Research Article

Habitat-Suitability Bounds for Nesting Cover of Northern Bobwhites on Semiarid Rangelands

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ABSTRACT Northern bobwhite (*Colinus virginianus*) is a species for which extensive knowledge exists regarding its ecology, life history, and habitat. Although the qualitative aspects of bobwhite habitat have been described and known for many decades, researchers have neglected to characterize bobwhite habitat quantitatively (i.e., habitat selection). Thus, biologists have been capable of identifying components that compose bobwhite habitat but have only been able to speculate on how much of each component was necessary. We documented selection–avoidance behavior of nesting bobwhites in Brooks County, Texas, USA, during May–August, 2004–2005. We measured 5 vegetation features (i.e., nesting-substrate ht and width, suitable nest clump density, herbaceous canopy coverage, and radius of complete visual obstruction) at nest sites ($n = 105$) and at random points ($n = 204$). We used continuous selection functions to assess habitat use and identify bounds of suitability. Selection domains for nesting-substrate height and radius of complete visual obstruction were 16.9–31.2 cm and 1.05–4.35 m, respectively. Across all measurements, bobwhites selected for nest sites with a nesting-substrate width ≥22.4 cm, suitable nest-clump density ≥730 nest clumps/ha, and herbaceous canopy coverage ≥36.7%. This knowledge will provide an important foundation for managers to evaluate current nesting conditions on semiarid rangelands and provide a basis for habitat management aimed at creating suitable nesting habitat for bobwhites.
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KEY WORDS *Colinus virginianus*, habitat selection, nesting habitat, northern bobwhite, radiotelemetry, Texas.

Effective wildlife management requires knowledge of species habitat requirements and habitat-use patterns. Such knowledge provides an important foundation for managers to evaluate current habitat conditions and provide a basis for habitat management aimed to create suitable habitat for target species or guilds. Qualitative knowledge of habitat requirements for wildlife is commonly known; however, quantitative knowledge of habitat use (i.e., outcome of habitat selection process resulting in disproportional use of available resources [Hall et al. 1997]) often is lacking. Wildlife management operates less effectively without habitat-use data because bounds of habitat suitability (i.e., lower and upper threshold values) are unknown.

Northern bobwhite (*Colinus virginianus*) is an example for which extensive knowledge exists regarding the species' ecology, life history, and habitat (Stoddard 1931, Rosene 1969, Lehmann 1984), but considerably less information exists regarding its selection of habitat (Kopp et al. 1998, Guthery et al. 2000) despite years of research. This research trajectory has resulted in a knowledge base that provides qualitative descriptions of bobwhite habitat but does not provide quantitative bounds of habitat suitability. Thus, biologists have been capable of identifying the components that characterize bobwhite habitat but only have been able to speculate how much of each component was required.

This lack of habitat-selection data forced early biologists to base habitat recommendations on their best educated guess. Recent research on selection–avoidance behavior of bobwhites (Johnson and Guthery 1988, Kopp et al. 1998, Guthery et al. 2000) has surfaced the tenuous nature of early recommendations. For example, bobwhites initially were thought to require landscapes consisting of 5–15% woody canopy coverage (Jackson 1969, Lehmann 1984, Guthery 1986). However, subsequent habitat-selection research revealed that bobwhites actually selected points with much higher woody canopy cover (20–90%; Johnson et al. 1990, Kopp et al. 1998). Other similar habitat recommendations have been propagated through time without empirical testing, such as amount of nesting cover. Lehmann (1976) speculated that nesting cover requirements for bobwhites ranged within 600–4,000 nest sites/ha, a recommendation restated later by Guthery (1986). Biologists have continued to issue this recommendation despite its speculative nature. A negative aspect of this iterative process has been that the speculative nature of recommendations has been supplanted with an element of truth through mere repetition.

Habitat-selection research provides an empirical basis from which bounds of habitat suitability can be identified. These habitat-suitability bounds represent the threshold values that collectively define usable space (Guthery 1997) for bobwhites. Because a goal of management is to create or maintain usable space, habitat-suitability bounds facilitate effective management. The objective of our study was to empirically determine the bounds of habitat suitability for 5 vegetation characteristics of bobwhite nesting cover (nesting-substrate ht and width, suitable nest-clump density, herbaceous canopy coverage, and radius of complete visual obstruction) deemed important in prior research (Lehmann

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1984, Kopp et al. 1998, Guthery et al. 2000). Our goal was to characterize the structural properties of nest sites and their surrounding area. Thus, we measured nesting-substrate height and width measurements because both compose structural characteristics of an actual nest site. We measured suitable nest-clump density, herbaceous canopy cover, and radius of complete visual obstruction because they described the structural properties surrounding a nest site.

STUDY AREA

We collected our data from an ongoing, long-term (>7 yr) radiotelemetry project (The South Texas Quail Research Project) conducted on the Encino Division of the King Ranch, Inc. since 1998. The Encino Division is located in Brooks County, Texas, USA, which lies within the Rio Grande Plains ecoregion of Texas (Gould 1975). Average annual rainfall within this area was 40–76 cm, with May and June receiving the highest amount of rainfall, and January and February receiving with the lowest (Corell and Johnston 1979).

Our study area consisted of 3 spatially independent study sites: Cuates, La Loba, and North Viboras. Each site was approximately 1,000 ha and supported a variety of habitat types, including mesquite (*Prosopis glandulosa*) savannahs, mixed-brush thorn shrub, and live oak (*Quercus virginiana*) communities. The plant community in all 3 pastures consisted predominately of honey mesquite, granjeno (*Celtis pallida*), pricklypear cactus (*Opuntia lindheimeri*), and huisache (*Acacia smallii*). Common grasses consisted of little bluestem (*Schizachyrium scoparium*), paspalum (*Paspalum* spp.), red lovegrass (*Eragrostis secundiflora*), gulf cordgrass (*Spartina spartinae*), and grassbur (*Cenchrus incertus*). Less common grasses included nonnative Kleberg bluestem (*Dichanthium annulatum*), King Ranch bluestem (*Bothriochloa ischaemum*), and buffelgrass (*Pennisetum ciliare*). Predominant forbs were croton (*Croton* spp.), dayflower (*Commelina erecta*), partridge pea (*Chamaecrista fasciculata*), and sunflower (*Helianthus annuus*). All 3 sites were grazed 1 animal unit/9–13 ha per year.

METHODS

Radiotelemetry

We captured bobwhites using standard funnel traps (Stoddard 1931) during January–August 2004–2005 such that we maintained $\geq$20 radiomarked bobwhites/site at all times. We baited funnel traps with grain sorghum (*Sorghum* spp.) and covered them with woody branches to conceal traps from predators. We spaced traps 150–200 m apart to ensure uniform trapping across the study area and minimize recapture of marked bobwhites. We marked every captured bird with an aluminum leg band, and we fitted birds weighing $\geq$150 g with a neck-loop radiotransmitter (American Wildlife Enterprise, Monticello, FL). We used a handheld 3-element Yagi antenna and an Advanced Telemetry Systems (Isanti, MN) receiver to monitor bobwhites 2–3 times per week to locate nests. When we located birds in the same location (>2 consecutive d), we assumed incubation was occurring. We marked brush surrounding nests (>10 m away) with fluorescent surveyor's flag on which we recorded the estimated distance and direction from the flag to the nest site. In addition, we obtained Global Positioning System (GPS) coordinates of the general nest area with a Garmin Legend GPS unit. Once incubation was complete or the nest was unsuccessful, we then obtained habitat measurements within 1–2 weeks following the determination of the nest's fate.

Habitat Measurements

We collected habitat data at 2 types of points: nest site and random. To establish random points, we constructed a 400 $\times$ 400-m grid and randomly placed this grid onto a map of each study site for the 2004 and 2005 nesting seasons. Thus, our first point was random, but thereafter, points were systematic random. We collected habitat data at each grid point, which produced 34, 34, and 35 random points in Cuates, La Loba, and North Viboras, respectively (n = 103 points/yr). At each type of point, we measured nesting-substrate height, width, density of suitable nest clumps, percent herbaceous cover, and radius of complete visual obstruction (Kopp et al. 1998). We considered a bunchgrass a suitable nest site if it was height $\geq$25.4 cm and width $\geq$25.4 cm (Lehmann 1984). We collected habitat data at random points during June–August of each year to coincide with the nesting season of bobwhites on our study area. It is important to note that when we obtained habitat measurements at random points, no nests were situated at any of the random points.

Nesting-substrate height and width.—We measured vegetation height (cm) and width (cm) at each type of point with a meter stick. We obtained one height measurement, centering the meter stick on each point and recording the effective maximum height of vegetation. We measured bunchgrass width once in 2 separate orientations (north–south and east–west) to calculate a mean diameter.

Suitable nest-clump density.—We determined suitable nest-clump density with the point-centered-quarter method (Cottam and Curtis 1949, 1956; Cottam et al. 1953). Briefly, we established 4 quadrants (north, east, south, and west) centered around each point. We measured the distance to the nearest suitable nest clump in each quadrant. We then used these distances in the calculation of density as described by Cottam and Curtis (1949).

Herbaceous canopy coverage.—We measured percent canopy coverage of herbaceous plants using a 1-m^2 sampling frame. We obtained 4 estimates at each point to obtain mean percent canopy coverage. We obtained these estimates by placing the sampling frame in such a manner that we measured the 4 quadrants (north, east, south, and west) surrounding a point.

Radius of complete visual obstruction.—We measured the radius of complete visual obstruction (Kopp et al. 1998) at each point type. To do so, we measured visual obstruction distance along 8 compass radii (north, northeast, east, southeast, south, southwest, west, and northwest) at each point. We defined visual obstruction distance (m) as the distance at which the 0- to 15.2-cm stratum on a 15 × 60-cm profile board was 100% visually obstructed to a kneeling observer (ht = 0.5 m). This stratum (0–15.2 cm) represented the average height of a bobwhite. We calculated a mean obstruction distance (m) for each point. This mean distance, known as the radius of complete visual obstruction, represents the distance at which a bobwhite nest would be visible to terrestrial predators (Kopp et al. 1998).

Statistical Analyses

We developed continuous selection functions for each habitat variable following the protocol of Kopp et al. (1998) to identify selection domains. We modeled the cumulative frequency distribution for each habitat variable using parametric (logistic, Gompertz, confined exponential, and Weibull) functions. We chose the model with the highest multiple coefficient of determination value for the particular cumulative frequency distribution. We differentiated and scaled the resulting cumulative distribution functions to obtain the respective probability density functions $f(x)$ for nest sites and $g(x)$ for random points. We then calculated a continuous selection function (Guthery 1997), as $u(x) = f(x)/g(x)$ for $g(x) > 0$. The continuous selection function is interpreted the same as the discrete selection ratio, defined as proportional use divided by proportional availability. A selection function value of $u(x) > 1$ indicates selection, a value of $u(x) < 1$ indicates avoidance, and a value of $u(x) = 1$ indicates no difference in proportional use and proportional availability (Kopp et al. 1998). Random use with respect to a habitat variable is interpreted as $u(x) = 1$ for all domain x.

For comparison, we also compared means of habitat variables between nest and random points using 95% confidence intervals (Ott 1992).

RESULTS

We obtained habitat data for 105 nest points and 204 random points. We collected habitat data at all 105 nest sites. We collected habitat data at all 204 random points for all habitat features except for vegetation height ($n = 187$), width ($n = 187$), and percent herbaceous cover ($n = 203$).

Nest Height and Width

Mean height of vegetation at nest sites (95% CI: 23.7 ± 1.3 cm) was similar to mean vegetation height at random points (95% CI: 23.3 ± 1.1 cm). Model fit was good for cumulative frequency distributions of both nest sites ($R^2 = 0.999$) and random points ($R^2 = 0.999$; Appendix). The continuous selection function indicated bobwhites selected for a nesting-substrate height of 16.9–31.2 cm (Fig. 1). The selection function value remained close to 1.0, indicating weak selection–avoidance behavior by bobwhites for this variable.

Nesting-substrate diameter was greater at nest sites (95% CI: 29.6 ± 1.7 cm) compared to random points (95% CI: 22.7 ± 1.1 cm). Model fit also was good for cumulative frequency distributions of nest sites ($R^2 = 0.994$) and random points ($R^2 = 0.997$; Appendix). The selection

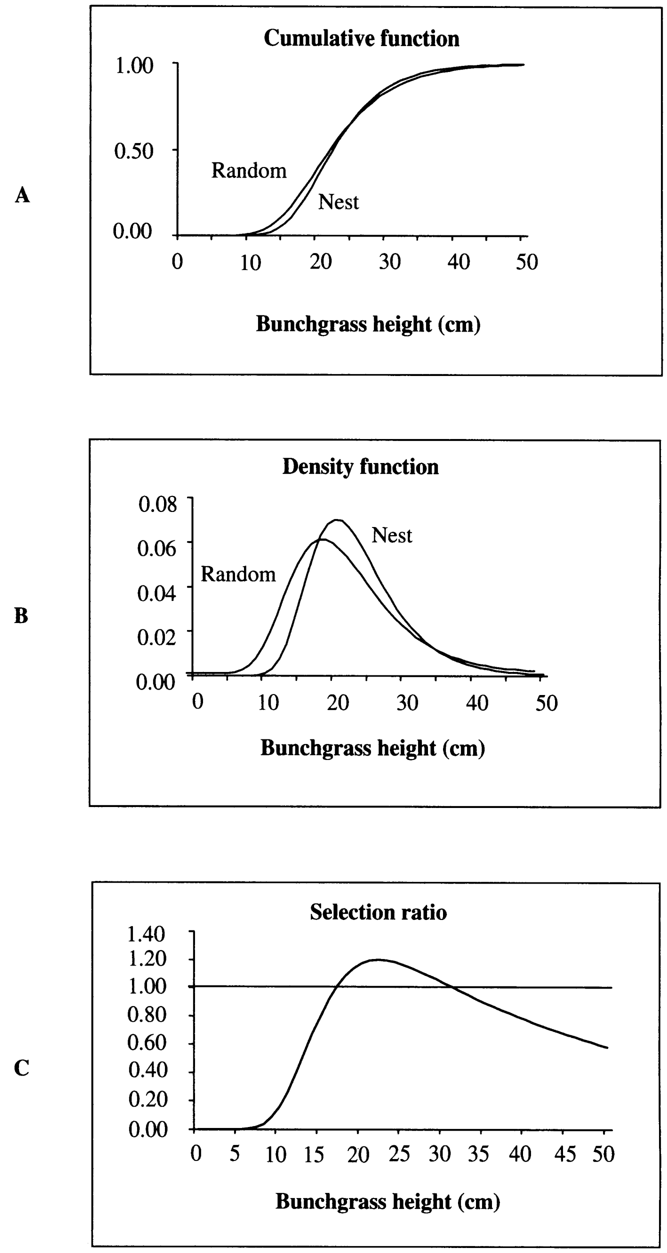

Figure 1. (A) Cumulative function and (B) probability density function of bunchgrass height for available (random) and used (nest site) points of northern bobwhites, and (C) selection function based on the probability density function in Brooks County, Texas, USA, during May–August, 2004–2005.

function indicated bobwhites selected nesting substrates with diameters ≥22.4 cm (Fig. 2).

Bobwhite nests were located in several grass species (Table 1). Little bluestem represented the most common nesting substrate (44%; $n = 97$ nests) followed by red lovegrass (13%), brownseed paspalum (*Paspalum plicatulum*; 9%), and gulf cordgrass (9%; Table 1). Two nonnative species, Kleberg bluestem and bermudagrass (*Cynodon dactylon*), also were used as nesting substrates.

Suitable Nest-Clump Density

We documented greater mean suitable nest-clump density at nest sites (95% CI: 0.1754 ± 0.0452 nest clumps/m^2) than at random points (95% CI: 0.1108 ± 0.0283 nest clumps/

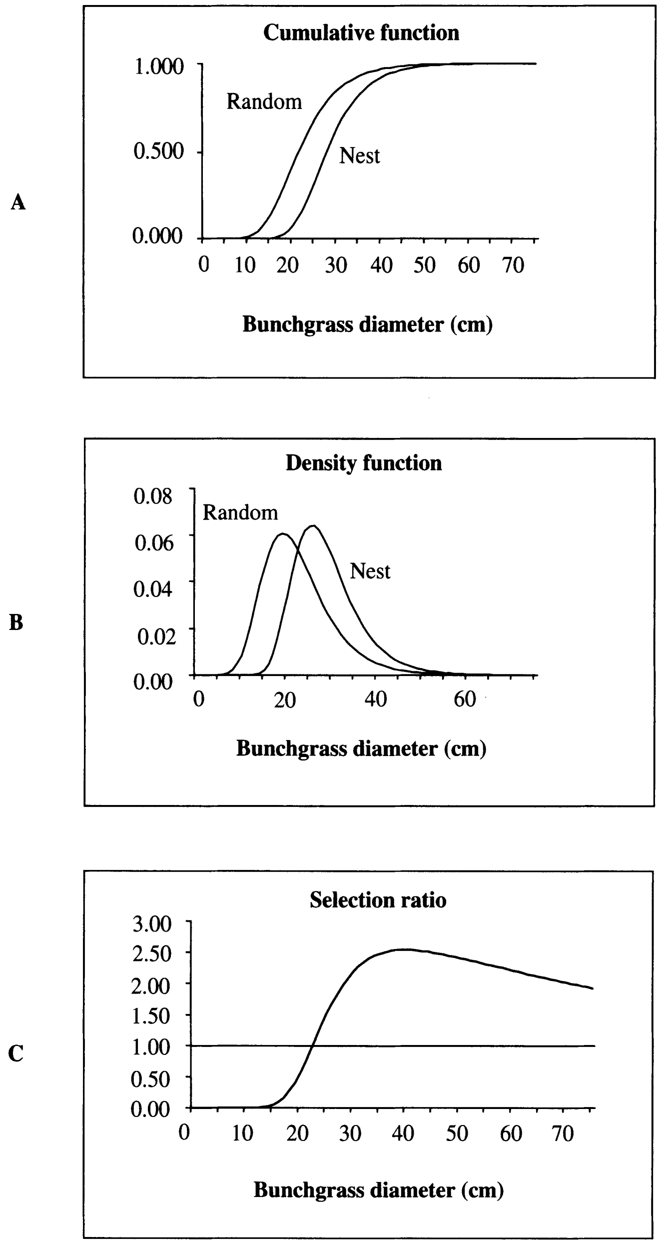

Figure 2. (A) Cumulative function and (B) probability density function of bunchgrass diameter for available (random) and used (nest site) points of northern bobwhites, and (C) selection function based on the probability density function in Brooks County, Texas, USA, during May–August, 2004–2005.

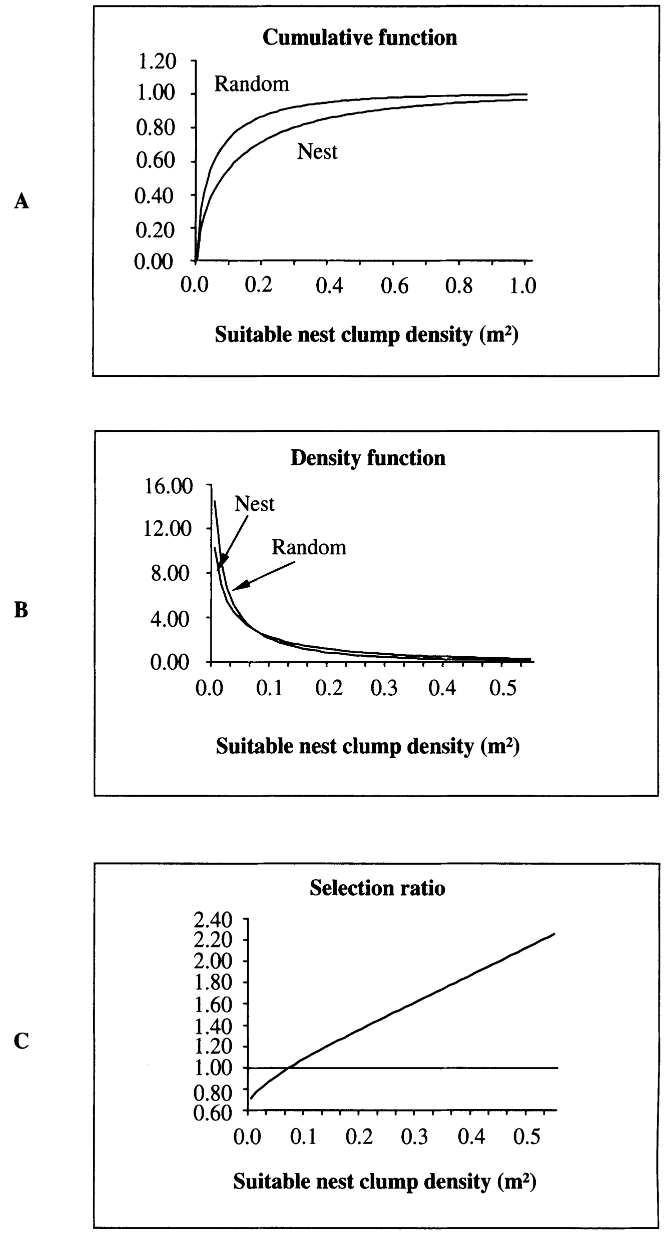

Figure 3. (A) Cumulative function and (B) probability density function of suitable nest-clump density for available (random) and used (nest site) points of northern bobwhites, and (C) selection function based on the probability density function in Brooks County, Texas, USA, during May–August, 2004–2005.

m^2). The exponential model used to obtain probability density functions for suitable nest-clump density provided a good fit for nest sites ($R^2 = 0.994$) and for random points ($R^2 = 0.987$; Appendix). Based on the selection function, bobwhites selected nest sites in areas with $\geq$730 nest clumps/ha (Fig. 3).

Herbaceous Canopy Coverage

Bobwhites selected nest sites with greater herbaceous canopy coverage (95% CI: 52.1 $\pm$ 3.7%) than randomly available (95% CI: 42.1 $\pm$ 3.0%). Modeling of cumulative frequency distributions provided a good fit for both nest sites ($R^2 = 0.99$) and random points ($R^2 = 0.99$; Appendix). The selection function suggested bobwhites selected nest sites with $\geq$36.7% herbaceous canopy coverage (Fig. 4).

Radius of Complete Visual Obstruction

Mean radius of complete visual obstruction was smaller at nest sites (95% CI: 3.3 $\pm$ 0.3 m) than at random points (95% CI: 5.5 $\pm$ 0.5 m). This suggests that a bobwhite nest would disappear from a terrestrial predator's view at an average radius of 3 m and 5 m at used and random points, respectively. Model fit was good for both nest sites ($R^2 = 0.997$) and random points ($R^2 = 0.990$; Appendix). The resulting selection function indicated the domain of selection for nest-site radius of complete visual obstruction was 1.05–4.35 m (Fig. 5).

Table 1. Vegetation height (cm) and width (cm) of grass species used by northern bobwhite as nesting substrate, Brooks County, Texas, USA, May–August, 2004–2005.

Tribe Common name	Scientific name	Origin	*n*	%	Ht (cm) $\bar{x}$	Ht (cm) SD	Width (cm) $\bar{x}$	Width (cm) SD
Andropoganeae								
Little bluestem	*Schizachyrium scoparium*	Native	44	45.4	25.0	5.6	30.4	7.3
Kleberg bluestem	*Dichanthium annulatum*	Introduced	4	4.1	19.8	5.7	23.4	6.7
Pooled			48	49.5	24.5	5.7	30.1	7.4
Aristideae								
Threeawn	*Aristida purpurea*	Native	6	6.2	21.2	6.2	26.6	2.0
Chlorideae								
Gulf cordgrass	*Spartina spartinae*	Native	9	9.3	30.8	10.7	39.9	18.8
Hooded windmillgrass	*Chloris cucullata*	Native	1	1.0	15.0	na[a]	21.5	na
Bermudagrass	*Cynodon dactylon*	Introduced	5	5.2	17.2	6.1	25.9	6.0
Pooled			15	15.5	25.2	11.3	34.3	16.5
Eragrosteae								
Red lovegrass	*Eragrostis secundiflora*	Native	13	13.4	21.0	3.0	24.1	4.6
Purpletop	*Tridens flavus*	Native	4	4.1	24.5	4.5	33.5	7.0
Pooled			17	17.5	21.8	3.6	26.4	6.4
Paniceae								
Brownseed paspalum	*Paspalum plicatulum*	Native	9	9.3	23.0	23.0	30.4	6.1
Switchgrass	*Panicum virgatum*	Native	1	1.0	41.0	na	37.0	na
Grassbur	*Cenchrus incertus*	Native	1	1.0	25.0	na	23.0	na
Pooled			11	11.3	24.8	7.4	30.6	6.3
Total			97		24.0	6.8	30.0	9.1

[a] na = not applicable.

DISCUSSION

Based on our data, bobwhite nesting habitat was characterized as 1) nesting-substrate height within 15–30 cm, 2) nesting-substrate width $\geq$22 cm, 3) suitable nest clump density $\geq$730 nest clumps/ha, 4) herbaceous canopy cover $\geq$37%, and 5) radius of complete visual obstruction within 1–4 m.

A collective view of our findings and the available research leads to a general characterization of bobwhite nest-site selection: 1) nesting substrates are taller and wider than available vegetation, and 2) nest sites are situated in areas with denser vegetation than surrounding habitat (Klimstra and Roseberry 1975, Taylor et al. 1999, Townsend et al. 2001, Hernández et al. 2003).

Regarding nesting substrates, our data provided evidence that bobwhites selected wider nesting substrates but only weakly supported the attribute of taller nesting substrates. No other study has quantified selection for nesting-substrate width for bobwhites besides our study; therefore, a comparative review of existing research is not possible. However, the mean width of bunchgrasses used by bobwhites in our study (30.5 cm) was similar to that reported by Lehmann (1984) for southern Texas (30 cm).

Our documentation of weak selection for nesting-substrate height is in contrast to Taylor et al. (1999), who reported that nest sites in Kansas, USA, were situated in taller vegetation (52 cm) than was available (35 cm). Our finding may have resulted from a landscape (habitat within all 3 study sites) in which the available habitat approximated the nesting-substrate height selected by bobwhites. Lehmann (1946) reported that on mixed-grass prairie of southern Texas, bobwhites used bunchgrasses 23 cm tall, a value closely approximating mean height of both nests (24 cm) and random points (23 cm) in our study. Thus, it is possible that bobwhites did not have an opportunity to express selection on our study area because available habitat was suitable. The qualitative similarity between the probability density function of available habitat and used habitat (selection ratios near 1.0) provides evidence for this view. Alternatively, nesting-substrate height may not have been an important habitat variable in nest-site selection, or we simply failed to measure it in a manner meaningful to bobwhites.

Regarding location of nest sites within the landscape, our data support the general characterization that nest sites are situated in areas of dense cover. We documented greater herbaceous canopy cover, smaller radius of complete visual obstruction, and greater suitable nest-clump density at nest sites than at available habitat. In our study, bobwhite nests became completely obstructed from view at a shorter distance (3 m) than at random points (5 m). Such a small difference in visual obstruction distance between nest sites and random points raises concern regarding the biological significance of this finding. However, the biological relevance lies not in the difference per se but rather in the behavioral pattern emerging from a collective interpretation of our and available research. Taylor et al. (1999) documented that bobwhite nests in Kansas contained greater visual obstruction than available habitat. Likewise, Townsend et al. (2001) and Hernández et al. (2003) reported a similar pattern in nesting behavior for bobwhites

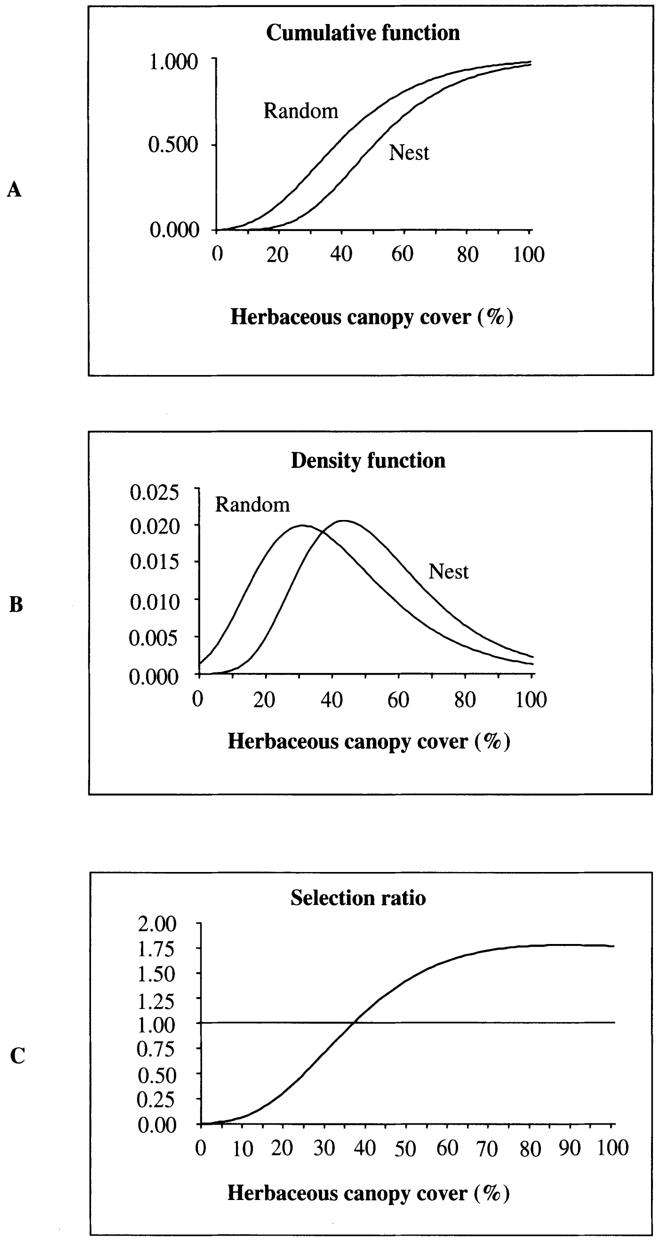

Figure 4. (A) Cumulative function and (B) probability density function of herbaceous canopy cover for available (random) and used (nest site) points of northern bobwhites, and (C) selection function based on the probability density function in Brooks County, Texas, USA, during May–August, 2004–2005.

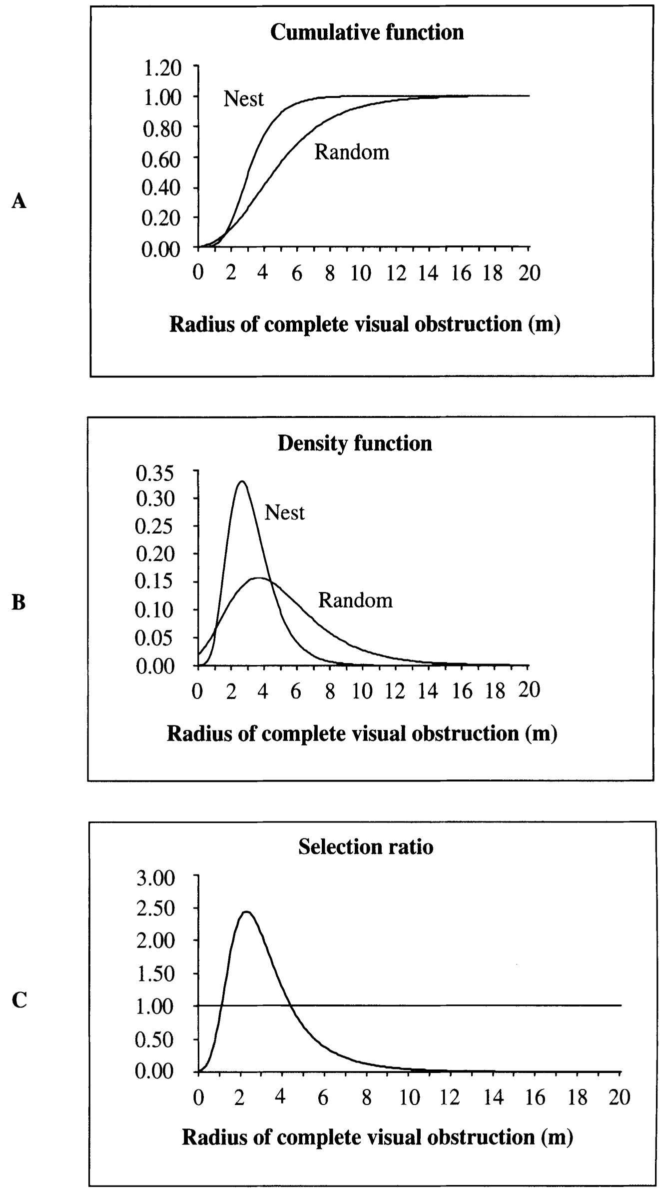

Figure 5. (A) Cumulative function and (B) probability density function of radius of complete visual obstruction for available (random) and used (nest site) points of northern bobwhites, and (C) selection function based on the probability density function in Brooks County, Texas, USA, during May–August, 2004–2005.

in Oklahoma, USA, and northern Texas, respectively. Given that these findings span a large geographic area (KS to OK to TX), the selection of nest sites with denser vegetation than is available suggests this nest-site attribute has adaptive value for bobwhites.

It is worthy to compare our empirical estimate of adequate nesting cover for bobwhites with early speculations. Our data suggested that bobwhites selected nest sites with $\geq$730 nest clumps/ha. Lehmann (1976) speculated that bobwhites required about 600–4,000 nest sites/ha for adequate nesting cover. The lower bound estimated by Lehmann (1976) is numerically lower but still comparable to our empirical estimate. Thus, our findings suggest that early recommendations (Lehmann 1976, Guthery 1986), although speculative, were reasonable.

MANAGEMENT IMPLICATIONS

Past research provided a variety of information regarding management of bobwhite habitat; however, management largely operated without the knowledge of habitat-suitability bounds. We determined selection domains for nesting cover of bobwhites. We emphasize that these suitability bounds need to be viewed as general and not definitive characteristics of bobwhite nesting because habitat availability is not a singular instance but rather dynamic through space and time. Nevertheless, our research findings provide an empirical foundation from which bobwhite nesting habitat can be managed (Holechek et al. 1982, Guthery 1996). For example, habitat-suitability bounds for nesting-substrate height (i.e., 15–30 cm) can be used to manage grazing pressure to meet bobwhite nesting requirements. Other habitat variables (% herbaceous canopy cover, radius of complete visual obstruction, and suitable nest-clump density) also can be used in a similar context to regulate grazing. However, monitoring grazing pressure using these latter variables may not be as readily assessable by managers.

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Appendix. Cumulative distribution and probability density functions for habitat variables at random points and nest sites used by northern bobwhites in Brooks County, Texas, USA, May–August, 2004–2005.

Variable	n	Model			Parameter		
		Type	Function	R^2	a	b	Coeff.
Vegetation ht (cm)							
Nest site	105	Cumulative	$F(x) = \exp[-a \exp(-bx)]$	0.999	48.2898	0.1914	0.1914
		Probability density	$f(x) = \text{coeff. } F(x)[-\ln(F(x))]$				
Random	187	Cumulative	$G(x) = \exp[-a \exp(-bx)]$	0.999	24.2642	0.1635	0.1635
		Probability density	$g(x) = \text{coeff. } G(x)[-\ln(G(x))]$				
Vegetation width (cm)							
Nest site	105	Cumulative	$F(x) = \exp[-a \exp(-bx)]$	0.994	84.6263	0.174	0.174
		Probability density	$f(x) = \text{coeff. } F(x)[-\ln(F(x))]$				
Random	187	Cumulative	$G(x) = \exp[-a \exp(-bx)]$	0.997	23.0315	0.1646	0.1646
		Probability density	$g(x) = \text{coeff. } G(x)[-\ln(G(x))]$				
Herbaceous canopy cover (%)							
Nest site	105	Cumulative	$F(x) = \exp[-a \exp(-bx)]$	0.989	11.2266	0.0559	0.0559
		Probability density	$f(x) = \text{coeff. } F(x)[-\ln(F(x))]$				
Random	203	Cumulative	$G(x) = \exp[-a \exp(-bx)]$	0.999	5.2325	0.0538	0.0541
		Probability density	$g(x) = \text{coeff. } G(x)[-\ln(G(x))]$				
Radius of complete visual obstruction (m)							
Nest site	105	Cumulative	$F(x) = \exp[-a \exp(-bx)]$	0.997	10.2007	0.8985	0.8985
		Probability density	$f(x) = \text{coeff. } F(x)[-\ln(F(x))]$				
Random	203	Cumulative	$G(x) = \exp[-a \exp(-bx)]$	0.990	4.5398	0.421	0.4255
		Probability density	$g(x) = \text{coeff. } G(x)[-\ln(G(x))]$				
Suitable nest-clump density (nest clumps/ha)							
Nest site	105	Cumulative	$F(x) = 1 - \exp[-(x/a)^b]$	0.994	0.134	0.5998	4.4862
		Probability density	$f(x) = \text{coeff. } (x/a)^{b-1} \times \exp[-(x/a)^b]$				
Random	204	Cumulative	$G(x) = 1 - \exp[-(x/a)^b]$	0.987	0.058	0.5704	9.7671
		Probability density	$g(x) = \text{coeff. } (x/a)^{b-1} \times \exp[-(x/a)^b]$				