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ORIGINAL PAPER

Aspects of northern bobwhite ecology on south Florida US pastureland

J. A. Martin · W. E. Palmer · J. P. Carroll

Received: 3 March 2012 / Revised: 26 July 2012 / Accepted: 18 September 2012 / Published online: 9 October 2012 © Springer-Verlag Berlin Heidelberg 2012

Abstract During 2004 and 2005, we monitored breeding season survival, home range, habitat use, density, and reproduction of northern bobwhite (Colinus virginianus) in the peninsular region of Florida, USA. We radio-tagged 81 birds across a 20-km² cattle ranch consisting predominately of rotationally grazed pastureland. Birds were radio-tracked three to five times per week until mortality or the transition to nonbreeding season. We found no difference in home range size among the sexes, ages, or their interaction. Mean home range size pooled for years, sexes, and age class was 56.28 ha (±7.87 SE). Home ranges of bobwhites were not distributed among habitats randomly (second order: $\Lambda = 0.10$; 7, 35 df; P = 0.002). In addition, bobwhites did not use the habitats within their home range at random (third order: $\Lambda = 0.14$, 5, 35 df; P = 0.02). Estimated seasonal survival was $0.28 (\pm 0.12 \text{ SE})$ and was best explained by the time-dependent model. Reproductive metrics indicated adequate reproduction and values consistent with the bobwhite literature. Bobwhite density (birds per hectare) in 2004 was 0.52 (±0.54 95 % confidence interval [CI]) and 0.75 (±0.51 95 % CI) for 2005. These results suggest that pastureland landscapes managed with rotational grazing can support

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Warnell School of Forestry and Natural Resources, University of Georgia, Georgia, GA 30602, USA bobwhite populations, albeit at low densities. More conservation attention should be directed towards improving these systems for bobwhite restoration.

Keywords *Colinus virginianus* · Florida · Game birds · Grazing · Northern bobwhite · Pastureland

Introduction

Historically, northern bobwhites (*Colinus virginianus*; hereafter, bobwhite) were abundant residents of fire-maintained prairie habitats in peninsular Florida USA (Frye 1954). However, over the past 40 years, bobwhite populations have declined at an annual rate of 4.3 % (Hines 2007), likely due to the degradation of native prairie habitats resulting from incompatible fire management and grazing practices and the conversion of native prairie habitats to pastureland dominated by exotic forages, principally bahia grass (*Paspalum notatum*) and Bermuda grass (*Cynodon dactylon*) (Dimmick et al. 2002; Hines 2007). Exotic pasturelands now occupy 1.2 million ha of what was once suitable bobwhite habitat in peninsular Florida.

Bobwhite habitat use and demographic parameters are well documented in most agroecosystems, but information is lacking for subtropical pasturelands in the Southeastern USA (Singh et al. 2011). However, Flanders et al. (2006) and Kuvlesky et al. (2002) described the negative impacts of exotic grasses on bobwhites in the Southwest. In Texas, Flanders et al. (2006) reported that bobwhite density was 2.72 birds/ha on native pastures (>50 % relative dominance); conversely, on exotic pastures (<50 % relative dominance), densities averaged 1.42 birds/ha. Habitat-based studies relative to bobwhite suitability have been conducted on tall fescue (*Festuca arundinacea*) pastures in the Southeast (Barnes et al. 1995; Burger et al. 1990;

Communicated by P. Acevedo

Washburn et al. 2000). Although these areas differ from the vast bahia grass pastures of south Florida, these authors concluded that the fescue pasture did not meet the biological requirements for bobwhites.

Understanding bobwhite ecology in altered habitats is important for determining conservation opportunities on pasturelands. Considering the spatial extent and economic importance of pastureland, it is important to identify ways to improve these areas for bobwhite conservation. It is also important to quantify the value of remaining native prairie habitats to bobwhites.

We could not experimentally test the effects of pastureland compared to more native habitats on bobwhite demographics simultaneously because the study area was predominately exotic pasture. Therefore, this study establishes baseline information for bobwhites in a landscape dominated by exotic pasture. Our objectives were to estimate the habitat use and selection of bobwhites in a peninsular Florida pastureland agrosystem, compare the population parameters to those of bobwhites in other habitats, and determine the density of bobwhites in this system. We also provide evidence that habitat management can affect bobwhite populations in a landscape dominated by exotic pastureland. This information can be used by conservation planners charged with modeling landscapes for bobwhite habitat suitability. Also, the Northern Bobwhite Conservation Initiative (NBCI) is keenly interested in manipulating pastureland habitats to make them more suitable for bobwhite populations (Dimmick et al. 2002; Palmer and Terhune 2010).

Materials and methods

Study area

This study was conducted on a 2,300-ha private ranch approximately 6 km south of Arcadia, FL, USA (Fig. 1). The ranch has been grazed under a deferred rotation grazing system since 1978 similar to that described by Merrill (1954). The ranch separated cattle into multiple herds (depending on season) that were rotated on regular intervals, rarely grazing >50 % of the herbage in a given paddock. The objective of the grazing systems was to reduce stress on the native grass species and legumes within pastures, reduce the probability of invasive exotic species occupation [e.g., cogon grass (Imperata cylindica) and tropical soda apple (Solanum viarum)], and limit fertilizer inputs (Capece et al. 2007). Annually, a moderate amount of bahia grass sod was removed for commercial sale. Also, the ranch maintained approximately 260 ha of citrus groves for commercial sale. The ranch habitat composition was 59 % pasture, 10 % woody, 7 % semi-improved pasture, 7 % fallow, 6 %



Fig. 1 Location of the study area near 6 km south of Arcadia, FL, USA

seasonal wetlands, 3 % unimproved pasture, 3 % young citrus grove, and <2 % other (e.g., developed areas).

Climate in south Florida is subtropical and humid with average annual temperatures in the mid-20 °C, ranging from approximately 16 °C in midwinter to approximately 27 °C in summer. Rainfall averages about 137 cm, with 50–60 % of it occurring during June to September (Obeysekera et al. 1999; USFWS 1999).

Habitat manipulations

During 2004, we manipulated approximately 7 % of the study area (approximately 400 ac) using several habitat management techniques that we believed would create a positive population response. These manipulations included: prescribed fire, seasonal disking, and mechanical brush control. This was not done in an experimental approach because of the spatial arrangement of the study area and the areas occupied by bobwhites. However, manipulations should be viewed as quasiexperimental; therefore, any response (positive or negative) should be considered correlative.

Data collection

We captured bobwhites using standard wire walk-in funnel traps (February and April, 2004 and 2005) baited with grain

sorghum (Stoddard 1931). Birds were banded and fitted with 6.4–6.9 g pendant-style radio transmitters and released at the site of capture (American Wildlife Enterprises, Monticello, FL, USA). All trapping, handling, and marking procedures were consistent with the guidelines in the American Ornithologists' Union Report of the Committee on the Use of Wild Birds in Research (American Ornithologists' Union 651988) and those of the University of Georgia, Institutional Animal Care and Use Committee (IACUC Protocol No. 2001-GB-01).

Radio-marked bobwhites were located using homing techniques (White and Garrott 1990) 3-5 days/week and approached to within 10-25 m. Locations were taken using a programmable telemetry receiver and a three-element handheld Yagi antenna. We approximated the bobwhite's location using geometric calculations which required a Global Positioning System (GPS) position of the observer, distance to the bird in meters, and compass bearing. We assumed that birds were nesting if they were recorded in the same location on two consecutive days, following Burger et al. (1995b). Once the nest had been initiated, it was flagged. Nests were checked twice daily, once in the morning to detect depredations from the previous night and in the afternoon to detect if bird was on recess. Egg counts were taken when birds were on recess. Nests were monitored until termination to determine fate (Burger et al. 1995b). A land cover map was created using the 2004 Digital Orthophoto Quarter Quads and GPS. The smallest mapping unit was approximately 1 ha. A total of eight macrohabitat types were delineated on the study area. Approximated bobwhite locations were overlaid on the Geographic Information System (GIS) map using the Animal Movement Extension (Hooge and Eichenlaub 1997). Land cover type was spatially joined to each telemetry location. Home range sizes were plotted on a scatter plot diagram to distinguish the minimum number of locations needed to include a bobwhite in the analysis. The minimum was set at 12, at which point home range size began to become asymptotic. All locations from 15 March to 18 October were used in home range estimations.

Data analysis

Home range and habitat analysis

The Animal Movement Extension (Hooge and Eichenlaub 1997) was used to create 100 % minimum convex polygons (MCP) for bobwhite home ranges. The ranch boundary was used to delineate the availability of habitats. We used general linear models (glm) in program R (R Development Core Team 2012) to compare home range sizes between sexes, between two age classes (juvenile and adult), and their interaction.

We described habitat use during the breeding season (March–October) at two spatial scales, corresponding to Johnson (1980), the second- and third-order selection using compositional analysis (Aebischer et al. 1993). Habitat composition of the ranch and within each bird's home range was defined by intersecting the polygons of the ranch and home ranges in GIS. We compared proportions of each habitat type in the study area (availability) with proportions found in each individual's home range (use) to determine second-order habitat selection (Aebischer et al. 1993; Johnson 1980). We then compared proportions of habitats in each home range (availability) with radio locations of each individual (use) to determine third-order selection (Aebischer et al. 1993; Johnson 1980). Multivariate analysis of variance was used to test the null hypothesis that bobwhite habitat use was random. The adehabitat package (Calenge 2006) for program R was used to conduct the analysis according to Aebischer et al. (1993). Prior to analysis, we replaced zero values for use with the value 0.001 which was one order of magnitude less than the smallest recorded nonzero proportion (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 nonmissing values for the respective log ratio (Aebischer et al. 1993).

Reproduction

Fecundity is the number of young successfully raised during a defined interval, generally 1 year or one breeding season (Gill 2000); annual fecundity reflects the number of nesting attempts, the success of each attempt and clutch size, and the experience of the breeding individual (Cowardin and Johnson 1979; Skalski et al. 2005). We derived an estimate of overall fecundity, *F*, calculated as the probability that a breeding female successfully hatches a clutch (π) multiplied by mean brood size (γ) and mean number of nests produced per year (ψ). Thus, the estimator for *F* is:

$$\widehat{F} = (\pi) \times \frac{\gamma}{2} \times (\psi) \tag{1}$$

where \hat{F} is the number of juvenile females hatched, ψ is the estimated probability that a breeding female successfully hatches a clutch (i.e., nest success rate), γ is the estimated mean brood size (see Eq. 4), and π is the mean number of nests built. The above estimator assumes an equal sex ratio (Skalski et al. 2005), which is a legitimate assumption for bobwhites (Faircloth 2008). We calculated variance using the delta method (Hilborn and Mangel 1997; Williams et al. 2002).

Additionally, we estimated productivity (P)—the total number of juveniles, males and females, produced per breeding female. A common estimator for P is:

$$\widehat{P} = \widehat{H} \times \overline{x} \tag{2}$$

where \hat{H} is the probability that a breeding female produces a successful clutch and \bar{x} is the mean clutch size. Because

Eq. 2 does not account for multiple nesting attempts, we used an adjusted productivity estimate using a conditional, joint binomial probability function. Thus, we estimated our total net productivity by using a weighted mean of the average brood size and separate hatching success rate relative to nest attempt:

$$\widehat{P} = \widehat{h}_1 \widehat{b}_1 + \widehat{h}_2 \widehat{b}_2 + \widehat{h}_i \widehat{b}_i \tag{3}$$

where \hat{h}_1 is the probability a female incubates and successfully hatches the *i*th nest and b_i is the mean brood size for the *i*th nesting attempt (Skalski et al. 2005). Following Skalski et al. (2005), the weighted mean brood size was calculated as:

$$\widehat{b} = \frac{1}{y_i} \sum_{j=1}^{y_i} b_{ij} \tag{4}$$

where b_{ij} is the mean brood size for the *i*th nesting attempt (i=1, 2, ..., n) for the *j*th breeding female $(i=1, 2, ..., y_i)$. We derived individual estimates of *b* as:

$$b = \widehat{CS} \times \widehat{HR} \tag{5}$$

where CS is the clutch size and HR is the hatch rate, and we estimated the variance using the delta method (Hilborn and Mangel 1997; Williams et al. 2002).

Survival analysis

We based breeding season survival rates on a 273-day interval (15 March-18 October). These dates correspond to known breeding activity from our telemetry records. Survival parameters were estimated using Program MARK (White and Burnham 1999), which allows flexibility in modeling survival parameters and estimates. Data structure followed a live-dead (LDLD) format and was read into MARK as a known-fate model (Williams et al. 2002). The known-fate model works similar to the Kaplan-Meier estimation method (Pollock et al. 1989). However, known-fate modeling within Program MARK allows for the integration of covariates, groups, and selection between models (White and Burnham 1999). We modeled survival with four groups: year (2004 and 2005) and sex (male or female). The delta method was used to calculate the variance for the survival estimate (Powell 2007).

Model selection

Survival and home range models were assessed on how well they fit the data using Akaike's Information Criterion (AIC; Burnham and Anderson 2002). The relative fit of each candidate model was assessed by calculating Akaike weights (Burnham and Anderson 2002), which can take a value from 0 to 1, with the best-fitting candidate model having the greatest Akaike weight. We then calculated AIC_c (AIC corrected for small sample sizes) values, AIC_c weights, model-averaged parameter or real estimates, and unconditional standard errors for each effect and overall survival (Burnham and Anderson 2002).

Population estimation

We estimated bobwhite density using autumn covey call point transects, a type of distance sampling (Buckland et al. 2001; Thomas et al. 2010; Wellendorf and Palmer 2005). Observers in our study were trained a minimum of two mornings prior to collecting data. At each point, observers recorded the distance and time of first call for each unique bobwhite covey (Wellendorf et al. 2004). To account for detection differences by distance, we estimated a detection function using the program DISTANCE (Thomas et al. 2010; Wellendorf and Palmer 2005). We developed a global detection probability curve from a larger dataset and poststratified by study area to obtain a density estimate for this study area. The type of distance function was selected with information theoretic procedures (AIC values; see above for AIC explanation), and model fit was assessed with chisquare model fit statistics.

We adjusted the density of bobwhite coveys by incorporating the availability of bobwhite coveys to be detected (Diefenbach et al. 2007, 2003). Wellendorf et al. (2004) developed a logistic regression equation to predict the probability of a bobwhite covey to call. The probability is influenced by several weather variables and the number of adjacent coveys that call (i.e., a density dependence response). Lastly, to convert the density of bobwhite coveys to the density of bobwhites, we used a year-specific covey size estimate, observed from intentionally flushed coveys, to derive the density of individuals.

We used descriptive statistics to present the bobwhite density results because of our low numbers of covey call surveys for each year. Each survey plot during each year was considered the experimental unit. Variance among these data was used to compute a 95 % confidence interval (CI).

Results

We radio-tagged 41 bobwhites in 2004 (26 females and 15 males) and 40 in 2005 (22 females and 18 males). Because of a limited sample for some individuals (i.e., <30 locations), we used 35 individuals for home range estimation, of which 23 were females and 12 were males. Twenty-five hens were alive on April 15 in 2004, which produced 12 nests. In 2005, 22 hens were alive on April 15, which produced 24 nests. Five covey call surveys were conducted

twice each year for each year of study, which produced 50 bobwhite detections during autumn.

Home range

Mean summer home range size pooled for both years, genders, and age classes was 56.28 ha (\pm 7.87 SE). Our models explain minor amounts of variation in home range size (Table 1 and Fig. 2). Model-averaged parameter estimates overlapped zero and the null model was the highest ranking model ($\omega_{(null)}$ =0.32).

Home ranges of bobwhites were not distributed among habitats on the study site randomly (second order: Λ =0.10; 7, 35 *df*; *P*=0.002). In addition, bobwhites did not use the habitats within their home range at random (third order: Λ = 0.14, 5, 35 *df*; *P*=0.02). At the second-order level, bobwhites preferred unimproved pasture (UNIMP) habitats, followed in order by young citrus groves and fallow areas (FALL; Table 2 and Fig. 3).

At the third-order level, bobwhites preferred fallow habitats, followed by semi-improved pasture (SEMIMP; Table 3 and Fig. 3). For the third-order analysis, two habitat categories were dropped because they were unavailable to bobwhites within their home ranges: other and woody.

Survival

Predation was the leading cause of mortality (98 % of all mortalities; 55 % of all radio-tagged birds); one bobwhite died from decapitation by a mowing machine while incubating a nest. Estimated survival for the breeding season was 0.28 (\pm 0.12 SE).

The best-approximating model indicated that bobwhite survival was best explained by time dependence ($\omega_{(t)}=0.32$; Table 4). The next best model contained a year effect ($\omega_{(t)}=0.27$). Other group effects such as sex and age were not well supported (Table 4).

Reproductive parameters

In 2004, predation was the leading cause of nest failure (n=3), one nest was abandoned for an unknown cause, and one nest was



Fig. 2 Box plots for home range size (in hectares) (n=35) for four groups of northern bobwhites on south Florida, US pastureland as estimated by 100 % MCP home range estimator, 2004–2005

flooded and then abandoned. In 2005, predation was the leading cause of nest failure (n=4), and three nests were abandoned for unknown causes. One nest failed because the incubating male was killed by farm machinery as stated above. All measured nesting parameters were higher in 2005 than in 2004 (Table 5).

In 2004, only one bobwhite had multiple nests; however, in 2005, five bobwhites had multiple nests. Nest success was higher in 2005 than in 2004 (0.67 ± 0.03 vs. 0.58 ± 0.07). Furthermore, the other reproduction metrics were higher in 2005 than in 2004, resulting in greater estimates of fecundity and productivity (Table 5).

Bobwhite abundance

We used 115 covey detections to construct the global detection function, including the 50 detections from this study. The best detection model was uniform with hermite polynomial adjustments (AIC=155.44, χ^2 =0.1214, P=0.94). A mean covey size of 10 and 12 was used for 2004 and 2005, respectively. Bobwhite density in 2004 was 0.52 [±0.54

Table 1General linear modelselection and model-averagedparameter estimates for homerange size among sex, age,and year groups for northernbobwhites on south Florida,USA pastureland, 2004–2005

Model	Model number	K^{f}	AIC _c	ΔAIC_{c}	ω_{i}	Parameter estimate (models included)	SE
Null (intercept)	1	2	82.3	0	0.32	3.54 (1-5)	0.23
SEX [male]	2	3	82.6	0.36	0.26	0.41 (2.4, 5)	0.32
AGE [juvenile]	3	3	83.2	0.88	0.20	0.35 (3.4, 5)	0.30
SEX+AGE	4	4	83.5	1.21	0.17	NA	NA
SEX×AGE	5	5	86.0	3.76	0.04	0.30 (5)	0.61

Table 2 Results of compositional analysis based on 100 % MCP home ranges (second order)

habitats (P < 0.05) is indicated by (+++) or (---)

order)	FALL		
	PAST		
	OTHER		
Within the matrix, (+) signifies	SEMIMP		
that the row habitat is preferred	UNIMP		
a(-) signifies the opposite	WET		
Significant difference between	WOOD		

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	FALL	PAST	OTHER	SEMIMP	UNIMP	WET	WOOD	YGROVE
FALL	0	+++	+++	+++	+++	+++	+++	+++
PAST		0	—	+	-		+++	+
OTHER		+	0	+	-	-	+++	+
SEMIMP		-	-	0			+++	-
UNIMP		+	+	+++	0	-	+++	+
WET		+++	+	+++	+	0	+++	+
WOOD							0	
YGROVE		-	_	+	—	-	+++	0

95 % CI (birds/ha)] and 0.75 [±0.51 95 % CI (birds/ha)] for 2005.

Discussion

Home range

Home range sizes of the bobwhites in our study are relatively large compared to those reported in ecosystems of the Southeastern USA. The most similar home range size estimates found in the literature were from a study conducted near the Flint Hills of Kansas (Taylor et al. 1999b). Their home range estimates in the rangeland habitats averaged near 103 ha for males and 54 ha for females. In south Texas, reported female bobwhite home ranges are <28 ha



Fig. 3 Manly's resource selection ratios (second order top and third order bottom) for northern bobwhites on pastureland in south Florida, USA, 2004-2005. Values above 1 indicate selection and those below 1 indicate avoidance

in grazed pastures (Whiting and Sloan 1993); however, unlike this study, their pastures consisted of mostly native plant species. In North Carolina, estimates of home range size in a row crop ecosystem were similar to that of Whiting and Sloan (1993), 32 ha (Puckett et al. 2000). In the wellmanaged quail plantations of south Georgia and north Florida, Sisson et al. (2000) and Wellendorf and Palmer (2009) found home ranges to be <5 ha. It has been postulated that home range size is correlated, if not casually related, to the quality of habitat (Odum and Kuenzler 1955), which suggests that the habitat in this study area is of poorer quality than other areas studied.

There were no biological differences detected in home range sizes among sex or age classes; this is likely because of low sample sizes and high variation within groups. However, ecologically, bobwhites, regardless of age or gender, had to transverse much of the same conditions on the study site. Both sexes participate in reproduction, reducing the chance of sex-specific home range estimates. Also, only breeding season home ranges were measured; therefore, juveniles had several months from the previous breeding season to adapt and familiarize themselves to the area.

Habitat use

Breeding season habitat use in this study is consistent with previous studies of bobwhite ecology (Cook 2004; Parnell 2002; Puckett et al. 2000; Taylor and Burger 2000; Williams et al. 2000). The fallow habitat type was the most preferred. Fallow areas mostly consisted of native grasses and shrubs that have been reported as preferred microhabitat (Kopp et al. 1998; Taylor et al. 1999a). Many of the fallow areas were on the fringe of pastures, suggesting that they received less grazing pressure from cattle. The unimproved pasture was very similar to the fallow areas and was also highly preferred. This habitat type contained very little exotic forage grass such as bahia. Bobwhites could transverse these areas freely (Burkhart 2004). The remaining pasture types, semi-improved and improved pastures received the least amount of use. These types consisted of mostly exotic forage grasses known to be detrimental to birds (Flanders et al. 2006; Kuvlesky et al. 2002).

 Table 3 Results of compositional analysis based on radio locations within a bird's home range (third order)

Within the matrix, (+) signifies that the row habitat is preferred over the column habitat, whereas a (-) signifies the opposite. Significant difference between habitats (*P*<0.05) is indicated by (+++) or (- - -)

	FALL	PAST	SEMIMP	UNIMP	WET	WOOD	YGROVE
FALL	0	+++	+	+	+++	+++	+++
PAST		0	-	-	+	-	-
SEMIMP	-	+	0	+	+++	+	+
UNIMP	-	+	_	0	+++	+	+
WET		-			0		
WOOD		+	_	-	+++	0	+++
YGROVE		+	-	-	+++	+++	0

Bobwhites avoided woody habitats at both spatial scales. Unlike some other studies, the woody habitat types of this study area are closed canopy oak hammocks and planted citrus

Survival

The survival rates derived from this study are lower estimates from those in a high-quality habitat (Palmer and Wellendorf 2007; Terhune et al. 2007), but higher than those reported in areas of limited habitat (Burger et al. 1995a; Corteville 1998). The analysis showed weak relationships between bobwhite breeding season survival and the explanatory variables—confidence intervals included zero for the parameter estimates. The top-ranking model suggests that survival varies significantly across biweekly periods. Weekly weather influences can change dramatically in south Florida during the breeding season. During the study time period, weeks with abundant rainfall >25 cm occurred, causing a significant area of the landscape to become flooded—a natural hydrological process in the region

groves. These cover types provide little understory vegetation

and are likely a refugia for predators (Seckinger et al. 2008).

(Obeysekera et al. 1999). Modeling these affects on survival is difficult, especially given the sample size. Furthermore, the weather variables are correlated with time, making it difficult to separate the influences of weather vs. random variation in time. The time-varying model likely ranked high because it acts as a surrogate for time-correlated weather patterns.

Breeding season survival was comparable to estimates for bobwhites in marginal habitats but less than that in managed habitats (Sisson et al. 2009). Survival rate is an important predictor of population growth (Sandercock et al. 2008). Habitat management designed to increase breeding season survival rates would be important to increasing bobwhite populations on ranches.

Nesting

Nest success was relatively high compared to other bobwhite studies (Burger et al. 1995b). The open pastureland has a limited amount of edge and human-induced travel corridors for predators (Gates and Gysel 1978; Martin 1995). In England, Potts (1986) found that partridge nests

Table 4 Models predicting breeding season survival for northern bobwhites in Florida, USA

Model	K ^a	AIC _c	ΔAIC_{c}	ω_{i}	Model likelihood	Deviance
$\overline{S(t)}^{\rm b}$	22.00	396.49	0.00	0.32	1.00	351.69
S(t+YEAR)	23	397.17	0.68	0.27	0.71	350.30
S(t+YEAR+SEX)	23	398.31	1.82	0.16	0.40	351.44
YEAR ^c	2.00	398.42	1.93	0.12	0.38	394.41
S(t+YEAR+SEX)	24	399.12	2.64	0.09	0.25	350.18
$S(.)^{d}$	1.00	399.19	2.70	0.10	0.26	397.19
S(SEX)	2.00	400.67	4.18	0.04	0.12	396.66

Models are ranked by differences in AIC_c values

^a Number of parameters in model

^b Time in this case is the weekly survival rate

^c Year of study

^d Null model

Parameter	Year	Number	\overline{x}	90 % CI
Clutch size	2004	12	10.90	2.53
	2005	24	11.72	1.58
	Pooled	36	11.36	1.13
Nest success	2004	12	0.58	0.07
	2005	24	0.67	0.03
	Pooled	36	0.64	0.02
Broods per hen	2004	25	0.28	0.05
	2005	22	0.73	0.06
	Pooled	47	0.49	0.02
Productivity index	2004	25	2.4	1.34
	2005	22	5.9	1.36
	Pooled	47	4.00	0.98
Fecundity	2004	25	1.20	0.42
	2005	22	4.26	1.07
	Pooled	47	2.52	0.50

Table 5Reproductive parameters for northern bobwhites on pasture-land in Florida, USA, 2004–2005

were relegated to nest near field edges because of insufficient cover in agriculture fields. He found that these nest were mostly unsuccessful because of predator movements along edges. Similarly, in North Carolina, bobwhite nest success was low in the narrow strips of habitat around row crop fields (Puckett et al. 1995). In our study area, nests were not directly tied to human-induced edges that may act as travel corridors for predators (Martin 1995), likely reducing predation pressure on nesting bobwhites. The expansive pastureland system is likely unsuitable for meso-mammal predators, reducing habitat space and decreasing their abundance. For example, the study area provides little mammalian predator refugia (e.g., oak hammocks and citrus groves; <5 %), essentially reducing the usable space for mammalian predators. Nest success may be limited in its application to capture changes in bobwhite demographics (Sandercock et al. 2008); other reproductive rates help explain the amount of reproduction occurring within the population. The flexible mating strategies for bobwhites allow them to renest and have multiple clutches (Burger et al. 1995b), reducing the effect of a failed nest on overall reproduction.

The productivity and fecundity estimates suggest that bobwhites were producing chicks at an adequate rate for viability. These estimates were much higher in the second year of study, while the estimates of the first year would not have likely been able to maintain the population. Although the estimates of fecundity may suggest that reproduction was occurring at levels to sustain the population, we have no data on chick recruitment. Driving factors of bobwhite chick survival remains poorly understood (DeMaso et al. 1997) as little experimental data exists on the stage of the bobwhite life cycle.

Bobwhite density

Bobwhite density data do suggest that bobwhite density was positively associated with habitat manipulations. This would be plausible considering higher survival and higher productivity during the second year of study. The increase in covey size between the years was a major factor in the density increase. Ellis et al. (1969) suggested that smaller increases in abundance were experienced in covey size, whereas large increases were caused by formation of new coveys of bobwhites.

Reported densities of bobwhites are sparse because techniques that incorporate detection rates have not been readily used in the past. Most studies report relative abundance (coveys per point) or an index value that is assumed to relate to the underlying abundance (sensu, Johnson 2008). Leif and Smith (1993) estimated the density of bobwhites to be between 0.43 and 0.60 birds/ha using line transect distance sampling on rangeland habitat in Texas. Smith and Burger (2009) found densities of bobwhites to be <0.36 birds/ha in an intensive agricultural landscape. Terhune et al. (2009) demonstrated a 75 % increase (0.86 to 1.48 birds/ha) in bobwhite density following habitat restoration of an agricultural landscape. These reported densities are comparable to those obtained in this study, providing support that the estimates are plausible.

The demographic parameters reported herein are relatively low compared to those reported for other agroecosystems, but not at levels that warrant the disregard of pastureland as a functional bobwhite habitat. Veech (2006) reported that more populations were increasing in pastureland landscapes than decreasing, further suggesting its potential value for management. Conversely, Guthery et al. (2001) suggests that bobwhite abundance is negatively associated with "tame pasture" throughout the Southwest. Management of pasturelands and type of grazing system employed (i.e., stocking rate) on the pasturelands will likely be the deciding factor on the utility of pastures for bobwhite conservation (Hammerquist-Wilson and Crawford 1981). Our study area was surrounded by large areas of open habitats, either pastureland, native rangeland, or agriculture, which likely bolstered populations on the study area. Pasturelands in areas surrounded by forest would likely produce different results because of increased predation pressure and lack of immigration.

Management implications

The NBCI plan's goal is to identify and prioritize areas of suitable or potentially suitable habitat throughout the range of the bobwhite (The National Bobwhite Technical Committee 2011). The plan identifies pastureland as a habitat type in need of conversion to a more suitable land cover type for bobwhites. The costs associated with restoration of pastureland to native rangeland are not conducive under most economic scenarios.

The conservation of bobwhites across large landscapes may be better served if pastureland is considered a habitat that is in need of management instead of restoration (i.e., conversion). We suggest the development of objective-based strategies to manage pastureland similar to the approach taken with intensive row crop agriculture landscapes (Burger 2006). However, the challenges will be greater in exotic grass pastures because of the constant encroachment of exotic grasses into the "native areas" and the disturbances created by cattle.

Acknowledgments We are grateful to the following organizations that provided funding, equipment, support, and/or assistance for this project: the Florida Fish, USDA Natural Resource Conservation Service and Wildlife Conservation Commission, the Tall Timbers Research Station and Land Conservancy, and the University of Georgia's Warnell School of Forestry and Natural Resources. We thank the owners and managers of the 2×4 Ranch. Valuable field assistance and data collection were provided by S. Wellendorf, Justin Fletcher, and Brad Pfeil. This paper was drastically improved by an anonymous reviewer.

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