

Patterns of space and habitat use by northern bobwhites in South Florida, USA

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Abstract The manner by which animals use space and select resources can have important management consequences. We studied patterns of habitat selection by northern bobwhites (*Colinus virginianus*) on Babcock-Webb Wildlife Management Area, Charlotte County, Florida and evaluated factors influencing the sizes of their home ranges. A total of 1,245 radio-tagged bobwhites were monitored for 19,467 radio days during 2002–2007. The mean (± 1 SE) annual home

range size, estimated using the Kernel density method, was 88.43 (± 6.16) ha and did not differ between genders. Winter home ranges of bobwhites (69.27 ± 4.92 ha) were generally larger than summer home ranges (53.90 ± 4.93 ha). Annual and winter home ranges were smaller for bobwhites whose ranges contained food plots compared to those that did not; however, the presence of food plots did not influence summer home ranges. We used distance-based methods to investigate habitat selection by bobwhites at two scales: selection of home ranges within the study site (second-order selection) and selection of habitats within home ranges (third-order selection). Across both scales, bobwhites generally preferred food plots and dry prairie habitat and avoided wet prairies and roads. This pattern was generally consistent between genders and across years. Our data indicate that management practices aimed at increasing and maintaining a matrix of food plots and dry prairie habitat would provide the most favorable environment for bobwhites.

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Introduction

Population declines of the northern bobwhite have been widely documented throughout the southeastern USA (Brennan 1991; Brennan and Kuvlesky 2005; Sauer et al. 2004; Williams et al. 2004). These declines have occurred despite the economic importance of the northern bobwhite as a game species and extensive efforts to maintain and improve its population welfare. Hypotheses proposed to explain local or regional population declines include reduction in fledgling survival due to predation by imported

fire ants (Allen et al. 1995; Giuliano et al. 1996; Mueller et al. 1999; Pedersen et al. 1996), loss and fragmentation of habitat (FenskeCrawford and Niemi 1997; Fleming and Giuliano 2001), extreme weather events such as drought and flooding (Guthery et al. 2000; Hernandez et al. 2005; Lusk et al. 2001; Robel and Kemp 1997), and hunting pressure (Burger et al. 1999; Guthery et al. 2004a; Madison et al. 2002; Peterson 2001). An exhaustive review of the dramatic range-wide population declines of bobwhites in the southeastern range of the species conducted by the Southeastern Quail Study Group concluded that habitat losses including qualitative changes (conversion of native warm season grasses to exotic cool season and warm season species) and quantitative habitat losses to urban expansion and transportation structures have been the most universally significant causes (Dimmick 1992).

The way that bobwhites utilize space and resources are an important aspect of the species' ecology and thus has significant management implications (Guthery 1997; Guthery et al. 2004b; Webb and Guthery 1983; Williams et al. 2004). Previous studies suggest that home range sizes of bobwhites vary regionally and also are influenced by several intrinsic and extrinsic factors (e.g., Bell et al. 1985; Taylor et al. 1999a; Terhune et al. 2006; Yoho and Dimmick 1972). Furthermore, resource selection and the proximate cues used by bobwhites in habitat selection may vary across spatial scales. Although bobwhites occupy a wide variety of habitats across their range in the USA (Barnes et al. 1995; Dixon et al. 1996; Roseberry et al. 1994; Taylor and Guthery 1994), they may exhibit preference for specific habitat types on a local scale. Furthermore, energetic demands for thermoregulation and nutritional requirements of bobwhites may vary among seasons (Townsend et al. 1999). A variety of foods is required to meet the special requirements of growing chicks, breeding hens, and all sex–age classes during fall and winter (Dimmick 1992). Cover that affords protection from weather, predators, and hunters is paramount in fall, winter, and early spring. Good nesting cover consists of vegetation suitable for building the nest and concealing it and the clutch of eggs. The degree of interspersed of the components of food and cover is a major determinant of the quality of the bobwhite's habitat. Thus, knowledge of site-specific patterns of space use and habitat selection is necessary for evaluating the suitability of different land cover types and for managing habitat to enhance bobwhite survival and reproduction. However, prior to the initiation of this study, data on space and habitat use by bobwhites in south Florida were scarce.

Harvest records indicate that the bobwhite population in Babcock-Webb Wildlife Management Area in Charlotte County, Florida, USA (hereafter Babcock-Webb WMA) has declined steadily since the 1970s (Dimmick et al. 2010). The numbers of bobwhites in the area remain low despite a significant effort to reverse this trend. Management of

bobwhites in south Florida could benefit from an understanding of the patterns of space and habitat use in this ecoregion. However, information on home range sizes and habitat preferences of bobwhites in south Florida is currently lacking. Our goal was to fill this gap in knowledge and provide information on space and habitat use by bobwhites on the Babcock-Webb WMA. Specifically, we estimated the size of annual and seasonal home ranges and investigated factors influencing home range sizes. Secondly, we tested for habitat selection by bobwhites at two scales: home range establishment within the study area and habitat selection at two scales (selection of home ranges within the study site and selection of habitats within home ranges) and examined variations in the pattern of habitat use over time and between genders.

Study area

The study was conducted on the Babcock-Webb WMA in Charlotte County, FL situated about 8 km east of the town of Punta Gorda (Fig. 1). The WMA admeasures 26,818 ha comprising dry prairie (9,737 ha, 36.30%), pine palmetto (9,145 ha, 34.10%), and wet prairie (7,047 ha, 26.28%) as the major habitat types. During the last two decades, 3-m-wide *Sesbania* sp. food plots have been planted in concentrated areas throughout the WMA. These strips comprise 0.56% (151 ha) of the area and are rejuvenated and fertilized on an annual basis. Other, essentially non-habitat, land cover types include buildings and other human use areas collectively called "odd areas" (508 ha, 1.89%), water bodies (192.35 ha, 0.71%), roads (18.42, 0.07%), and road grade (18.75 ha, 0.07%). We follow the vegetation descriptions of Frye (1954) throughout.

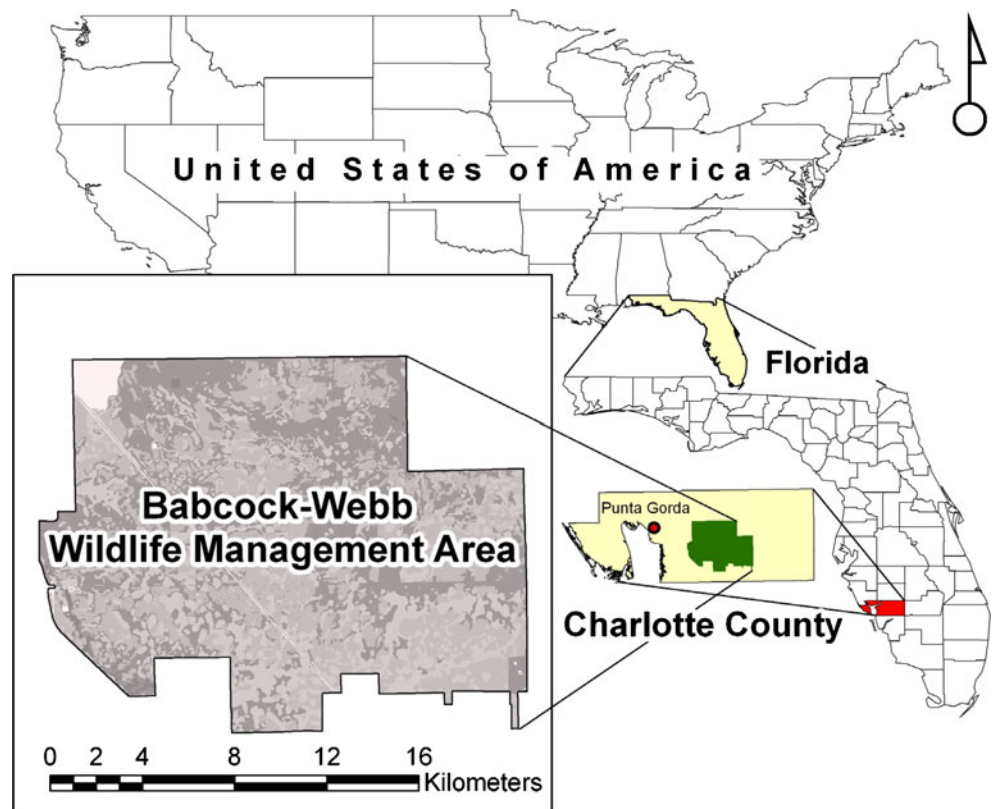
Topography of the WMA is flat, and the soil is sandy. The surface floods periodically following heavy rains, but drains rapidly when rainfall ceases. The area is subject to prolonged drought, sometimes lasting several years. Water depths of several centimeters may cover more than 50% of the surface for several days. Both of these weather extremes likely affect bobwhite space use and habitat selection across seasons and years.

Materials and methods

Trapping and radiotelemetry

We captured bobwhites during all months of the year from October 2002 through March 2007. We used baited funnel traps during the breeding and non-breeding seasons; however, in the breeding season, we placed a female in a small enclosure in the main trap to entice males (callback trapping). The callback trapping was enhanced by playing

Fig. 1 Location of the Webb-Babcock Wildlife Management Area in Charlotte County, south Florida, USA



recordings of females using tape players capable of playing a continuous loop of calls. Cast nets approximately 3 m in diameter were used to capture birds throughout the year. During daylight hours, birds were located with radios and cast nets were used to capture associated unmarked birds. We used bird dogs to locate bobwhites when radio-tagged birds were not in an area where we wished to capture birds. At night, we located radio-tagged birds on their roost and captured them and their associated covey mates with the cast net. Multiple capture methods were used to ensure adequate sample sizes; capture methods are unlikely to influence home range sizes or habitat selection by bobwhites. Birds were weighed to the nearest gram, aged, sexed, and leg-banded. Age determination was difficult for many birds and was therefore excluded as a factor from all analysis. All trapping and handling protocols were approved by the University of Florida Institutional Animal Care and Use Committee (Protocol no. A-794).

We located radio-tagged birds using handheld receivers and Yagi antennas. We searched for individual birds at 3- to 5-day intervals. The location of each radio-tagged bird was established using the homing procedure and logged into a GPS unit.

Data analysis

Home range sizes

We monitored 1,245 radio-tagged bobwhites (approx. 43% males) from October 2002 to March 2007. We used radio-

locations collected from October 1 of year 1 to September 30 of year 2 to investigate factors influencing variations in annual home ranges. The annual period thus spanned both winter (1 October–31 March) and summer (1 April–30 September) seasons. We did not include data for 2006–2007 for these analyses because they included radiolocations from the winter season only. Annual home ranges were estimated for birds that had ≥ 30 radiolocations spanning at least 3 months in each season. The literature suggests that the number of locations used to estimate home ranges in our study is adequate (Haines et al. 2004; Hiller et al. 2007; Taylor et al. 1999b) and also reflects a trade-off between the number of radiolocations per bird as compared to monitoring a large number of birds. On average, individual birds were monitored for 110.52 ± 5.29 days/year; the average number of locations was 37.90 ± 0.49 (Table 1). We estimated annual home ranges using the 95% Kernel density method (Seaman and Powell 1996; Worton 1989) using the least cost cross-validation procedure in ArcView[®] Animal Movement Analyst (Hooze and Eichenlaub 2000). To analyze seasonal home ranges, we selected all birds that had ≥ 20 radiolocations within a season and estimated home ranges as described previously.

Estimates of home range sizes were right-skewed and were therefore log-transformed prior to analyses. We analyzed annual and seasonal home ranges separately. We first tested separately for the effect on annual home range size of gender, year of study (2002–2003, 2003–2004, 2004–2005, 2005–2006), and a variable describing whether a home range

Table 1 Estimates of annual and seasonal home range size (mean \pm 1 SE) of the northern bobwhite quail at the Babcock-Webb Wildlife Management Area, Florida, 2002–2006

	Annual		Winter		Summer	
	<i>n</i> (no. of locations)	Mean ha \pm 1 SE (range, ha)	<i>n</i> (no. of locations)	Mean ha \pm 1 SE (range, ha)	<i>n</i> (no. of locations)	Mean ha \pm 1 SE (range, ha)
By year						
2002–2003	10 (38.60 \pm 1.77)	97.30 \pm 23.29 (5.69–235.64)	5 (23.40 \pm 1.54)	160.28 \pm 66.20 (33.64–401.58)	14 (27.21 \pm 1.56)	58.54 \pm 10.13 (5.28–114.99)
2003–2004	44 (38.86 \pm 1.01)	84.30 \pm 16.33 (10.69–544.30)	36 (26.44 \pm 0.80)	79.35 \pm 11.31 (10.40–278.71)	23 (21.70 \pm 0.30)	35.31 \pm 5.95 (7.23–113.48)
2004–2005	78 (37.24 \pm 0.74)	92.96 \pm 8.36 (9.07–475.83)	75 (26.41 \pm 0.35)	69.15 \pm 6.97 (5.59–236.86)	40 (24.00 \pm 0.33)	64.07 \pm 12.81 (10.10–530.06)
2005–2006	42 (37.95 \pm 0.96)	82.25 \pm 9.84 (14.02–331.47)	13 (24.23 \pm 0.63)	58.79 \pm 9.95 (29.21–141.94)	46 (23.67 \pm 0.50)	52.95 \pm 5.41 (9.68–148.38)
2006–2007			38 (25.84 \pm 0.52)	51.57 \pm 7.50 (6.60–188.29)		
By gender						
Female	75 (38.89 \pm 0.83)	84.06 \pm 8.58 (5.69–362.93)	72 (26.14 \pm 0.37)	62.25 \pm 7.30 (5.59–278.71)	46 (24.17 \pm 0.60)	51.51 \pm 11.62 (5.28–530.06)
Male	99 (37.15 \pm 0.58)	91.74 \pm 8.69 (9.07–544.30)	95 (25.95 \pm 0.39)	74.59 \pm 6.63 (5.59–401.58)	77 (23.60 \pm 0.35)	55.33 \pm 3.82 (9.59–148.38)
Home range intersected a food plot						
Yes	148 (38.32 \pm 0.54)	80.50 \pm 6.24 (5.69–544.30)	124 (25.73 \pm 0.33)	66.84 \pm 5.83 (5.59–401.58)	113 (21.80 \pm 0.71)	54.60 \pm 5.26 (5.28–530.06)
No	26 (35.50 \pm 1.10)	133.57 \pm 19.02 (10.69–475.83)	43 (26.88 \pm 0.44)	76.29 \pm 9.11 (9.25–223.33)	10 (23.99 \pm 0.33)	46.06 \pm 12.95 (7.23–148.38)

Home range sizes were estimated using the 95% Kernel density method. Home range sizes are presented by the year of the study (2002–2006), gender, and based on whether or not home range of a bird intersected at least one food plot (Yes=a home range intersected a food plot; No=a home range did not intersect a food plot). The number of home ranges (*n*) and the mean (\pm 1 SE) number of radiolocations used for estimating home ranges are also presented

intersected a food plot using generalized linear mixed models. For these analyses, we considered the effect of one variable at a time and with individual bird as a random effect and Gaussian error. Next, we pooled all data to simultaneously analyze the influence of aforementioned variables on annual home ranges. Denominator degrees of freedom for the F test of the mixed model were estimated with the Kenward–Roger method (Kenward and Roger 1997). Seasonal home ranges were analyzed in a similar fashion. Generalized mixed models were implemented using GLIMMIX procedure in SAS version 9.2 (SAS 2009; Zuur et al. 2009).

In both cases (annual and seasonal home range analyses), we tested for all main and two-way interaction effects and sequentially removed non-significant ($\alpha=0.05$) interaction terms in a stepwise fashion such that the least significant interaction term was removed each time (sensu Slade et al. 1997). The models were refitted sequentially until all main effects and only significant interaction effects remained in the model (Moyer et al. 2007; Slade et al. 1997). We further explored the significant interaction effects in the final models using the least-square means (i.e., estimated marginal means) multiple comparison procedures. All data were analyzed using the SAS software, version 9.2 (SAS Institute Inc., Cary, NC, USA).

Habitat selection

We used a distance-based method (Conner et al. 2003) to investigate habitat selection and to examine if the pattern of habitat selection differed between genders and seasons and varied across years. We preferred this method because two of our habitat types (food plots and road grades) were essentially linear features; this precluded the use of methods that require area-based estimates of habitat availability (e.g., compositional analysis; Aebischer et al. 1993). The distance-based approach compares observed distances from radiolocations to a given habitat type with the expected distance to that habitat type in order to test the hypothesis that habitat types are used in proportion to their availabilities (Conner et al. 2003, 2005; Perkins and Conner 2004). When compared to classification-based methods, inferences based on the distance-based analysis are more robust with respect to habitat misclassifications (Bingham and Brennan 2004).

We examined habitat selection at two scales: second-order selection (selection of home range within the study area) and third-order selection (selection of habitat types within home ranges (Johnson 1980). To evaluate habitat selection at the second-order selection level, we generated a 95% kernel home range using radiolocations pooled from all birds. This home range defined the analysis “study area.” We generated random points inside this cumulative home range with a uniform distribution at the density of 200 points per square kilometer using custom scripts written in ArcView. This

density of points was selected because the variance of the average distance to a given habitat type stabilized at a density of approx. 200 points/km². These points defined habitat “availability.” Habitat “use” for the second-order of selection was defined by generating random points with the same density within each quail’s home range.

The distance from each random point was measured in each home range to the nearest patch of each habitat type. We created vectors of distances of these random points to each habitat type (\mathbf{r}). Entries in \mathbf{r} represented expected values of distances under the null hypothesis of no habitat selection (Conner et al. 2003). We also created a vector \mathbf{u} ; entries in \mathbf{u} represented distances from radiolocations to each habitat type. Entries in \mathbf{u} represented habitat use. A vector of ratios (\mathbf{d}) was created by dividing each entry in \mathbf{u} by the corresponding entry in \mathbf{r} . Entries equaling 1.0 in \mathbf{d} indicated that habitat use equaled habitat availability for a given habitat type. These ratios were averaged over all individual quail to produce a vector $\mathbf{\rho}$. The null hypothesis that $\mathbf{\rho}$ is not significantly different from a vector of 1’s was tested using multivariate analysis of variance (MANOVA). Rejection of the null hypothesis of no habitat selection indicated that use differed from availability for at least one habitat type. If the null hypothesis was rejected, we used a paired t test to compare each entry in $\mathbf{\rho}$ to 1.0 to determine which habitat types were used differently than expected (Conner et al. 2003). When an entry in $\mathbf{\rho}$ was <1 , radiolocations were closer than expected (indicating preference), and when an entry in $\mathbf{\rho}$ was >1 , radiolocations were farther away than expected (indicating avoidance). The entries in $\mathbf{\rho}$ were then used to rank the habitat types in order of preference. Significant differences among habitat types were determined using a paired t test (Conner et al. 2003). We tested for habitat selection using all data to examine the pattern of overall habitat selection. We then repeated the analyses by year, gender, and season to test for annual, gender-specific, and seasonal patterns of habitat selection, respectively.

Analysis for the third-order of habitat selection (Johnson 1980) proceeded in a similar fashion with a slight difference. Habitat availability for the third order selection was defined using random points generated within each bird’s home range. Habitat use for the third-order selection was defined using actual radiolocations for each bird. The statistical analyses proceeded as described for the analysis of second-order habitat selection.

Results

Annual home ranges

Data were adequate for estimating annual home ranges for 174 birds (37.90 ± 0.49 locations/bird). The mean (± 1 SE)

size of annual home was 88.43 ± 6.16 ha (range, 5.69–544.3 ha). When the effect of each factor was tested separately on (log-transformed) home range size, we found that annual home ranges did not differ significantly between genders ($F=1.06$, $df=1,161.7$, $P=0.3038$), nor did they vary across years of study ($F=2.24$, $df=3,49.6$, $P=0.094$). However, annual home ranges of bobwhites that contained food plots were significantly smaller ($F=10.27$, $df=1,163.8$, $P=0.0016$) than those that did not contain food plots (Table 1).

When the effect of year, gender, and the presence of food plots was evaluated simultaneously using a generalized mixed model, we found that the main effect of year ($F=4.65$, $df=3,130.2$, $P=0.004$) and gender ($F=6.13$, $df=1,158.8$, $P=0.014$) was significant. Moreover, the interaction effect of year and the presence of food plots was significant ($F=4.76$, $df=2,161.4$, $P=0.009$), indicating that the influence of food plots on home range size varied across years (Fig. 2a). Least-square mean comparison procedures

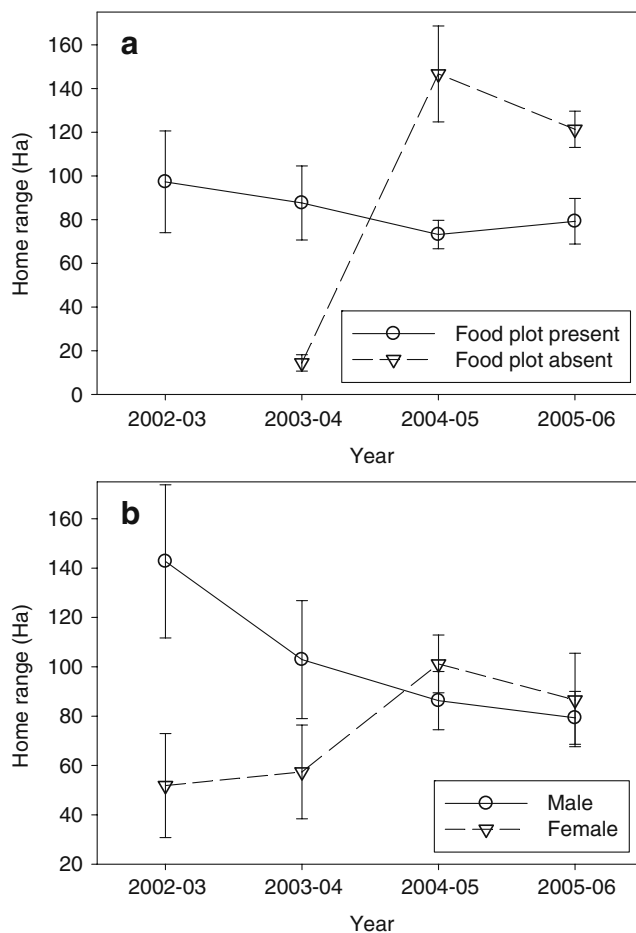


Fig. 2 Size of bobwhite annual home ranges (ha; mean \pm 1 SE) for each year of the study in Babcock-Webb Wildlife Management Area, FL. Home range sizes are presented by whether a home range contained a food plot (a) and gender (b). There were no home ranges that did not intersect food plots in 2002–2003; only two and three home ranges did not intersect food plots in 2003–2004 and 2005–2006, respectively

revealed that in 2004–2005, home ranges that did not contain food plots were significantly larger (146.66 ± 21.94) than those that did (73.17 ± 6.14 ha; $F=3.73$, $df=162.9$, $P=0.0055$); the small number of home ranges without food plots in other years precluded similar comparisons ($N=0, 2$, and 3 in 2002–2003, 2003–2004, and 2005–2006, respectively). The interaction effect of gender and year also was significant ($F=3.77$, $df=3, 76.18$, $P=0.014$), indicating that neither males nor females had consistently larger (or smaller) home ranges during all years of study (Fig. 2b).

Seasonal home ranges

The mean size of summer home ranges was 53.90 ± 4.93 ha (range, 5.28–530.06 ha, $n=123$, 23.81 ± 0.31 locations/bird) and that of winter home range was 69.27 ± 4.92 ha (range, 5.59–401.57, $n=167$, 26.03 ± 0.27 locations/bird). Tests of single factor effects revealed that winter home range size did not differ between bobwhites whose home range did or did not contain food plots ($F=2.39$, $df=1,162.2$, $P=0.1241$) and between genders ($F=2.49$, $df=1,158.5$, $P=0.1163$). However, winter home ranges varied significantly across years ($F=2.45$, $df=4,162$, $P=0.0483$) with larger home ranges during 2002–2003 than in 2006–2007 (Table 1). When the effect of all factors was evaluated simultaneously, the main effect of the presence of food plots was significant ($F=6.93$, $df=1,160$, $P=0.0093$); winter home ranges that contained food plots were significantly smaller than those that did not (Table 1). The main effect of year was also significant ($F=3.17$, $df=4,149.5$, $P=0.0156$). None of the interaction effects was significant.

Single-factor analysis revealed that summer home ranges differed significantly between genders ($F=6.67$, $df=1,121$, $P=0.011$), with males (55.33 ± 3.82 ha) maintaining larger summer home ranges than females (51.51 ± 11.6282 ha; Table 1). Annual variations in summer home range size were also significant ($F=2.73$, $df=3,119$, $P=0.0469$), with smaller summer home ranges during 2003–2004 than most other years (Table 1). The effect of food plots on summer home range size was not significant. When the effect of all factors was tested simultaneously, the only significant main effect was that of gender ($F=5.88$, $df=1,117$, $P=0.0168$). None of the interaction effects were significant.

Habitat selection

Second-order habitat selection: selection of home range within the study area

Distance ratios analyzed using the MANOVA procedure revealed that bobwhite radiolocations differed significantly from random locations overall ($F=401.48$, $P<0.0001$) and when considered separately for each gender ($F=354.88$,

Table 2 Results of *t* tests testing for the second-order habitat selection

Habitat	Overall (<i>n</i> =252 birds; 17,856 locations)				By sex				By season				Rank			
	<i>t</i>	<i>P</i>	Rank	Rank	Female (<i>n</i> =101 birds; 7,069 locations)		Male (<i>n</i> =151 birds; 10,787 locations)		Summer (<i>n</i> =123 birds; 6,332 locations)		Winter (<i>n</i> =129 birds; 11,524 locations)					
					<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>				
DP	-33.89	<0.0001	1	1	-23.78	<0.0001	1	-24.47	<0.0001	2	-17.37	<0.0001	2	-29.46	<0.0001	1
FP	-20.32	<0.0001	2	7	9.34	<0.0001	7	-55.24	<0.0001	1	-77.5	<0.0001	1	4.52	<0.0001	6
OA	2.44	0.0148	5	4	-4.63	<0.0001	4	7.11	<0.0001	5	17.85	<0.0001	7	-10.54	<0.0001	3
PP	11.03	<0.0001	6	8	14.52	<0.0001	8	1.15	0.2501	4	4.48	<0.0001	4	10.36	<0.0001	7
RD	11.36	<0.0001	7	5	3.39	0.0007	5	11.71	<0.0001	7	-0.14	0.8865	3	14.15	<0.0001	8
RG	-0.83	0.405	4	2	-14.98	<0.0001	2	7.48	<0.0001	6	12.19	<0.0001	6	-12.83	<0.0001	2
WA	23.28	<0.0001	8	6	8.32	<0.0001	6	23.25	<0.0001	8	37.97	<0.0001	8	1.29	0.1981	5
WH	-2.7	0.007	3	3	-5.84	<0.0001	3	1.06	0.2904	3	7.29	<0.0001	5	-10.21	<0.0001	4

Results are presented as overall and stratified by gender and season (sample sizes in parentheses). The *t* tests test for differences between the vector of ratios of the average distances of random points and distances of radiolocations to each habitat type and a vector of 1's. Values of *t*-statistic and associated *P* values are presented. Negative *t*-statistics indicate that radiolocations were closer to the corresponding habitat type than expected by chance, the magnitude of *t*-statistics signifies the strength of the association. Non-significant *P* values indicate that the vector of distance ratios was not significantly different from a vector of 1's (i.e., no evidence of selection). Ranking of the habitat type are based on the habitat ranking matrix presented in Appendix A of [Electronic supplementary material](#) (1=most preferred; 8 = least preferred)

DP dry prairie, FP food plot, OA odd area, PP pine palmetto, RD road, RG road grade, WA water, WP Wet prairie

Table 3 Results of *t* tests testing for second-order habitat selection

Habitat	2002–2003 (<i>n</i> =19 birds; 1,546 locations)			2003–2004 (<i>n</i> =59 birds; 3,274 locations)			2004–2005 (<i>n</i> =115 birds; 7,438 locations)			2005–2006 (<i>n</i> =59 birds; 3,083 locations)		
	<i>t</i>	<i>P</i>	Rank	<i>t</i>	<i>P</i>	Rank	<i>t</i>	<i>P</i>	Rank	<i>t</i>	<i>P</i>	Rank
DP	-33.95	<0.0001	3	-7.39	<0.0001	2	-23.21	<0.0001	2	-14.32	<0.0001	2
FP	-43.57	<0.0001	2	-214.88	<0.0001	1	-4.35	<0.0001	6	-30.72	<0.0001	1
OA	-52.25	<0.0001	1	12.16	<0.0001	5	3.27	0.0011	7	19.07	<0.0001	8
PP	7.4	<0.0001	4	-2.02	0.0439	3	5.78	<0.0001	8	0.34	0.7316	6
RD	19.92	<0.0001	8	22.13	<0.0001	6	-18.97	<0.0001	3	-13.63	<0.0001	3
RG	19.52	<0.0001	7	25.21	<0.0001	7	-33.7	<0.0001	1	-3.5	0.0005	5
WA	17.04	<0.0001	6	36.69	<0.0001	8	-10.83	<0.0001	5	9.99	<0.0001	7
WH	9.65	<0.0001	5	8.34	<0.0001	4	-11.57	<0.0001	4	-5.6	<0.0001	4

Results are stratified by year (sample sizes in parentheses). See Table 2 for interpretation of *t*-statistics, *P* values, and habitat ranking
 DP dry prairie, FP food plot, OA odd area, PP pine palmetto, RD road, RG road grade, WA water, WP wet prairie

$P < 0.0001$), season, ($F = 439.84$, $P < 0.0001$), and year ($F = 529.33$, $P < 0.0001$). Thus, bobwhites exhibited habitat selection while establishing home ranges within the study site.

Overall, dry prairie was the most preferred habitat type, followed by food plots and wetland hammock. Pine palmetto habitat, roads, and water bodies were generally avoided by both males and females. Despite some variations, dry prairie and food plots were the most preferred habitat types for both sexes and seasons and in most years (Tables 2 and 3; Appendix 1 in [Electronic supplementary material](#)).

Third-order habitat selection: selection of habitat within home ranges

Bobwhites exhibited strong habitat selection while selecting habitat within home ranges overall ($F = 166.6$, $P < 0.0001$) and when considered separately for each gender ($F = 150.12$, $P < 0.0001$), season, ($F = 209.56$, $P < 0.0001$), and year ($F = 198.75$, $P < 0.0001$).

Food plots were strongly preferred by both males and females in both seasons (Table 4) and across most years of study (Table 5; Appendix 1 in [Electronic supplementary material](#)). Pine palmetto habitat was preferred by male bobwhites, but not by females (Table 4). Pooled across genders, pine palmetto habitat was preferred by bobwhites across both seasons (Table 4) and in all years except 2002–2003 and 2004–2005 (Table 5). Dry prairie habitat was generally preferred by bobwhites, but the pattern of selection was not consistent across genders, seasons, or years. Females preferred dry prairie habitat, but males did not (Table 4). When data were pooled across genders, bobwhites strongly preferred dry prairie habitat in winter, but not in summer (Table 4). Across years, dry prairie habitat was preferred in all years except 2003–2004 (Table 5).

Bobwhites generally avoided wet prairie habitat, but the pattern of selection varied. Male bobwhites were found farther than expected from wet prairie habitats; however, females used wet prairies randomly (Table 4). Across seasons, wet prairie habitats were preferred in winters but avoided in summers. Across years, bobwhites generally avoided wet prairie habitats except in the years 2004–2005 (Tables 4 and 5). Bobwhites were generally found farther than expected from water bodies, road grades, and odd areas; the pattern was consistent across genders and seasons (Table 4). Water bodies and road grades were generally avoided (Table 5).

Discussion

Effective management of game species requires knowing how the species utilizes available landscapes and selects resources within them. Landscapes are inherently heterogeneous, and the choice of habitat can influence an individual's survival and reproduction, as well as individual fitness (Fretwell and Lucas 1970; Holt 1985; Pulliam 1988). Quantifying behavioral responses to habitat heterogeneity may help identify essential resources and environmental conditions that affect population dynamics and may aid in the management of wildlife populations (Boyce and McDonald 1999; Sutherland 1996).

During the period of this study, the bobwhite population on the majority of the Babcock-Webb WMA existed at a very low density, in contrast with many other managed habitats across the species' range (Dimmick et al. 2010). The population reached this very low density following several decades of decline from the 1970s when annual harvests often exceeded 5,000 birds per year (Florida Fish and Wildlife Conservation Commission, unpublished data). The population decline probably reflected deterioration in

Table 4 Results of *t* tests testing for third-order habitat selection

Habitat	Overall (<i>n</i> =252 birds; 17,856 locations)			By gender			By season								
	<i>t</i>	<i>P</i>	Rank	<i>t</i>	<i>P</i>	Rank	Female (<i>n</i> =101 birds; 7,069 locations)		Male (<i>n</i> =151 birds; 10,787 locations)		Summer (<i>n</i> =123 birds; 6,332 locations)		Winter (<i>n</i> =129 birds; 11,524 locations)		
	<i>t</i>	<i>P</i>	Rank	<i>t</i>	<i>P</i>	Rank	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	Rank	<i>t</i>	<i>P</i>	Rank	
DP	-2.35	0.019	4	-2.26	0.0241	3	-1.18	0.2381	3	0.56	0.5773	4	-3.65	0.0003	4
FP	-33.53	<0.0001	1	-12.77	<0.0001	1	-37.62	<0.0001	1	-58.06	<0.0001	1	-12.03	<0.0001	1
OA	21.56	<0.0001	8	14.24	<0.0001	8	16.2	<0.0001	8	20.18	<0.0001	8	11.86	<0.0001	8
PP	-7.12	<0.0001	2	-1.57	0.1174	5	-8.33	<0.0001	2	-8.42	<0.0001	2	-2.72	0.0066	7
RD	-3.95	<0.0001	3	-9.29	<0.0001	2	2.03	0.0423	4	-2.73	0.0064	3	-2.86	0.0043	6
RG	9.22	<0.0001	7	-1.82	0.069	4	12.11	<0.0001	7	17.17	<0.0001	6	-3.71	0.0002	3
WA	7.49	<0.0001	6	2.03	0.0423	7	7.99	<0.0001	6	19.43	<0.0001	7	-5.22	<0.0001	2
WP	3.36	0.0008	5	-0.29	0.7708	6	4.54	<0.0001	5	8.3	<0.0001	5	-3.33	0.0009	5

Overall results and those stratified by gender and season are presented (sample sizes in parentheses). See Table 2 for interpretation of *t*-statistics, *P* values, and habitat ranking

*DP=Dry Prairie, FP=Food Plot, OA=Odd Area, PP=Pine Palmetto, RD=Road, RG=Road Grade, WA=Water, WP=Wet prairie

the quality of the habitat mediated by changes in management practices as well as other activities occurring on the area or its perimeter. It is also possible that the population has been overharvested, particularly during recent years when legal harvest removed birds at a rate believed to be unsustainable (Dimmick et al. 2010). Efforts to reverse the decline in the bobwhite population are currently underway; our goal was to assist the Florida Fish and Wildlife Conservation Commission in this effort by providing data on space and habitat use by bobwhites on the WMA.

Characteristically, bobwhites occupy home ranges as small as ≤5 ha in excellent habitat (Sisson et al. 2000; Wiseman and Lewis 1981) and ≤40 ha in good habitat (Bell et al. 1985; Dixon et al. 1996; Guthery et al. 2004b; Haines et al. 2004; Terhune et al. 2006). The mean annual home range size in our study area was 88.43±6.16 ha, which is substantially larger than most previously reported bobwhite home ranges. Resource availability and habitat productivity have been shown to have tremendous influences on home range sizes in many wildlife species (Koehler and Pierce 2003; Moyer et al. 2007; Samson and Huot 1998), and extremely large bobwhite home ranges observed in our study likely reflect that some component of the habitat is poor on the WMA.

Several intrinsic and extrinsic environmental factors, alone or in concert, can influence annual or seasonal home range sizes (e.g., Badyaev et al. 1996; Moyer et al. 2007; Slade et al. 1997; Whitaker et al. 2007). For example, stochastic variation in the environment can influence home range size, but the pattern of influence can vary depending on other factors, such as gender and resource availability. We found that although there was a significant interaction between gender and year, the difference was not consistent. Likewise, there was no gender difference in winter home ranges; this was expected because bobwhites of both sexes and all age classes form coveys during winter. However, we found that males generally maintained larger summer home ranges than females. Taylor et al. (1999a) found that male bobwhites had significantly larger home ranges than females in one study site, but the pattern was reversed in another study site. Thus, bobwhites apparently do not follow systematic gender differences in home range size observed in many species of birds and mammals (Begg et al. 2005; Favaron et al. 2006; Oka 1992)

We believe that the generally larger home ranges during winter than in summer observed in our study are probably a consequence of food resource limitation, particularly limited availability of slough grass (*Spartina pectinata*), an important food source for bobwhites in our study area. Animals tend to roam more widely during seasons of lower resource abundance in search of scarce and patchily distributed resources, which would lead to larger home ranges (e.g., Chapman et al. 1993; Ndithia and Perrin 2006; Yo et al. 1992). Another possibility is that larger home

Table 5 Results of *t*-tests testing for third-order habitat selection

Habitat	2002–2003 (<i>n</i> = 19 birds; 1,546 locations)			2003–2004 (<i>n</i> =59 birds; 3,274 locations)			2004–2005 (<i>n</i> =115 birds; 7,438 locations)			2005–2006 (<i>n</i> =59 birds; 3,083 locations)		
	<i>t</i>	<i>P</i>	Rank	<i>t</i>	<i>P</i>	Rank	<i>t</i>	<i>P</i>	Rank	<i>t</i>	<i>P</i>	Rank
DP	-6.71	<0.0001	3	4.86	<0.0001	3	-5.1	<0.0001	6	-0.35	0.7289	4
FP	-32.04	<0.0001	1	-180.51	<0.0001	1	-8.28	<0.0001	3	-26.37	<0.0001	1
OA	-20.93	<0.0001	2	14.98	<0.0001	7	11.51	<0.0001	8	15.26	<0.0001	8
PP	0.2	0.8391	4	-15.57	<0.0001	2	-0.75	0.4542	7	-4.27	<0.0001	3
RD	16.64	<0.0001	6	13.02	<0.0001	6	-18.5	<0.0001	1	-7.63	<0.0001	2
RG	21.37	<0.0001	8	18.95	<0.0001	8	-7.74	<0.0001	4	4.02	<0.0001	7
WA	17.39	<0.0001	7	12.44	<0.0001	5	-9.72	<0.0001	2	2.92	0.0036	6
WP	11.85	<0.0001	5	8	<0.0001	4	-6.66	<0.0001	5	2.47	0.0138	5

Results are stratified by year (sample sizes in parentheses). See Table 2 for interpretation of *t*-statistics, *P* values, and habitat ranking
 DP dry prairie, FP food plot, OA odd area, PP pine palmetto, RD road, RG road grade, WA water, WP wet prairie

ranges during winter may also be due to hunting-induced disturbances, as is commonly observed in other game birds (Whitaker et al. 2007).

Bobwhites generally showed a strong response to food plots in our study area. Annual home ranges were smaller for birds whose ranges contained food plots compared to those that did not; Sisson et al. (2000) and W.E. Palmer (Tall Timbers Research Station, 2009, personal communication) both observed a similar response to supplemental feeding. The fact that there were few home ranges that did not intersect food plots is probably an indication that food plots influenced habitat selection by bobwhites on the WMA. The same pattern was observed for winter home ranges as well. Food plots and supplemental feeding are widely used practices for managing bobwhite populations in North America (Guthery et al. 2004b; Haines et al. 2004; Townsend et al. 1999). Our results, along with those of Guthery et al. (2004b), suggest that bobwhite home ranges may be influenced by food availability and that bobwhites inhabiting poor quality habitat (or within a site, during seasons of lower food availability) would typically need larger home ranges to satisfy their resource needs (Sisson et al. 2000; W.E. Palmer, Tall Timbers Research Station, 2009, personal communication). The effects of supplemental food on home range size may, however, vary depending perhaps on local habitat conditions (e.g., Haines et al. 2004).

Apart from home range sizes, distance-based habitat selection analyses revealed that bobwhites were generally found closer to food plots as compared to other habitat types, indicating a preference for this habitat type. Furthermore, preference for food plots was consistent across both second- and third-order habitat selections (i.e., establishment of home ranges within the study site and habitat selection within home ranges, respectively). Other habitat types preferred by bobwhites included dry prairie and pine palmetto, and these

patterns were generally consistent between sexes and seasons. One notable difference between second- and third-order habitat selections was that pine palmetto habitat was generally preferred when selecting habitats within home ranges (third-order selection), but not when establishing home ranges within the study site (second-order selection). These results suggest that cues used by bobwhites to select habitat might vary depending on the scale of habitat selection.

Management implications

Bobwhites in our study site had substantially larger home ranges compared to those in other parts of their range. If larger home ranges are indicative of lower habitat quality, as typically assumed, the quality of habitat in our study site in south Florida may be considered suboptimal, most likely due to limited abundance of food resources. There may be other habitat issues, but food resources are clearly identified as an important factor by the data reported here. This is supported by the observation that bobwhites whose ranges contained food plots had substantially smaller home ranges compared to those that did not and that bobwhites exhibited a strong preference for food plots. Thus, management practices that will lead to an increase in quantity and quality of food (e.g., through fertilization and rejuvenation), interspersed within well-managed dry prairie and pine palmetto habitats, will most likely have a positive impact on bobwhite populations in south Florida. This strategy would likely help release the bobwhite population from food limitations while avoiding potential negative effects of highly localized feeders (e.g., Frye 1954; Oberheu and Dabbert 2001).

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