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HABITAT SELECTION MODELING FOR NORTHERN BOBWHITES ON SUBTROPICAL RANGELAND

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Abstract: Knowledge of habitat preference–avoidance behavior by a wildlife species provides a theoretical background for habitat management decisions. We studied habitat selection by northern bobwhites (*Colinus virginianus*) on subtropical rangeland in Texas during 1994–95 and developed a continuous selection function for describing preference–avoidance behavior. Our results validated use of canopy coverage by woody and herbaceous vegetation and exposure of bare ground in habitat modeling for bobwhites. Bobwhites were not sensitive to dry mass of herbaceous vegetation in the landscape we studied. The birds seemed sensitive to cover screening based on indices of exposure to ground and aerial predators. Continuous selection functions provide a means of prioritizing habitat management needs on an area. Managers should consider probability distributions of habitat features in space and time to develop sound habitat management programs.

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Key words: *Colinus virginianus*, habitat selection, northern bobwhite, selection modeling, Texas.

Knowledge of habitat properties that influence the occurrence of an animal in space and time provides a theoretical basis for habitat management decisions. Management may seek to alter habitat to which a target species is ill-adapted, and therefore avoids, and to foster habitat to which the species is well-adapted, and therefore prefers. A large literature exists on the theory of preference–avoidance analysis (Manly et al. 1993). However, application of preference–avoidance results in management decisions is less well developed.

Based on descriptive biology (Stoddard 1932, Rosene 1969) and species–habitat modeling (Schroeder 1985, Bidwell et al. 1991, Rice et al. 1993), several habitat features are considered diagnostic for assessing the quality of habitat for northern bobwhites (hereafter, bobwhite). These features include percent canopy coverage of woody and herbaceous vegetation, percent exposure of bare ground, and screening cover and height of vegetation, among others. Univariate habitat suitability models, which reflect known or presumed habitat quality for a specific value of a habitat feature, have been written for several variables (Schroeder 1985, Bidwell et al. 1991, Rice et al. 1993).

We developed a selection (preference–avoidance) function that may be considered a habitat suitability model, after scaling. This function can be used to assess utility of variables used in habitat modeling for bobwhites. We also introduce and test variables not previously used in habitat modeling for bobwhites. These variables include herbaceous dry mass and indices of exposure to ground and aerial predators. We dis-

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Table 1. Properties of study sites used for collection of data on habitat selection by northern bobwhites, southern Texas, 1994–95.

County Site	Size (ha)	Elevation (m)	Mean annual Precipitation (cm)[a]	Mean annual Temperature (C)
Duval				
Bomer	48	94	59.4	22.3
Private ranch	600	94	59.4	22.3
Kleberg				
TAMUK Farm	220	20	68.5	22.4
Jim Wells				
La Copita	1,103	62	72.0	22.4
San Patricio				
Welder	2,960	14	90.0	22.2
Brooks				
San Tomas	13,600	33	62.5	22.3

[a] Larkin and Bomar (1983).

cuss implications of the approach and results for inferences about landscapes. Finally, we present an approach for applying results of preference–avoidance studies in habitat management.

STUDY AREA AND METHODS

Field Sampling

Data were collected on 6 study sites in 5 counties of southern Texas (Table 1) during June 1994–August 1995. The sites are in a subtropical, subhumid region of Texas with level to slightly undulating topography. Soils range from deep sands to heavy clays. The sites supported a variety of habitat types including open prairie, old fields, low- to high-density mixed brush, and closed-canopy, live oak (*Quercus virginiana*) forest. Sites with a diversity of habitat types were selected so that bobwhites could exercise preference–avoidance behavior.

The sampling effort within study sites was proportional to the area of the site; sampling was distributed randomly in space (randomly chosen X-Y coordinates of sites) and systematically in time (days, seasons). This approach provided an unbiased image of available habitat features in space and time from which bobwhites were selecting in the total area sampled (18,531 ha; Table 1).

We collected data at 3 types of points: random, flushing, and landing. Flushing and landing points were centered at locations where groups of bobwhites flushed and landed. Two observers walked on study sites to flush groups, with location of searches governed by location of random points (i.e., on a search occasion, a randomly selected point served as the center of the search area and the search effort radiated outward from that point).

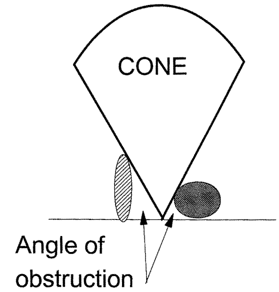

Fig. 1. Schematic representation of the cone of vulnerability, a volume of air space within which a raptor could attack a northern bobwhite with no obstruction in the line of flight. The bobwhite would occur at the point of the cone.

We considered a point to be centered within a patch (small area) of habitat. We collected subsamples at each point because of uncertainty over the exact point of flushing or landing (i.e., not knowing the precise point, we obtained data on average conditions near the point). For measurement purposes, each point was associated with 8 compass radii: north, northeast, east, southeast, south, southwest, west, and northwest. We estimated percent canopy coverage of woody plants with 4-m line intercepts (Canfield 1941) along the 8 radii. We defined visual obstruction distance (m) as the distance at which the 0–15-cm stratum on a 2.5-cm-diameter profile pole disappeared from view (100% visual obstruction) of a kneeling observer (height = 1 m). We recorded obstruction distance along the 8 radii, and we used the mean distance to estimate the area of a circle, defined as the disc of vulnerability, within which a bobwhite might be visible to a terrestrial predator. This stratum (0–15 cm aboveground) represents the average height of a bobwhite (Bidwell et al. 1991). Finally, we determined the visual obstruction angle along each of the 8 radii (Fig. 1). We used a 2-m profile pole to aim at the top of vegetation obstructions and a clinometer or compass laid on the pole to determine the angle. From the mean angle, we estimated a cone of vulnerability (Fig. 1), which we defined as a volume of air space within which a raptor would have an unobstructed line of flight to an exposed bobwhite. Beyer (1984:127–128) provided formulas for determining the volume of a right circular cone and cap of cone (spherical segment of 1 base). When estimating volume of the cone, we assumed bobwhites would be vulnerable within a radius of 100 m. The cone of vulnerability provided a general index of structural conditions associated with used and random points.

We used a 2- × 5-dm sampling frame (Daubenmire 1959) to sample properties of herbaceous cover at points. The frame was centered on the point and placed randomly (4 times) within a 2-m radius of the point to give 5 placements/point. At each placement, we estimated percent canopy coverage of herbaceous vegetation (Daubenmire 1959), percent exposure of bare ground, and aboveground biomass of herbaceous vegetation. Herbaceous vegetation was clipped, placed in paper bags, dried at 37.8°C for ≥3 days, and weighed to the nearest 0.1 g. Bare-ground exposure was determined after clipping as the percentage of the frame not occupied by the basal area of plants or by plant litter.

Statistical Analysis

We fit cumulative frequencies of habitat variables to parametric curves (logistic, Gompertz, confined exponential, Weibull) and to linear models. Cumulative frequencies were modeled to obtain probability density functions for random, flushing, and landing points (see below). The asymptote (K) for the logistic, Gompertz, confined exponential, and Weibull functions was set at $n + 2$, where n is sample size because visual inspection of cumulative frequencies indicated the asymptote was near n. Banks (1991) provided methods of estimating parameters for the asymptotic models. Parameters for linear models were estimated with standard least-squares procedures.

Because of the flexible nature of the cumulative frequency models, it was possible for >1 model to explain a significant ($P < 0.001$) portion of the variation in observed frequency distributions. We considered parsimony (no. of estimated parameters) and precision in selecting the models for further analysis (Burnham and Anderson 1992). The estimated number of parameters was 2 with all models. Therefore, the models used were equally parameterized under our assumption of known asymptote. We therefore used models with the highest r^2 value to describe frequency distributions.

For a given habitat feature and point type, cumulative frequency for used points was defined as $F(x)$, and that for random points as

Table 2. Sample size by data-pooling strata and point type for determining habitat selection models for northern bobwhites in southern Texas, 1994–95.

Stratum	Point type		
	Random	Flushing	Landing
Biological season[a]			
Pair–nest	132	105	49
Nest–brood	287	189	103
Covey	187	106	86
Time of day[b]			
Morning–evening	277	233	146
Midday	329	167	92

[a] Pair–nest = Mar–Jun; nest–brood = Jul–Sep; covey = Oct–Feb.
[b] Morning–evening = daylight–1100 and 1600–dusk; midday = 1100–1600.

$G(x)$. These distributions were differentiated and scaled to the probability density functions $f(x)$ and $g(x)$ (Mendenhall et al. 1990:145). We then calculated a continuous selection function (Guthery 1997), $u(x)$, as

$$u(x) = f(x)/g(x),\ g(x) > 0.$$

The continuous selection function may be interpreted in the same manner as the discrete selection ratio, defined as proportional use/proportional availability within an arbitrary class for the habitat feature (Manly et al. 1993): $u(x) < 1$ indicates avoidance, $u(x) = 1$ indicates use in proportion to availability, and $u(x) > 1$ indicates preference. Random use with respect to a habitat feature would manifest as $u(x) = 1$ for all x. We defined the domain of selection as the range of x values where $u(x) > 1$, and the domain of avoidance as the range where $u(x) < 1$. We used discrete theory (Manly et al. 1993:50–51) to test for significant preference–avoidance effects within 5 classes of use and availability for each habitat variable. Our experimental design had estimated proportional availability. We used equation 4.24 of Manly et al. (1993:50) to obtain simultaneous confidence intervals for discrete selection ratios.

We analyzed annually pooled data and data stratified by biological seasons and time-of-day (Table 2). For economy of presentation, we present results from annually pooled data in this paper. Kopp (1997) provides a complete set of models for habitat variables. All means are presented ± standard error.

RESULTS

We obtained data at 606 random points, 400 flushing points, and 238 landing points (Table 2). Sample size was smaller at landing than at

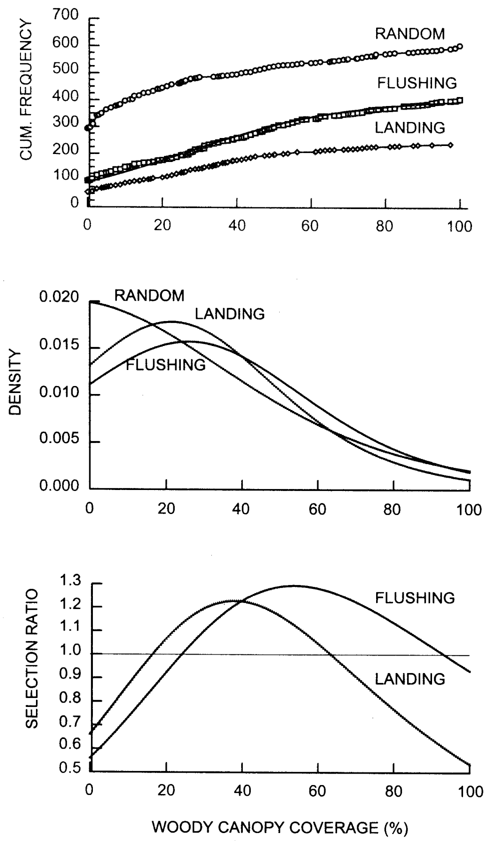

Fig. 2. Cumulative (cum.) frequency distributions (top) and probability density functions (center) for mean canopy coverage of woody vegetation at random points and at flushing and landing points used by northern bobwhites, and selection ratios based on the density functions (bottom), southern Texas, 1994–95. See Appendix A for descriptions of cumulative frequency and frequency models.

flushing points because it was not always possible to determine where groups landed after being flushed. Highly significant models for cumulative frequency ($r^2 > 0.92$, $P < 0.001$) were found for all habitat features, types of points, and data-pooling categories (Kopp 1997; Appendix A). Therefore, we make no further reference to P-values in the text. Appendix A gives cumulative frequency models, frequency models, and associated statistics for the variables discussed in this paper.

Before presenting further results, we offer these comments on continuous selection functions to assist readers in interpreting results. Percent canopy coverage of woody vegetation (Fig. 2) serves as the example. Readers may use the top figure to interpret how well our cumulative frequency models fit the observed cumulative frequency distributions. The top figure also shows the range for any variable encountered at flushing, landing, and random points. The middle figure shows the probability distributions (density curves) of variables at point types; the areas under these curves are 1.0. The selection function curves, $u(x)$, (bottom) represent the density curves for used points, $f(x)$, (for flush, land) divided by the density curve for random points, $g(x)$. Wherever the density curves of used and random points intersect, the selection function takes a value of 1.0, where use equals availability and $f(x) = g(x)$. The selection function curve is >1 (use greater than availability) if the density curve for used points exceeds the density curve for random points, $f(x) > g(x)$, and <1 (use less than availability) if the density curve for used points falls below the density curve for random points, $f(x) < g(x)$. The area under the random-point density curve where the used point density curves fall below the random point density curve represents the proportion of the space–time landscape avoided relative to a specific habitat feature. Reference to the discrete results (Table 3) provides a framework for drawing inferences based on the continuous selection functions.

Canopy Coverage of Woody Vegetation

Bobwhites selected patches with higher mean values for canopy coverage of woody vegetation than were randomly available in the landscape under study (Fig. 2). Mean coverage was 16.7 ± 1.10% at random points, 31.7 ± 1.97% at flushing points, and 26.6 ± 1.47% at landing points (see Table 2 for sample sizes). On an annual basis, the domain of selection appeared broader for flushing points (>25 to <90% canopy coverage) than for landing points (>15 to <65% canopy coverage). Analysis of the classified data indicated significant avoidance for patches with <20% canopy coverage of woody vegetation, preference for patches with 20–60% canopy coverage, and random use for patches with >60% canopy coverage (Table 3).

Disc of Vulnerability

The continuous selection function declined rapidly as the disc of vulnerability (m^2) increased linearly from 0 m^2 for annually pooled data (Fig. 3). The domain of selection was approximately 0–425 m^2; the domain of avoidance was >425 m^2. These results were strongly supported with the classified data because

Table 3. Discrete analysis of preference–avoidance behavior for comparisons with continuous selection functions (Figs. 2–7) for northern bobwhites in southern Texas, 1994–95. Avoidance (−) is indicated when the upper 95% confidence limit (UCL) on the selection ratio is <1, preference (+) is indicated when the lower 95% confidence limit (LCL) is >1, and neither preference nor avoidance (o) is indicated when the upper and lower limits contain 1. The selection ratio is estimated as proportional use (u_i) divided by proportional availability (a_i).

Habitat variable		Flush				Land			
Class	a_i	u_i	LCL	UCL	Use	u_i	LCL	UCL	Use
Canopy coverage of woody vegetation (%)									
0–20	0.72	0.44	0.53	0.70	−	0.49	0.58	0.76	−
>20–40	0.13	0.23	1.14	2.60	+	0.25	1.23	2.77	+
>40–60	0.08	0.18	1.14	3.35	+	0.16	1.02	3.05	+
>60–80	0.05	0.10	0.72	3.48	o	0.07	0.47	2.58	o
>80–100	0.02	0.05	0.12	3.55	o	0.03	0.00	2.40	o
Disc of vulnerability (m²)									
0–500	0.55	0.70	1.11	1.44	+	0.73	1.16	1.49	+
>500–1,000	0.25	0.20	0.52	1.02	o	0.19	0.51	0.99	−
>1,000–1,500	0.12	0.07	0.26	0.91	−	0.06	0.19	0.78	−
>1,500–2,000	0.06	0.03	0.03	0.85	−	0.02	0.00	0.69	−
>2,000	0.02	0.00	0.17	0.94	−	0.00	0.00	0.64	−
Cone of vulnerability ($m^3 \times 10^{-3}$)									
0–400	0.24	0.58	1.91	2.97	+	0.48	1.55	2.48	+
>400–800	0.28	0.21	0.52	0.96	−	0.29	0.76	1.29	o
>800–1,200	0.28	0.13	0.28	0.63	−	0.16	0.37	0.76	−
>1,200–1,600	0.15	0.06	0.17	0.63	−	0.06	0.16	0.60	−
>1,600	0.05	0.02	0.03	0.86	−	0.01	0.02	0.65	−
Canopy coverage of herbaceous vegetation (%)									
0–20	0.28	0.52	1.47	2.26	+	0.55	1.54	2.54	+
>20–40	0.33	0.10	0.18	0.43	−	0.10	0.13	0.44	−
>40–60	0.26	0.11	0.27	0.62	−	0.11	0.20	0.63	−
>60–80	0.10	0.13	0.67	1.82	o	0.12	0.51	1.80	o
>80–100	0.03	0.14	1.50	8.08	+	0.12	1.11	7.71	+
Dry mass of herbaceous vegetation (kg/ha)									
0–500	0.38	0.42	0.89	1.34	o	0.44	0.89	1.44	o
>500–1,000	0.35	0.35	0.77	1.23	o	0.33	0.67	1.19	o
>1,000–1,500	0.18	0.16	0.54	1.20	o	0.16	0.47	1.27	o
>1,500–2,000	0.07	0.05	0.25	1.28	o	0.06	0.19	1.52	o
>2,000	0.02	0.02	0.14	1.48	o	0.01	0.30	1.96	o
Exposure of bare ground (%)									
0–20	0.17	0.13	0.45	1.07	o	0.17	0.56	1.43	o
>20–40	0.20	0.23	0.78	1.51	o	0.15	0.41	1.08	o
>40–60	0.21	0.33	1.14	2.00	+	0.26	0.81	1.67	o
>60–80	0.21	0.16	0.49	1.03	o	0.21	0.62	1.38	o
>80–100	0.21	0.15	0.45	0.97	−	0.21	0.62	1.38	o

bobwhites exhibited preferences for discs <500 m² and avoidance for larger discs, except for random use of discs between 500 and 1,000 m² at flushing points (Table 3). For annually pooled data, the mean discs were 522.8 ± 44.1 m² (flushing), 472.9 ± 56.7 m² (landing), and 791.5 ± 55.3 m² (random). These latter results indicate a bobwhite would disappear from human view at an average radius of 12–13 m at used points and a radius of 16 m at random points.

Cone of Vulnerability

When we assumed a level land surface, bobwhites were potentially vulnerable to attack from 2,094,395 m³ of air space. This number is the volume of a hemisphere with radius of 100 m, which represents a situation with no vegetation cover. The mean cone of vulnerability at random sites was 852,911 ± 21,443 m³, whereas annually pooled data for cones averaged 455,700 ± 25,847 m³ at flushing points and 500,380 ± 28,756 m³ at landing points. Thus,

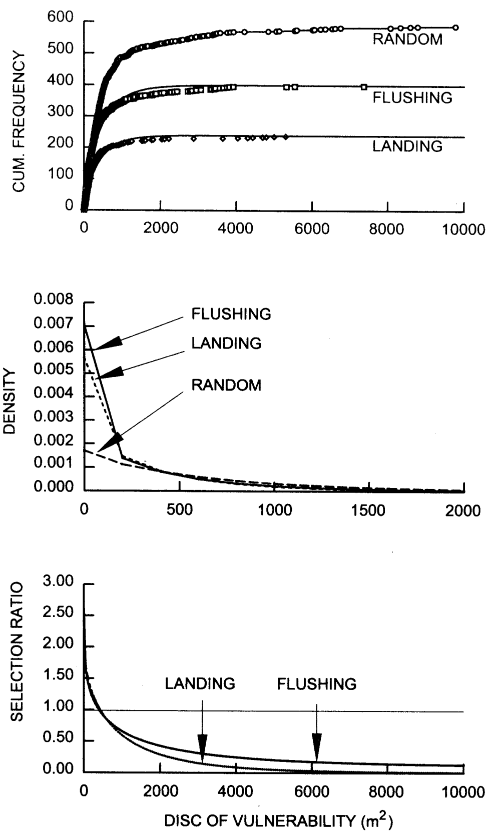

Fig. 3. Cumulative (cum.) frequency distributions (top) and probability density functions (center) for the disc of vulnerability at random points and at flushing and landing points used by northern bobwhites, and selection ratios based on the density functions (bottom), southern Texas, 1994–95. See Appendix A for descriptions of cumulative frequency and frequency models.

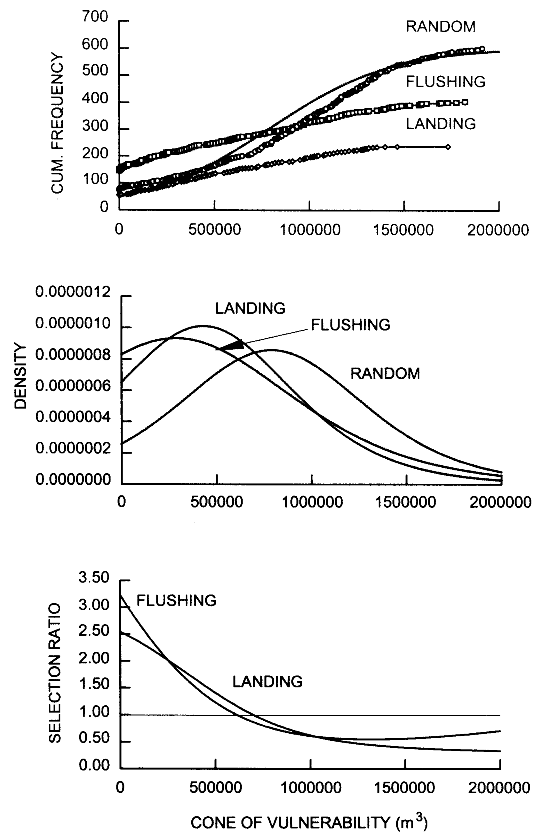

Fig. 4. Cumulative (cum.) frequency distributions (top) and probability density functions (center) for the cone of vulnerability at random points and at flushing and landing points used by northern bobwhites, and selection ratios based on the density functions (bottom), southern Texas, 1994–95. See Appendix A for descriptions of cumulative frequency and frequency models.

on average, bobwhites were vulnerable within 21.8% of air space at flushing points and 23.9% at landing points. Bobwhites exhibited maximum selection for points with total overhead cover (cone = 0 m^3; Fig. 4), and the domain of selection ranged between 0 and 500,000–750,000 m^3. Analysis of the classified data revealed selection for cones <400,000 m^3 and, in general, avoidance of habitat patches with larger cones of vulnerability (Table 3).

Canopy Coverage of Herbaceous Vegetation

The mean canopy coverage of herbaceous vegetation was similar at flushing points (29.4 ± 1.04%), landing points (32.2 ± 1.46%), and random points (34.5 ± 0.98%). Selection occurred within the domain 0 to <35% (Fig. 5). Analysis of the classified data revealed a preference for low canopy coverage values (<20%), avoidance or null use of moderate values (>20–80%), and preference for higher values (>80%; Table 3). The continuous selection-function models detected increasing preference at higher coverage values, especially at landing points (Fig. 5).

Biomass of Herbaceous Vegetation

The probability distributions for herbaceous biomass were qualitatively similar for annually pooled data at flushing, landing, and random points, which resulted in selection functions that remained near 1.0 as biomass varied from 0 to 2,500 kg/ha (Fig. 6). The mean values for pooled data were 744.3 ± 24.99 at flushing points, 773.1 ± 52.60 at landing points, and 932.8 ± 39.71 at random points. Likewise, analysis of the classified data revealed neither selec-

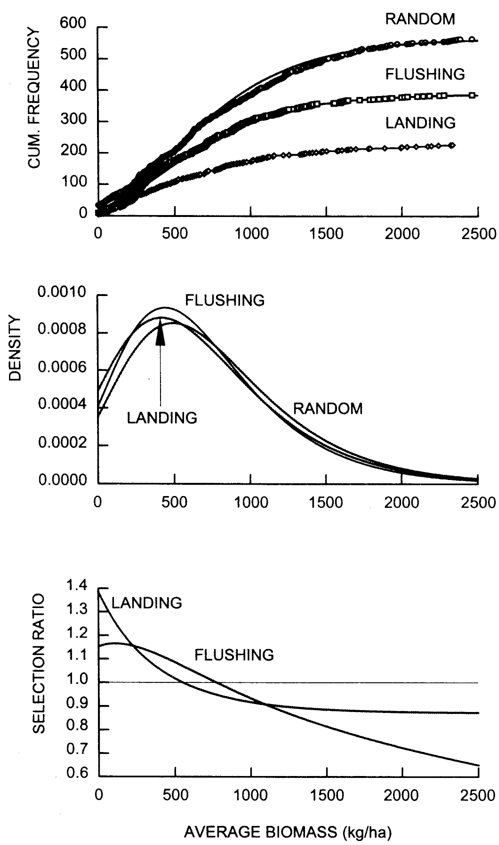

Fig. 5. Cumulative (cum.) frequency distributions (top) and probability density functions (center) for mean canopy coverage of herbaceous vegetation at random points and at flushing and landing points used by northern bobwhites, and selection ratios based on the density functions (bottom), southern Texas, 1994–95. See Appendix A for descriptions of cumulative frequency and frequency models.

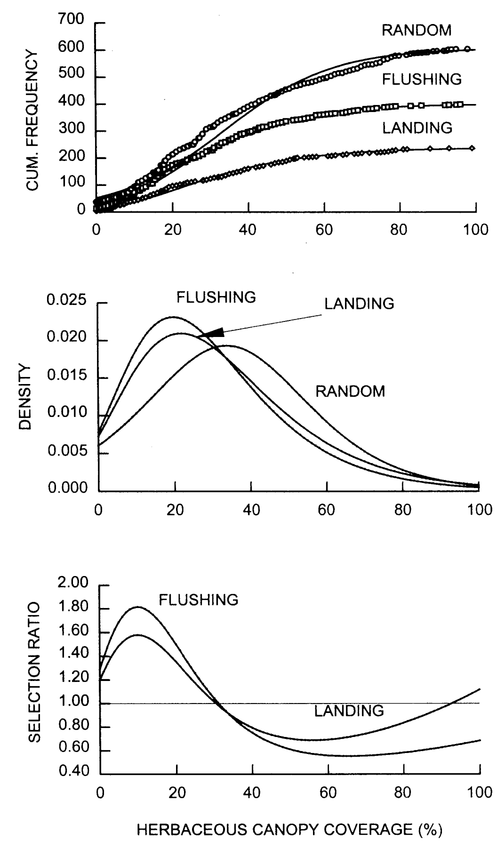

Fig. 6. Cumulative (cum.) frequency distributions (top) and probability density functions (center) for mean dry mass of herbaceous vegetation at random points and at flushing and landing points used by northern bobwhites, and selection ratios based on the density functions (bottom), southern Texas, 1994–95. See Appendix A for descriptions of cumulative frequency and frequency models.

tion nor avoidance of herbaceous biomass classes within random and used patches (Table 3).

Exposure of Bare Ground

Mean exposure of bare ground was 48.7 ± 1.20% at flushing points, 50.7 ± 1.63% at landing points, and 51.3 ± 1.13% at random points. These similarities suggested weak selection for this habitat feature in the landscape under study, which held true for landing points (Fig. 7). Cumulative frequencies fit linear models for landing and random points, which suggests bare-ground exposure was uniformly distributed in space and time. For annually pooled data, there was evidence of selection at flushing points in the domain >10–<60% bare-ground exposure. Analysis of classified data suggested selection for patches with >40–60% exposure of bare ground and avoidance of patches with >80% exposure at flushing points.

DISCUSSION

The selection functions we developed (Figs. 2–7) represent quantitative images of bobwhite selection for habitat features in the landscape we studied. Although sample size was 606 for the random background, this number is small in the context of space and time (infinitely many points available). The tails of the selection models (especially the right tail) are subject to greater uncertainty than the central portions. Hence, the models may behave irrationally in the tails because of the small values that density functions may take in the tails, potentially resulting in divisors near zero and selection ratios near infinity. Research indicates bobwhites select for

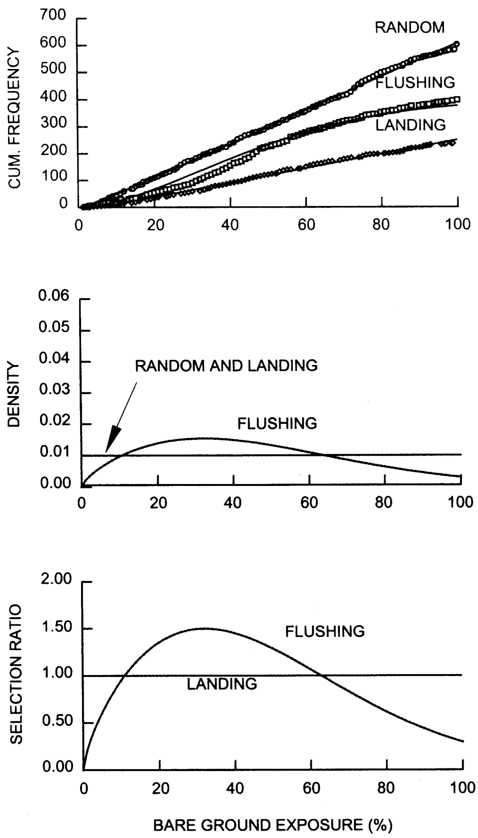

Fig. 7. Cumulative (cum.) frequency distributions (top) and probability density functions (center) for mean exposure of bare ground at random points and at flushing and landing points used by northern bobwhites, and selection ratios based on the density functions (bottom), southern Texas, 1994–95. See Appendix A for descriptions of cumulative frequency and frequency models.

habitat features within their home range at a patch (8-m radius) scale (Kuvlesky 1990), but the precise radius over which bobwhites evaluate habitat and make use decisions remains unknown. The scale of our habitat measurements at patches represents an assumption.

Nevertheless, continuous selection functions provide a useful adjunct to discrete selection modeling. For example, analysis of discrete data suggested avoidance of habitat patches with >20–40% canopy coverage of herbaceous vegetation (Table 3). The selection function revealed ambivalent behavior within this class, with evidence of selection at values slightly >20% and avoidance at values near 40% (Fig. 6). The continuous models have the advantage that discrete classes (a human decision) need not be specified. However, the selection functions lack a rigorous inferential basis at this time. Refinement of selection function analysis will require development of variance estimators and confidence bands, and investigation of the robustness of models used for density functions.

Selection Behavior

The domain of selection for any habitat feature depends upon adaptations of the species under study and probability distributions of available habitat features in a landscape; this statement holds for discrete and continuous selection models. Therefore, there is some danger in generalizing the results of 1 preference–avoidance study to other situations, because probability distributions of available features differ among areas. Variable probability distributions may lead to area-specific functions and domains of selection.

Given the preceding admonition, bobwhites on our study sites exhibited rather large domains of selection for canopy coverage of woody plants, the cone of vulnerability, canopy coverage of herbaceous plants, and exposure of bare ground. For these variables, selection occurred within ≥25% of the available domain. These results are open to 4 interpretations: (1) bobwhites were weakly sensitive to these features from an adaptive standpoint; (2) the probability distributions of available features tended toward the ideal distribution for bobwhites on our study sites, in which case use relative to a habitat feature could appear random despite adaptive importance of the feature; (3) broad domains for these features are compatible with the adaptations of bobwhites; or (4) some combination of the above. The original geographic range of northern bobwhites spans latitudes from Guatemala to Michigan and longitudes from Colorado to Virginia (Johnsgard 1973: 413). Flora, fauna, and climate vary hugely among areas within this geographic region. Thus, whereas features such as woody plants and bare ground may be essential components of habitat in most environments, bobwhites may have great flexibility in finding acceptable values for these features within a landscape.

Generally, bobwhites exhibited similar preference–avoidance behavior for properties of habitat patches at flushing and landing points (Figs. 2–7, Table 3). The major exception was for exposure of bare ground (selection behavior exhibited only at flushing points; Table 3). This contrasting behavior could have arisen because

Table 4. Hypothetical properties of ideal landscapes for northern bobwhites, based on inferences from habitat selection modeling, southern Texas, 1994–95.

Habitat feature	$\bar{x}$	SD	Domain	Proportional frequency by class[a] 1	2	3	4	5
Canopy coverage of woody vegetation (%)	53	26.6	0–100	0.14	0.21	0.24	0.23	0.18
Disc of vulnerability (m^2)	1,170	1,033.8	0–10,000	0.80	0.18	0.02	0.00	0.00
Cone of vulnerability ($m^3 \times 10^{-3}$)	691	594.1	0–2,000	0.44	0.21	0.12	0.11	0.12
Canopy coverage of herbaceous vegetation (%)	38	29.3	0–100	0.37	0.23	0.14	0.12	0.14
Dry mass of herbaceous vegetation (kg/ha)	1,117	715.1	0–2,500	0.25	0.23	0.19	0.17	0.16
Exposure of bare ground (%)	44	23.8	0–100	0.19	0.30	0.26	0.17	0.08

[a] Classes represent 20% of the domain with equal spacing. For example, Class 1 for woody coverage represents 0–20% coverage, Class 2 represents >20–40% coverage, and so on.

flushing points are associated with more time for the perception–decision–use process, whereas the process must be completed in an average of 5.1 ± 0.2 sec at landing points, which represents the average duration of a flight (Kassinis and Guthery 1996). Also, flushing points are associated with more behaviors (forage, loaf, dust, roost) than landing points (escape), potentially leading to more variable habitat selection at flushing than at landing points. Selection at flushing and landing points was similar for the visibility variables (cone and disc of vulnerability), despite differences in selection for variables that contribute to the cone and disc. This latter outcome indicates vegetation structure is similar at flushing and landing points, and that escape cover is contained within the cover preferred for other activities.

Inferences About Landscapes

A set of selection ratios (u_i/a_i) provides an unscaled image of how an animal would occupy space and time in a hypothetical landscape with a complete set of habitat classes equally available for each decision on habitat use (Manly et al. 1993:41) By analogy, a selection function, $u(x)$, provides an image of space and time occupation if a complete set of values of a habitat feature is equally available at each decision instant. One may extract properties of used habitat from the hypothetical landscape and obtain information, perhaps qualitative, about an ideal landscape (i.e., a landscape that would in theory permit more or less random use of space and time because the probability distribution for available features exactly matches the probability distribution for use through time). The process involves taking $u(x)$ as an image of the probability distribution of features in an ideal landscape. The image may be converted to a probability density function via numerical techniques, and properties of the ideal landscape (mean, variance) may be determined according to standard statistical theory (Mendenhall et al. 1990:152–153).

Our results indicate the ideal landscape would exhibit high relative variability (CVs ≥50%) in the variables we modeled (Table 4). This result is expected because the bobwhite is broadly adapted, as discussed earlier, and because it uses patches with different properties for daily and seasonal activities. The expected values (means) for percent canopy coverage of herbaceous plants and woody plants and percent exposure of bare ground fell within the optimum range in Schroeder's (1985) habitat suitability models. The ideal landscape, as modeled, had substantially higher canopy coverage of woody vegetation than Rice et al. (1993) considered optimum (5–15% coverage at the landscape level). The Schroeder (1985) model permitted 8–80% woody canopy cover in optimum landscapes, a range compatible with our landscape inferences. Although the disc of vulnerability was associated with high variability in the ideal landscape, an estimated 80% of the landscape would have discs <2,000 m^2 (Table 3; i.e., cover preferred by bobwhites seems associated with a high level of visual obstruction in space and time).

The above discussion of ideal landscapes based on habitat structure in space and time cannot be divorced from the question of fitness (e.g., Van Horne [1983] argued that rates of survival and reproduction are valid general measures of habitat quality). Guthery (1997) showed that populations of bobwhites exhibit similar mean demographics wherever populations persist. He argued that populations have maximum opportunity to express their demographic potential when landscapes provide the opportunity for unconstrained use of space through time. The question of fitness is therefore embodied in our discussion of ideal landscapes because the modeled landscapes would, in theory, permit random use of space and time.

MANAGEMENT IMPLICATIONS

Our approach to selection modeling provides a process for prioritizing habitat management needs, given a need for habitat management. The probability distributions for random and used points in space and time (Figs. 2–7) provide information on the proportion of a landscape that is avoided. Presumably, the greater the proportion of a landscape avoided because of some habitat feature, the greater the need to redress this problem through habitat management, thereby maximizing functional space–time and demographic potential of a population (Guthery 1997). For example, in the landscape we studied, a higher proportion of locations were avoided because of insufficient screening cover at ground level (disc of vulnerability) than because of any other feature measured. This deficiency seemed tied primarily to deficiencies in woody canopy because bobwhites were not especially sensitive to herbaceous dry mass, and they seemed to prefer screening cover provided by brush over that provided by herbaceous plants.

Finally, management will benefit by thinking not only of the mean properties of habitat in patches and landscapes, but also of the probability distributions of these properties relative to the needs of bobwhites. The probability distributions of habitat features in a space–time landscape address habitat interspersion. Landscapes are 4-dimensional (length, width, height, time) relative to the needs of bobwhites and other species. For example, consider an inferior landscape with 2 blocks of habitat. One block has 100% canopy coverage of woody vegetation for all time, whereas the other block has 0% coverage. This configuration would lead to mean coverage of 50%, which is theoretically acceptable for bobwhites (Schroeder 1985). Sampling the hypothetical landscape through space and time would reveal a binomial probability distribution with $P(100\%\ \text{coverage}) = P(0\%\ \text{coverage}) = 0.5$, whereas the ideal probability distribution would be shaped similarly to the woody coverage models shown in Figure 2. The hypothetical probability distributions we obtained (proportional frequencies; Table 4) may serve as frames of reference for existing landscapes and as hypotheses for further testing. Researchers may calculate probabilities for different habitat class sizes from models in Appendix A (e.g., 10% coverage intervals for woody vegetation).

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APPENDIX A. CUMULATIVE FREQUENCY (*F*) AND FREQUENCY DISTRIBUTIONS (*f*) FOR HABITAT VARIABLES AT RANDOM POINTS AND AT FLUSHING AND LANDING POINTS USED BY NORTHERN BOBWHITES IN SOUTHERN TEXAS, 1994–95. ALL MODELS EXPLAINED A SIGNIFICANT ($P < 0.001$) PROPORTION OF THE VARIATION IN CUMULATIVE FREQUENCY. SAMPLE SIZE FOR CUMULATIVE FREQUENCY MAY BE LESS THAN SAMPLE SIZE FOR OBSERVATIONS (TABLE 2), BECAUSE OF REPEATED OBSERVATIONS AT A PARTICULAR *x* VALUE

Canopy Coverage of Woody Vegetation (%)

Random ($n = 93$, $r^2 = 0.9367$)

$$F = 1/[1 + 0.832\exp(-0.0344x)]$$

$$f = 0.0804F(1 - F)$$

Domain: 0–100

Flushing ($n = 104$, $r^2 = 0.9649$)

$$F = 1/[1 + 3.349\exp(-0.0465x)]$$

$$f = 0.0629F(1 - F)$$

Domain: 0–100

Landing ($n = 75$, $r^2 = 0.9909$)

$$F = 1/[1 + 3.092\exp(-0.0528x)]$$

$$f = 0.0713F(1 - F)$$

Domain: 0–99

Disc of Vulnerability (m^2)

Random ($n = 518$, $r^2 = 0.9246$)

$$F = 1 - \exp[-(x/654.827)^{0.9892}]$$

$$f = 0.0015(x/654.827)^{-0.0108} \times \exp[-(x/654.827)^{0.9892}]$$

Domain: 1.5–9,777.4

Flushing ($n = 365$, $r^2 = 0.9455$)

$$F = 1 - \exp[-(x/412.41)^{0.8879}]$$

$$f = 0.0021(x/412.41)^{-0.1121} \times \exp[-(x/412.41)^{0.8879}]$$

Domain: 3.1–7,363.2

Landing ($n = 216$, $r^2 = 0.9301$)

$$F = 1 - \exp[-(x/378.73)^{0.9195}]$$

$$f = 0.0024(x/378.3)^{-0.0805} \times \exp[-(x/378.73)^{0.9195}]$$

Domain: 1.1–5,303.6

Cone of Vulnerability (m^3)

Random ($n = 198$, $r^2 = 0.9499$)

$$F = 1/[1 + 11.302\exp(-0.000003073x)]$$

$$f = 0.000003433F(1 - F)$$

Domain: 0–1,971,095

Flushing ($n = 139$, $r^2 = 0.9470$)

$$F = 1/[1 + 2.003\exp(-0.000002432x)]$$

$$f = 0.000003731F(1 - F)$$

Domain: 0–1,821,020

Landing ($n = 101$, $r^2 = 0.9629$)

$$F = 1/[1 + 3.949\exp(-0.000003197x)]$$

$$f = 0.000004039F(1 - F)$$

Domain: 0–1,730,706

Canopy Coverage of Herbaceous Vegetation (%)

Random ($n = 127$, $r^2 = 0.9752$)

$$F = 1/[1 + 10.696\exp(-0.0699x)]$$

$$f = 0.0764F(1 - F)$$

Domain: 0–98

Flushing ($n = 119$, $r^2 = 0.9931$)

$$F = \exp[-3.275\exp(-0.0599x)]$$

$$f = 0.0628F[-\ln(F)]$$

Domain: 0–96

Landing ($n = 94$, $r^2 = 0.9848$)

$F = \exp[-3.237 \exp(-0.0539x)]$

$f = 0.0570F[-\ln(F)]$

Domain: 0–99

Dry Mass of Herbaceous Vegetation (kg/ha)

Random (n = 398, r^2 = 0.9865)

$F = \exp[-2.973 \exp(-0.0022x)]$

$f = 0.0023F[-\ln(F)]$

Domain: 0–8,180

Flushing (n = 297, r^2 = 0.9949)

$F = \exp[-2.896 \exp(-0.0024x)]$

$f = 0.0025F[-\ln(F)]$

Domain: 0–6,722

Landing (n = 190, r^2 = 0.9860)

$F = \exp[-2.509 \exp(-0.0022x)]$

$f = 0.0024F[-\ln(F)]$

Domain: 0–7,508

Exposure of Bare Ground (%)

Random (n = 127, r^2 = 0.9990)

$F = 0.01x$

$f = 0.01$

Domain: 1–100

Flushing (n = 121, r^2 = 0.9807)

$F = 1 - \exp[-(x/54.241)^{1.6982}]$

$f = 0.0313(x/54.241)^{0.6982} \times \exp[-(x/54.241)^{1.6982}]$

Domain: 2–100

Landing (n = 101, r^2 = 0.9954)

$F = 0.01x$

$f = 0.01$

Domain: 3–99

ASSESSING THE SUITABILITY OF LANDSCAPES FOR NORTHERN BOBWHITE

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Abstract: Widespread declines of northern bobwhite (*Colinus virginianus*) populations may reflect habitat alteration at both site and landscape level. To investigate the latter, we quantified landscape composition and pattern throughout Illinois (>145,900 km^2) using classified satellite imagery and FRAGSTATS software. We then compared landscape structure with indexes of northern bobwhite abundance using county-level harvest and North American Breeding Bird Survey (BBS) data. Analyses at both scales suggested bobwhite were primarily associated with diverse, patchy landscapes that contained moderate amounts of grassland and row crops and abundant woody edge. These findings were used to develop a PATREC model to identify and map Illinois landscapes potentially suitable for bobwhite. Whether or not such areas actually support good bobwhite populations depends upon site conditions generally not discernable by remote sensing. Nevertheless, knowledge of the extent and distribution of potentially suitable landscapes can enhance and focus management efforts.

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Key words: *Colinus virginianus,* habitat modeling, Illinois, landscape, northern bobwhite, PATREC, remote sensing, satellite imagery.

Northern bobwhite (hereafter, bobwhite) are mainly found in diverse, patchy, predominantly open landscapes with abundant woody edge (Rosene 1969, Roseberry and Klimstra 1984). At a finer scale, they require a variety of successional stages (Ellis et al. 1969) and types of vegetative structure (Burger et al. 1990). However, changing agricultural and silvicultural practices over the past 30+ years have altered both macro- and microhabitat conditions, resulting in range-wide declines of bobwhite populations (Klimstra 1982, Brennan 1991). To address this problem, effective management and planning will require the ability to inventory, analyze, and interpret habitat at various spatial

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