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HABITAT USE BY BREEDING NORTHERN BOBWHITES IN MANAGED OLD-FIELD HABITATS IN MISSISSIPPI

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ABSTRACT

To better understand the proximate and ultimate cues associated with habitat selection in breeding northern bobwhites *(Colinus virginianus)*, we compared habitat use vs. availability at 2 spatial scales equivalent to Johnson's (1980) 2nd and 3rd order selection. We conducted the study in managed old-field habitats in Mississippi, from 1994 to 1996. We also estimated habitat use by broods with respect to availability, and quantified micro-habitat characteristics (4th order selection) at brood-rearing sites and nesting sites. Breeding bobwhites did not establish home ranges at random or allocate resources among patches in proportion to their availability. Breeding bobwhites, given a mosaic of seasonally manipulated old-field habitats, consistently used burned fields, disked fields, and areas with advanced woody succession to define breeding season home ranges. Bobwhites allocated their time and resources more to woody areas and fields that had received a combination of burning and disking. Broods consistently used burned/disked fields in proportion to availability; consistently avoided row crops and pastures; and generally preferred woody corridors. Vegetation characteristics at nest sites did not differ from random sites located within the same patch of habitat. Characteristics among nest sites were similar, yet successful nests were located in the proximity of more bare ground and less litter cover than unsuccessful nest sites. Brood site habitat characteristics were similar to nest sites; however, woody canopy (44.3%) and visual obstruction readings (59.0cm) at brood sites were significantly greater than nest sites (26.6% and 32.5cm).

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INTRODUCTION

Use of the habitat concept is often inconsistent among researchers (Karr 1980), and has throughout the progression of avian ecology, been used to define, in part, the species "niche". Supporters of Grinnell's (1917) conceptualization of niche maintain that (1) relationships exist between a species' distribution and underlying environmental conditions and (2) that niche components reveal relationships with other organisms, and ultimately the community structure where it resides (Rotenberry 1980). In contrast, Elton (1927) defined the niche concept as the functional role of an organism within the community, and adherents to this definition have suggested a distinct separation between a species' habitat and its role (Whitaker et al. 1973). Regardless of the definition used, it becomes obvious that habitat variables illustrate an integral part of a bird species' niche. Quantification of these habitat variables provides insight as to how, when and why birds allocate their time and resources to portions of the plant community, and subsequently the vertebrate community in which they occur.

The process of habitat selection by birds may be described as an adaptive process where individuals develop patterns based on their perception of environmental conditions (Rotenberry 1980). These patterns can be viewed in a hierarchal sense in which a bird first chooses a general place to live (habitat), and then makes subsequent decisions about how to allocate its time within different patches, the search mode it uses, and its responses to physical cues that it encounters (Charnov and Orians 1982). Selection may be based on a specific search image, early learned experience, genetic programming, or any combination of these factors (Klopfer 1970). Although birds should prefer environments in which their survival and reproductive success is good (Levins 1968, Orians 1980, Orians and Whittenberger 1991), the recognition stimuli which cause a bird to settle in a particular habitat patch may not directly influence the survival and reproductive success (fitness) of that bird (Hildén 1965). These proximate cues, however, are associated with ultimate factors which allow a species to exist under selective pressures (Hildén 1965, Rotenberry 1980). Bobwhites, through an undetermined combination of genetic and behavioral factors, are adapted to cue on characteristics of their surrounding habitat, which through evolutionary history enhanced individual survival and ultimate fitness. However, in modern landscapes which have been altered by humans, proximate ques may have become uncoupled with ultimate rewards measured in terms of fitness gains. Johnson (1980), recognizing that habitat selection operates at multiple spatial scales, introduced the concept of selection order (1st, 2nd, 3rd, 4th), in which orders of higher selection are conditional on the previous level. This approach is useful in ranking habitat components used by animals

Table 1. Area of available habitat types (ha) to breeding northern bobwhites on Trim Cane Wildlife Research and Demonstration Area, MS, 1 April–27 September, 1994 to 1996.

Habitat type	1994		1995		1996	
	ha	%	ha	%	ha	%
Control	59.68	15.7	28.20	7.4	36.45	8.1
Burn	75.76	19.9	77.21	20.3	97.90	21.8
Disk	54.92	14.4	69.10	18.2	45.75	10.2
Burn/Disk	43.97	11.6	58.08	15.3	76.38	17.0
Pasture	25.12	6.6	19.66	5.2	44.55	9.9
Row Crops	39.91	10.5	32.93	8.7	45.99	10.2
Woody	81.26	21.3	94.59	24.9	102.46	22.8
Total	380.62	100.0	379.76	100.0	449.48	100.0

with respect to their availability at multiple hierarchical spatial scales (Johnson 1980).

During the breeding season, habitats used by bobwhites typically contain components that provide escape, nesting, brood-rearing, foraging, and roosting covers (Stoddard 1931, McRae et al. 1979). Several researchers have studied the habitat needs of bobwhites (Stoddard 1931, Errington and Hamerstrom 1936, Lay 1940, Rosene 1969, Moore 1972, Yoho and Dimmick 1972, Simpson 1972, Bell et al. 1985, Mueller et al. 1988, Shaffery 1989, Burger et al. 1990); however, most analyses of habitat use or selection have been conducted at a single, and often undefined, spatial scale. Radio-telemetry facilitates quantification of habitat selection at multiple spatial and temporal scales (i.e., macro- and micro-habitat use throughout a defined period of time). Although application of radio-telemetry in bobwhite research is nearly 3 decades old (Bartholomew 1967), few studies address resource selection in relation to quantified spatiotemporal mosaics. Until recently, habitat use and movements by bobwhites have been quantified almost exclusively during winter (Yoho and Dimmick 1972, Wiseman and Lewis 1981, Bell et al. 1985), with few studies addressing habitat use by breeding bobwhites (Shaffery 1989, Taylor and Guthery 1994). In general, these studies reflect use at the macro-habitat level. In 1994, 3 studies in Mississippi addressed habitat use of bobwhite during the breeding season (Fuller 1994, Lee 1994, Manley 1994). In each study, macro-habitat use was tested with respect to available habitat types, and floristic characteristics were quantified to predict micro-habitat use. These studies provided insight into breeding season habitat selection, however, they did not consider habitat use relative to specific biological processes occurring within the breeding season (pre-laying, laying, incubation, and brood-rearing).

Habitat use by bobwhite broods is one of the least studied components of bobwhite ecology (Speake and Sermons 1986, DeVos and Mueller 1993, Taylor and Guthery 1994, Puckett et al. 1995). Roseberry and Klimstra (1984) stated that the life history and ecology of bobwhite chicks during the brood-rearing period is the least documented aspect of the species' biology. This can be attributed to the lack of technical and logistical tools necessary to adequately monitor chicks from hatch to first autumn. In this study, we used radio-marked adult bobwhite to (1) determine breeding bobwhite habitat use at multiple scales, relative to availability of habitats resulting from seasonal habitat manipulations and (2) quantify habitat characteristics at bobwhite nest sites and bobwhite brood sites.

STUDY AREA

We trapped, radiomarked, and monitored bobwhites on a 320 ha managed wildlife area, 10 km north of Starkville, Oktibbeha County, Mississippi. The Trim Cane Wildlife Research and Demonstration Area (TCWA) was under rowcrop production until 1986. Natural plant succession began following crop harvest in 1986. The developing vegetation community consisted primarily of broomsedge (*Andropogon virginicus*), Johnsongrass (*Jorghum halepense*), and annual and perennial forbs, interspersed with woody ditchbank and fencerow habitat (Manley 1994). TCWA was dissected by a network of drainage canals left after the channelization of Trim Cane Creek, and most of the area was subject to frequent inundation during winter and spring. Pioneer hardwood species such as box elder (*Acer negundo*) and green ash (*Fraxinus pennsylvanica*) took control of moist areas in fields adjacent to Trim Cane Creek, and areas of poor drainage throughout the study area.

In 1992, TCWA was divided into 50 fields, each averaging 6.5 ha (Manley 1994). The use of prescribed burning and strip-disking have been considered as beneficial to bobwhites for some time (Stoddard 1931);

Table 2. Simplified ranking matrix[a] comparing proportional habitat use within 100% kernel estimated home ranges with proportions of total available habitat types for Trim Cane Wildlife Research and Demonstration Area, MS, 1 April to 27 September 1994 to 1996.

Habitat type	Habitat type							
	Control	Burn	Disk	Burn/Disk	Pasture	Crops	Woody	Rank[b]
Control		–	–	+++	+++	+++	+	4
Burn	+		+	+++	+++	+++	+	6
Disk	+	–		+++	+++	+++	+	5
Burn/Disk	–––	–––	–––		–––	–––	–––	0
Pasture	–––	–––	–––	+++		+	–––	2
Crops	–––	–––	–––	+++	–		–––	1
Woody	–	–	–	+++	+++	+++		3

[a] Positive and negative signs denote selection and avoidance, respectively. Triple signs represent significant deviations from random ($P < 0.05$).
[b] An increase in rank value signifies increased use of habitat in selecting breeding season home ranges.

Table 3. Simplified ranking matrix[a] comparing the proportions of radio locations for each bird in each habitat type with the proportion of each habitat type within the birds 100% kemel estimated home range for Trim Cane Wildlife Research and Demonstration Area, MS, 1 April to 27 September 1994.

Habitat type	Habitat type							
	Control	Burn	Disk	Bum/Disk	Pasture	Crops	Woody	Rank[b]
Control		+	+	−	+++	+++	−	5
Burn	−		−	−−−	+	+	−−−	3
Disk	−	+		−−−	+	+	−−−	4
Burn/Disk	+	+++	+++		+++	+++	−	6
Pasture	−−−	−	−	−−−		−	−−−	1
Crops	−−−	−	−	−−−	+		−−−	2
Woody	+	+++	+++	+	+++	+++		7

[a] Positive and negative signs denote selection and avoidance, respectively. Triple signs represent significant deviations from random ($P <$ 0.05).
[b] An increase in rank value signifies increased use within home ranges.

therefore, we applied 3 experimental treatments on TCWA to improve bobwhite habitat: prescribed burning, strip-disking, and burn-disk combinations (Manley 1994, Taylor 1996). Control areas were added as a fourth experimental category and were allowed to undergo natural plant succession (Manley 1994). Habitat manipulations were applied at the same annual intervals with the same intensity throughout the study. TCWA contained no pasture, hayfields or fields planted to rowcrops; however, these habitat types were in close proximity to the boundary of the area, and thus were included in use and availability measures.

METHODS

Bobwhites were captured with walk-in funnel traps baited with commercial 3-grain chicken scratch or cracked corn (Stoddard 1931). Birds were aged, sexed, weighed to the nearest 1 g, banded with a #7 aluminum legband, radio-marked with a 5–6 g pendant-style transmitter, and released at the capture site. Radio-transmitters operated on the 148.000 to 149.999 MHz band and included a mortality sensor switch and a 25-cm antenna. Trapping began in late winter, while coveys were still formed and well into the breeding season to maintain an appropriate sample size.

Radio-marked birds were located 5 days/week using a programmable scanning receiver and handheld Yagi, and H-series antennas. Locations were obtained by homing and circling the bird at 25 to 50 m, then plotted on reproductions of aerial photos (Burger 1993). Additionally, we monitored hourly movements of each bobwhite brood during 1 of 3 5-hour intervals each day (0530 to 1030, 0930 to 1530, 1430 to 1930).

We describe habitat use of bobwhite during the reproductive season at 3 spatial scales equivalent to Johnson's (1980) 2nd, 3rd and 4th order selection using compositional analysis (Aebischer et al. 1993). Within the reproductive season, we quantified overall habitat selection and selection at 2 temporal scales: pre-hatch and post-hatch. The pre-hatch interval coincided with specific biological processes including prelaying, laying, and incubation, while the post-hatch interval included the brood-rearing period. Habitat use during the prelaying interval was estimated by reviewing daily telemetry locations of individual birds prior to their initiation of laying. The laying interval was estimated by backdating from known incubation initiation dates (1.2 days/egg multiplied by the number of eggs in clutch) (Klimstra and Roseberry 1975). A bird was classified as incubating when it stayed at the same location for 2 consecutive days during the breeding period. The nest site was then flagged at >10 m from 2 directions, and the following information was recorded: incubation initiation date, clutch size, and general habitat type. Upon hatching of the clutch, we continued to locate the parent bird daily using radio-telemetry. At 3 weeks of age, broods were flushed from the

Table 4. Simplified ranking matrix[a] comparing the proportions of radio locations for each bird in each habitat type with the proportion of each habitat type within the birds 100% kemel estimated home range for Trim Cane Wildlife Research and Demonstration Area, MS, 1 April to 27 September 1995.

Habitat type	Habitat type							
	Control	Burn	Disk	Burn/Disk	Pasture	Crops	Woody	Rank[b]
Control		−	−	−−−	+	−	−−−	2
Burn	+		+	−	+	+	−−−	5
Disk	+	−−−		−−−	+	+	−−−	4
Burn/Disk	+++	+	+++		+++	+++	−	6
Pasture	−	−	−	−−−		−	−−−	1
Crops	+	−	−	−−−	+		−−−	3
Woody	+++	+++	+++	+	+++	+++		7

[a] Positive and negative signs denote selection and avoidance, respectively. Triple signs represent significant deviations from random ($P <$ 0.05).
[b] An increase in rank value signifies increased use within home ranges.

Table 5. Simplified ranking matrix[a] comparing the proportions of radio locations for each bird in each habitat type with the proportion of each habitat type within the birds 100% kernel estimated home range for Trim Cane Wildlife Research and Demonstration Area, MS, 1 April to 27 September 1996.

Habitat type	Habitat type							
	Control	Bum	Disk	Burn/Disk	Pasture	Crops	Woody	Rank[b]
Control		+++	+	−	+++	+++	+	6
Bum	−−−		−−−	−−−	+	+	−	3
Disk	−	+++		−−−	+++	+++	+	5
Bum/Disk	+	+++	+++		+++	+++	+	7
Pasture	−−−	−	−−−	−−−		−	−−−	1
Crops	−−−	−	−−−	−−−	+		−	2
Woody	−	+	−	−	+++	+		4

[a] Positive and negative signs denote selection and avoidance, respectively. Triple signs represent significant deviations from random ($P < 0.05$).
[b] An increase in rank value signifies increased use within home ranges.

roost at dawn to estimate chick survival, and the parent bird was considered brood-rearing as long as 1 or more chicks were present. If a parent bird made a large move in 1 day or paired with another bird, we flushed the bird to determine brood loss or brood abandonment. At times, parent birds were inadvertently flushed during collection of daily telemetry locations or vegetation measurements, and their association with chicks was recorded. We were not able to distinguish between brood abandonment, brood loss or brood mixing (Burger et al. 1995).

We used the adaptive kernel 100% home range estimator (Worton 1989) in program CALHOME (Kie et al. 1996) to delineate home range boundaries. We compared mean home range size between years using a one-way analysis of variance [(PROC GLM) SAS Inst. Inc. 1988]. For each year, we combined all home range boundaries to determine study area availability. Habitat composition in the study area, and within each bird's home range, were determined by intersecting home range polygons with a geographic information system of available habitats on the study area. We compared proportions of each habitat type in the study area (availability) with proportions found in each individual's home range (use) to determine 2nd order selection (Johnson 1980, Aebischer et al. 1993). We then compared proportions of habitats in each home range (availability) with radio locations of each individual (use) to determine 3rd order selection (Johnson 1980, Aebischer et al. 1993). Using multivariate analysis of variance (MANOVA), we tested the null hypotheses that (1) breeding bobwhite define home ranges at random and (2) allocate their time and resources at random. We replaced missing values in MANOVA with a value of 0.00001 (Aebischer et al. 1993). We used paired t-tests to compare relative use of each habitat with all others individually, and ranked habitats in order of use. Due to insufficient degrees of freedom for MANOVA (Aebischer et al. 1993), we used Neu et al. (1974) to test hypotheses regarding brood habitat selection.

Assuming that a bird had selected a patch, habitat variables were quantified at 4th order (Johnson 1980) for the incubation and brood-rearing periods. Nests were monitored daily, and visually examined when the radio-marked bird was away from the nest. Hatching and termination days were determined to within 1 day. Upon hatching or nest termination, vegetation measurements were taken at the nest site to determine 4th order structural characteristics (Johnson 1980). Measurements included: litter depth; percentage ground cover for grasses, forbs, and woody species, litter and bare ground; percentage canopy cover for grasses, forbs, and woody species; and Robel visual obstruction index (Robel et al. 1970). Structural characteristics at the nest site were determined from 1 0.1-m^2 plot centered on the nest (Robel et al. 1970), from line intercept readings along a 4-m transect in each of the 4 cardinal directions from the nest (Canfield 1941), and from a 0.1-m^2 plot at the end of each transect (Robel et al. 1970).

Methods for locating and measuring brood-rearing sites closely follow that of nest sites. Brooding adult birds were located $\leq$5 times/day using hand-held telemetry equipment to walk within 10m of each brood/day and flag the position. Vegetative measurements similar to nest site measurements were taken the following day to quantify 4th order characteristics (Johnson 1980).

We used a comparison of 2 sample means [(PROC TTEST) SAS Inst. Inc. 1988] to test for differences between vegetative characteristics at nest sites and random sites, within the same patch. The same procedure was used to test for differences between vegetative characteristics at successful and unsuccessful nest sites, and to test for vegetative differences between nest sites and brood sites. We used logistic regression to model nest selection and nest success.

RESULTS

From 1994 to 1996, we radio-marked 88 and 51 male and female bobwhites, respectively. We used 24 male and 19 female radio-marked adult bobwhites to estimate habitat use at 2nd and 3rd orders of selection. Of these, 16 females and 5 males incubated 21 nests, 9 of which were successful (5 female and 4 male). These broods, in addition to 2 broods encountered at random (adopted by radio-marked bird or hatched outside study area) yielded 189 brood locations.

Table 6. Habitat use by northern bobwhite broods on Trim Cane Wildlife Research and Demonstration Area, Oktibbeha County, MS, 1 April to 27 September 1994.

Habitat type	Number of locations	Expected use	Observed use	Bonferroni[a] confidence interval	Result
Control	1	0.1568	0.0270	$-0.0458 < P < 0.0998$	Avoided
Burn	4	0.1990	0.1081	$-0.0313 < P < 0.2475$	Proportional
Bum/Disk	6	0.1155	0.1622	$0.0033 < P < 0.3276$	Proportional
Disk	8	0.1443	0.2162	$0.0315 < P < 0.4010$	Proportional
Woody	18	0.2135	0.4865	$0.2622 < P < 0.7108$	Preferred
Crops	0	0.1049	0.0000		Avoided
Pasture	0	0.0660	0.0000		Avoided

[a] After Neu et al. (1974) test conducted at $\alpha = 0.05$.

Overall Use of Habitat

Study area habitat availability for the breeding seasons of 1994, 1995, and 1996 totaled 380.6, 379.8, and 449.5 ha, respectively (Table 1). Juxtaposition of habitat types and seasonal treatments were similar between years; however, treatment of some fields was altered to deter hardwood encroachment. Home ranges of some bobwhites extended beyond the managed boundary of the study area; therefore, pasture and row crops were available at 2[nd] order selection. Mean home range size was similar among years ($F = 2.65$; df = 2, 42; $P = 0.08$). Overall habitat use differed from random at 2[nd] order ($\lambda = 0.36$; df = 6, 40; $P < 0.001$) and was not affected by year ($\lambda = 0.82$; df = 12, 68; $P = 0.84$) or sex ($\lambda = 0.91$; df = 6, 34; $P = 0.74$); therefore, bobwhites exhibited selection in home range establishment. Habitat use at 3[rd] order selection was similar between sexes ($\lambda = 0.87$; df = 6, 34; $P = 0.55$), yet differed between years ($\lambda = 0.42$; df = 12, 68; $P = 0.002$). Bobwhites did not allocate time among patches in proportion to availability in 1994 ($\lambda = 0.29$; df = 6, 13; $P = 0.006$) or 1995 ($\lambda = 0.12$; df = 6, 10; $P < 0.001$); however, habitat use at 3[rd] order was proportional to availability in 1996 ($\lambda = 0.09$; df = 6, 2; $P = 0.25$).

Habitats used in home range selection were ranked in increasing order of use, and were similar among years (Table 2). Burned fields, disked fields, woody areas and control fields were used significantly more than burned/disked fields, pastures and row crops at the 2[nd] order of selection (Table 2). Burned/disked fields were used significantly less than all other habitats, suggesting avoidance in home range definition during the breeding season.

Given that individual bobwhites chose home ranges, habitats used in patch selection (3rd order) were ranked in increasing order of use, and were similar between years (Tables 3, 4 and 5). Individuals used woody areas and burned/disked fields significantly more than burned fields, disked fields, pastures, and row crops for 1994 (Table 3). Similarly, in 1995, woody areas and burned/disked fields were used significantly more than disked fields, pastures, row crops and control fields (Table 4). Woody areas also were selected over burned fields in 1995; however, use of burned fields did not differ significantly from burned/disked fields (Table 4). Bobwhite use of burned/disked fields was more than all other available habitats in 1996, yet was not significantly different from use of control fields (Table 5). Pastures and row crops were used significantly less than control fields, disked fields and burned/disked fields in 1996 (Table 5).

Habitat Use by Broods

Habitat available to bobwhite broods was based on overall study area availability for both years (Table 1). Each year broods used burned/disked fields in proportion to their availability, while avoiding pastures and rowcrops (Tables 6, 7 and 8). Woody corridors were preferred over all other available habitats in 1994 and 1996, while use of other available habitats was stochastic (Tables 6, 7 and 8). Many brood locations were reported in areas recently relieved of standing water, thus providing bare ground with a significant overhead canopy component.

Microhabitat Characteristics at 4[th] Order Selection

We collected data on vegetation for 3 nest sites in 1994, 9 nest sites in 1995, and 4 nest sites in 1996 (*n*

Table 7. Habitat use by northern bobwhite broods on Trim Cane Wildlife Research and Demonstration Area, Oktibbeha County, MS, 1 April to 27 September 1995.

Habitat type	Number of locations	Expected use	Observed use	Bonferroni[a] confidence interval	Result
Control	14	0.0743	0.1556	$-0.0513 < P < 0.2599$	Proportional
Burn	21	0.2033	0.2333	$-0.1116 < P < 0.3551$	Proportional
Burn/Disk	20	0.1529	0.2222	$-0.1026 < P < 0.3419$	Proportional
Disk	20	0.1820	0.2222	$0.1026 < P < 0.3419$	Proportional
Woody	15	0.2491	0.1667	$0.0594 < P < 0.2739$	Proportional
Crops	0	0.0867	0.0000		Avoided
Pasture	0	0.0518	0.0000		Avoided

[a] After Neu et al. (1974) test conducted at $\alpha = 0.05$.

Table 8. Habitat use by northern bobwhite broods on Trim Cane Wildlife Research and Demonstration Area, Oktibbeha County, MS, 1 April to 27 September 1996.

Habitat type	Number of locations	Expected use	Observed use	Bonferroni[a] confidence interval	Result
Control	5	0.0811	0.0820	$-0.0139 < P < 0.1779$	Proportional
Burn	6	0.2178	0.0984	$-0.0057 < P < 0.2025$	Avoided
Burn/Disk	9	0.1699	0.1475	$0.0236 < P < 0.2715$	Proportional
Disk	0	0.1018	0.0000		Avoided
Woody	41	0.2280	0.6721	$0.5080 < P < 0.8362$	Preferred
Crops	0	0.1023	0.0000		Avoided
Pasture	0	0.0991	0.0000		Avoided

[a] After Neu et al. (1974) test conducted at $\alpha = 0.05$.

= 16); 1 random site per nest within the same patch (n = 16); and 78 brood locations. Of the 16 nests, 7 were successful and 9 were unsuccessful.

Logistic regression models did not identify vegetation variables or combinations thereof that were useful in predicting nest selection or nest success; therefore, we report univariate results. Vegetation characteristics at nest sites did not differ from random sites located within the same patch of habitat (Table 9), and successful nest sites were similar to unsuccessful nest sites (Table 10). Brood site vegetation characteristics were similar to nest sites; however, woody canopy (44.3%) and visual obstruction readings (59.0cm) at brood sites were significantly higher than at nest sites (26.6% and 37.5cm) (Table 11).

DISCUSSION

Overall Use of Habitat

The specific proximate and ultimate cues associated with habitat selection by breeding bobwhite remain an enigma. Such cues may vary throughout the geographic range of the species. However, breeding bobwhite at TCWA, given a mosiac of seasonally manipulated old-field habitats, consistently used burned fields, disked fields, control fields and woody areas to define their breeding season home ranges. Manley (1994) reported similar habitat use by breeding bobwhite on TCWA during 1993.

Throughout the 1994 and 1995 breeding seasons, woody areas and burned/disked fields were the most used habitat types within each bird's home range. In 1996, bobwhite use of control fields (unmanipulated old fields in more advanced state of plant succession) increased, and was second only to burned/disked fields. Control fields contained a significant and increasing woody component by 1996 and may have increased the proportion of available woody habitat. Woody corridors may have provided advertising posts for male bobwhite, escape cover, and corridors for movement between habitat types. Increased canopy cover also may have provided a cool, dry micro-climate for loafing during extreme heat and excessive rainfall (Johnson and Guthery 1988). The distribution and amount of woody cover available in the landscape may determine the proportion of usable space. Given that bobwhite used woody habitats in greater proportion than their availability (21 to 25%) at both 2nd and 3rd order levels of selection, we suggest optimal percent woody cover is somewhat greater than 20 to 25%.

Burned/disked fields were selected at 3rd order and likely provide annual weed seeds and invertebrates that enhance foraging habitat quality. Additionally, Manley (1994) reported that fields treated with burning and disking contained less litter and more bare ground than other treatments (Manley 1994), and may have provided increased mobility for breeding bobwhites.

Nest Site Microhabitat Selection

Although bobwhites exhibited macrohabitat selection at multiple scales, we did not detect fine scale selection for vegetation characteristics at nest sites. This may imply that bobwhites select patches in which to nest, but within the patch they are less selective with respect to the specific location for nest construction. That is, selection occurs at the spatial scale of the patch, instead of at the nest site spatial scale. If vegetation structure at the nest site has little effect on the probability of a nest hatching, given that a suitable patch is selected for nesting, there may be little pressure for selection of a specific vegetation structure. In support of this hypothesis, we observed no structural differences in habitat patches between successful and unsuccessful nests.

Brood Habitat Selection

Components of brood habitat are rarely defined and probably vary throughout the geographic range of the bobwhite. Stoddard (1931:40–41) recognized that brooding bobwhites require protection from intense sunlight, as well as rain. During this study, broods selectively used woody habitats. Woody cover and high percentages of bare ground have been identified as important components of bobwhite brood habitat (Cantu and Everett 1982, DeVos and Mueller 1993). Our sample of radio-marked adult bobwhites with broods used a variety of habitat types with 19.4% mean bare ground, similar to that reported in central Alabama (22.9%) and northern Missouri (25%) (Speake and Sermons 1986, Burger et al. 1994). Grasses (33.4%), forbs (40.0%) and woody plants (44.3%) provided ≤3 strata of overhead cover. Woody canopy cover (44.3%) was similar to overstory canopy cover (40%) reported by DeVos and Mueller (1993). Brood habitat was structurally different from nesting habitat. Brood sites

Table 9. Mean (cm)[a] vegetative characteristics of bobwhite nest sites and random sites at Trim Cane Wildlife Research and Demonstration Area, MS, 1994 to 1996.

	Nest site			Random			
Variable	x̄	%	S.E.	x̄	%	S.E.	*P*
Grass Canopy[b]	143.60	35.9	22.42	165.58	41.4	21.45	0.4847
Forb Canopy[b]	133.31	33.3	19.03	128.02	32.0	22.65	0.8593
Woody Canopy[b]	106.38	26.6	23.45	86.93	21.7	18.39	0.5193
Bare Ground[b]	97.95	24.5	19.03	140.28	35.1	27.31	0.2141
Litter Cover[b]	243.51	60.9	23.36	190.15	47.5	30.05	0.1719
Grass Ground[b]	48.94	12.2	8.40	56.95	14.2	8.12	0.4987
Woody Ground[b]	4.80	1.2	1.97	7.44	1.9	2.08	0.3643
Litter Depth[c]	0.64		0.09	0.52		0.11	0.3914
Nest VOR[d]	45.71		4.21	34.46		4.91	0.0930
VOR[e]	37.52		3.96	38.58		5.17	0.8716

[a] Means computed across all habitat types (nest: n = 16 random: n = 16).
[b] Values represent mean abundance along a 400 cm transect.
[c] Values represent mean litter depth taken at 50 cm intervals along a 400 cm transect.
[d] Mean Robel reading taken at nest site from 4 cardinal directions.
[e] Mean Robel readings from 4 m radius around nest site in 4 cardinal directions.

had greater woody cover and vegetation density than nest sites.

Taylor and Guthery (1994) reported that brush canopy cover in southern Texas differed among activity sites, and was more dense at midday loafing sites than feeding sites. They suggested that bobwhite managers should manipulate the habitat to accommodate within-day variation of habitat selection by broods. We concur with their recommendation and submit that combinations of burning and strip-disking be imposed on quail lands with a 20 to 25% interspersion of shrubby woody corridors. We also realize the importance of invertebrate abundance and accessibility to quail chicks, and suggest that these seasonal manipulations offer a mosaic of invertebrate rich habitat types while impeding succession.

MANAGEMENT AND RESEARCH IMPLICATIONS

Despite the relatively intensive disturbance regime implemented on TCWA, and selective use of manipulated fields by bobwhites, population density decreased during the study. This was in part attributable to consistently high nest predation and increasing mammalian cause-specific mortality of breeding adults over the life of the study (Taylor and Burger 1997, Taylor et al. this volume). Regrettably, we did not have information on temporal trends in predator community composition or abundance, illustrating that studies examining bobwhite ecology independent of predator context may provide an incomplete picture of population processes.

Bobwhites are adapted to exploit early successional habitats. Bobwhite management is largely control of vegetation successional processes. In old-field habitats, control of advancing natural succession in an ongoing process, but suitable bobwhite habitat can be maintained through combinations of strip-disking and prescribed burning. The disking and burning management practices implemented on TCWA provided early succession habitats which apparently met the annual cycle needs of bobwhites. However, neither this study, nor any previous studies, have clearly defined what con-

Table 10. Mean (cm)[a] vegetative characteristics of successful and unsuccessful bobwhite nest sites at Trim Cane Wildlife Research and Demonstration Area, MS, 1994 to 1996.

	Nest fate						
	Unsuccessful			Successful			
Variable	x̄	%	S.E.	x̄	%	S.E.	*P*
Grass Canopy[b]	178.08	44.5	29.21	104.46	26.1	25.35	0.0873
Forb Canopy[b]	122.11	30.5	27.99	149.96	37.5	20.25	0.4586
Woody Canopy[b]	98.19	24.5	23.82	116.11	29.0	43.17	0.7058
Bare Ground[b]	64.64	16.2	13.23	131.11	32.8	34.63	0.0694
Litter Cover[b]	278.50	69.6	13.42	210.75	52.7	46.45	0.1404
Grass Ground[b]	50.33	12.6	8.76	45.04	11.3	14.96	0.7523
Woody Ground[b]	5.42	1.4	2.61	3.50	0.9	2.77	0.6256
Litter Depth[c]	0.78		0.11	0.52		0.14	0.1604
Nest VOR[d]	49.17		6.45	42.32		6.29	0.4689
VOR[e]	34.13		4.76	43.88		8.98	0.3241

[a] Means computed across all habitat types by nest fate (successful: n = 7; unsuccessful: n = 9).
[b] Values represent mean abundance along a 400 cm transect.
[c] Values represent mean litter depth taken at 50 cm intervals along a 400 cm transect.
[d] Mean Robel reading taken at nest site from 4 cardinal directions.
[e] Mean Robel readings from 4 m radius around nest site in 4 cardinal directions.

Table 11. Mean (cm)[a] vegetative characteristics of bobwhite nest sites and brood sites at Trim Cane Wildlife Research and Demonstration Area, MS, 1994 to 1996.

Variable	Nest			Brood			P
	$\bar{x}$	%	S.E.	$\bar{x}$	%	S.E.	
Grass Canopy[b]	143.60	35.9	22.42	133.77	33.4	9.58	0.6824
Forb Canopy[b]	133.31	33.3	19.03	160.06	40.0	10.67	0.3017
Woody Canopy[b]	106.38B[c]	26.6	23.45	177.20A	44.3	12.71	0.0237
Bare Ground[b]	97.96	24.5	19.03	77.70	19.4	8.34	0.3321
Litter Cover[b]	243.51	60.9	23.36	267.24	66.8	10.65	0.3705
Grass Ground[b]	48.94	12.2	8.40	36.46	9.1	3.79	0.1875
Woody Ground[b]	4.80	1.2	1.97	14.36	3.6	2.86	0.1512
Litter Depth[d]	0.64		0.09	0.89		0.07	0.1386
Center VOR[e]	45.71		4.21	61.71		3.50	0.0544
VOR[f]	37.52B[c]		3.96	59.03A			0.0069

[a] Means computed across all habitat types (nest: n = 16; brood sites: n = 78).
[b] Values represent mean abundance along a 400 cm transect.
[c] Different letters within rows denote significance ($P < 0.05$).
[d] Values represent mean litter depth taken at 50 cm intervals along a 400 cm transect.
[e] Mean Robel reading taken at site point center from 4 cardinal directions.
[f] Mean Robel readings from 4 m radius around nest site in 4 cardinal directions.

stitutes optimal habitat composition. We propose that management as experimentation could be used in an adaptive resource context to identify optimal landscape composition at multiple spatial scales across a temporal gradient. Such management experiments should include covariates such as predator context and abundance and they should contain control areas where treatments are not applied. We support the contention that a nationally coordinated approach to management and research is required to reverse bobwhite population declines (Church et al. 1993, Brennan 1991, 1993).

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