. L., K. M. Puckett, and B. Lonnie-Brogdon. 2002. Breeding season movements and dispersal of northern bobwhites in fragmented habitats of Virginia. *Proceedings of the National Quail Symposium* 5:173–179.
- Hamrick, R. G. 2002. Evaluation of northern bobwhite (*Colinus virginianus*) population monitoring methods and population trends in agricultural systems in the upper coastal plain of Georgia. Master's thesis, University of Georgia, Athens, GA, USA.
- Hooe, P. N., and B. Eichenlaub. 1997. *Animal Movement Extension to ArcView*, ver. 1.1. Alaska Biological Science Center, U. S. Geological Survey, Anchorage, AK, USA.
- Hughes, D. W., T. M. Terhune, D. C. Sisson, and H. L. Stribling. 2005. Demographics of northern bobwhites on agricultural and intensively managed bobwhite plantation landscapes. *Proceedings of the Annual Conference of the Southeastern Associations of Fish and Wildlife Agencies* 59:30–42.

- Institute, S. 1999. SAS/STAT software, version 8.2. SAS Institute, Cary, North Carolina, USA.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- Kabat, C., and D. R. Thompson. 1963. Wisconsin quail, 1834–1962, population dynamics and habitat management. *Wildlife Bulletin* 30, Wisconsin Conservation Department.
- Kaplan, E. L., and P. Meier. 1958. Non-parametric estimation from incomplete observations. *Journal of the American Statistical Association* 53:457–481.
- Kenward, R. E. 2001. A manual for wildlife radio tagging. Academic Press, San Diego, CA, USA.
- Klimstra, W. D. 1972. Population dynamics of bobwhite on an intensively managed area in Southern Illinois. Pages 356–360 in J. A. Morrison and J. C. Lewis, editors. *Proceedings of the First National Bobwhite Quail Symposium*, volume 1. Oklahoma State University, Research Foundation, Stillwater, OK, USA.
- Manley, S. W., J. M. Lee, R. S. Fuller, J. P. Carroll, and L. A. Brennan. 2000. Comparison of two methods for quantifying northern bobwhite habitat use. Pages 213–218 in L. A. Brennan, W. E. Palmer, L. W. Burger, Jr., and T. L. Pruden, editors. *Quail IV: Proceedings of the Fourth National Quail Symposium*. Tall Timbers Research Station, Tallahassee, FL, USA.
- Mueller, B. S., J. B. Atkinson, Jr., and T. DeVos. 1988. Mortality of radio-tagged and unmarked northern bobwhite quail. Pages 139–144 in *Biotelemetry Symposium*, volume 10.
- Palmer, W. E., S. D. Wellendorf, L. A. Brennan, W. R. Davidson, and F. E. Kellogg. 2002. Hunting success and northern bobwhite density on Tall Timbers Research Station: 1970–2001. *Proceedings of the National Quail Symposium* 5:213–216.
- Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management* 53:7–15.
- Puckett, K. M., W. E. Palmer, P. T. Bromley, J. R. Anderson, Jr., and T. L. Sharpe. 1995. Bobwhite nesting ecology and modern agriculture: A management experiment. *Proceedings of the Annual Conference of the Southeastern Associations of Fish and Wildlife Agencies* 49:505–515.
- Puckett, K. M., W. E. Palmer, P. T. Bromley, J. R. Anderson, Jr., and T. L. Sharpe. 2000. Effects of filter strips on habitat use and home range of northern bobwhites on Alligator River National Wildlife Refuge. Pages 26–31 in L. Brennan, W. Palmer, L. W. Burger, Jr., and T. Pruden, editors. *Quail IV: Proceedings of the Fourth National Quail Symposium*. Tall Timbers Research Station, Tallahassee, FL, USA.
- Rollins, D., and J. P. Carroll. 2001. Impacts of predation on northern bobwhite and scaled quail. *Wildlife Society Bulletin* 29:39–51.
- Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer. 2004. Modeling nest-survival data: A comparison of recently developed methods that can be implemented in MARK and SAS. *Animal Biodiversity and Conservation* 27:187–204.
- Sisson, D. C., H. L. Stribling, and J. F. Sholar. 2002. Northern bobwhite population response to an intensive mechanical hardwood clean-up. Page 159 in L. Brennan, W. Palmer, L. W. Burger, Jr., and T. Pruden, editors. *Quail IV: Proceedings of the Fourth National Quail Symposium*, volume 5. Tall Timbers Research Station, Tallahassee, FL, USA.
- Sisson, D. C., H. L. Stribling, and D. W. Speake. 2000. Effects of supplemental feeding on home range size and survival of northern bobwhites in south Georgia. Pages 128–131 in L. Brennan, W. Palmer, L. W. Burger, Jr., and T. Pruden, editors. *Quail IV: Proceedings of the Fourth National Quail Symposium*. Tall Timbers Research Station, Tallahassee, FL, USA.
- Sisson, D. C., T. M. Terhune, H. L. Stribling, J. Sholar, and S. Mitchell. 2009. Survival and cause of mortality of Northern Bobwhites (*Colinus virginianus*) in the southeastern USA. Pages 467–478 in S. B. Cederbaum, B. C. Faircloth, T. M. Terhune, J. J. Thompson, and J. P. Carroll, editors. *Gamebird 2006: Quail VI and Perdix XII*. 31 May - 4 June 2006. Warnell School of Forestry and Natural Resources, Athens, GA, USA.
- Smith, P. G. 2005. Compos Analysis, version 6.2 plus [software]. Smith Ecology Ltd., Abergavenny, UK.
- Sotherton, N. W., P. A. Robertson, and S. D. Dowell. 1993. Manipulating pesticide use to increase the production of wild game birds in Britain. Pages 92–101 in K. E. Church and T. V. Dailey, editors. *Quail III: National Quail Symposium*. Kansas Department of Wildlife and Parks, Pratt, KS, USA.
- Stephens, S. E. 2003. The influence of landscape characteristics on duck nesting success in the Missouri Coteau region of North Dakota. Ph.D.

- thesis, Montana State University, Bozeman, MT, USA. URL <http://etd.lib.montana.edu/etd/view/item.php?id=138>.
- Stoddard, H. L. 1931. The bobwhite quail: Its habits, preservation, and increase. Charles Scribner's Sons, New York, NY, USA.
- Stribling, H. L., and D. C. Sisson. 2009. Hunting success on Albany, Georgia plantations. Pages 338–347 in S. B. Cederbaum, B. C. Faircloth, T. M. Terhune, J. J. Thompson, and J. P. Carroll, editors. *Gamebird 2006: Quail VI and Perdix XII*. 31 May - 4 June 2006. University of Georgia, Athens, GA, USA.
- Taylor, J. D., II, L. W. Burger, Jr., S. W. Manley, and L. A. Brennan. 2000. Seasonal survival and cause-specific mortality of northern bobwhite in Mississippi. Pages 103–107 in L. Brennan, W. Palmer, L. W. Burger, Jr., and T. Pruden, editors. *Quail IV: Proceedings of the Fourth National Quail Symposium*. Tall Timbers Research Station, Tallahassee, FL, USA.
- Terhune, T. M., D. C. Sisson, J. B. Grand, and H. L. Stribling. 2007. Factors influencing survival of radio-tagged and banded bobwhites in Georgia. *Journal of Wildlife Management* 71:1288–1297.
- Wellendorf, S., W. E. Palmer, and P. T. Bromley. 2004. Estimating call rates of northern bobwhite coveys and censusing population. *Journal of Wildlife Management* 68:672–682.
- White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46 Supplement:120–138.
- White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, Inc., San Diego, CA, USA.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168.