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# COMPARATIVE HABITAT ECOLOGY OF TEXAS AND MASKED BOBWHITES

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**Abstract:** The habitat ecology of masked bobwhites (*Colinus virginianus ridgwayi*) is poorly understood, which hampers recovery efforts for this endangered bird. During 1994–96, we analyzed the habitat ecology of masked bobwhites in Sonora, Mexico, and Arizona, and compared these findings with the habitat ecology of Texas bobwhites (*C. v. texanus*) in southern Texas. Mean values for the quantity of low screening cover (<50 cm aboveground), operative temperature (°C), and exposure to aerial predators were relatively constant across regions (CV <14.2%), indicating these variables are important in adaptive habitat-use decisions by bobwhites. Bobwhites exhibited preference in all regions for higher canopy coverage of woody vegetation, lower exposure to aerial predators, and lower operative temperatures in comparison with randomly available conditions. The major habitat deficiencies for masked bobwhites were lack of woody and herbaceous cover, which led to high exposure to aerial predators in Sonora and Arizona. High operative temperatures at quail level were associated with the loss of ≥24% of potential habitat space–time in Texas, Sonora, and Arizona. Management to improve habitat for masked bobwhites includes any practice that increases canopy coverage of woody vegetation, and height and coverage of herbaceous vegetation.

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**Key words:** Arizona, *Colinus virginianus*, endangered species, habitat, masked bobwhite, Mexico, northern bobwhite, operative temperature, Sonora, Texas.

Masked bobwhites and Texas bobwhites are subspecies of the northern bobwhite (Johnsgard 1973:409). Whereas Texas bobwhites are numerically secure in southern Texas and northern Mexico, the masked bobwhite was classified as endangered in 1969 (U.S. Fish and Wildlife Service 1995). Masked bobwhites persist today as native populations on a few ranches in Sonora, Mexico, and as a reintroduced population on Buenos Aires National Wildlife Refuge, Arizona (Kuvlesky et al. 1999).

A paucity of information on the habitat ecology of masked bobwhites and on habitat management priorities has hampered recovery efforts (Kuvlesky et al. 1999). While there is substantial information on the management of Texas bobwhites, which occur in semiarid

environments physiognomically similar to areas inhabited by masked bobwhites, the applicability of this information for management of masked bobwhites remains speculative.

We undertook a field study to determine the habitat ecology of masked bobwhites. Our objectives were to (1) provide descriptive data on the properties of habitat patches used by masked bobwhites in Sonora and Arizona, (2) analyze preference–avoidance behavior associated with habitat features in patches, and (3) compare these outcomes with Texas bobwhites. The third objective was executed to determine whether and to what degree information on Texas bobwhites could be applied in the management of masked bobwhites. We also prioritized habitat deficiencies based on the results of habitat selection modeling.

## STUDY AREAS

Study areas were in regions similar with respect to general climate (semiarid, subtropical with high summer temperatures), the occurrence of peak precipitation during the growing

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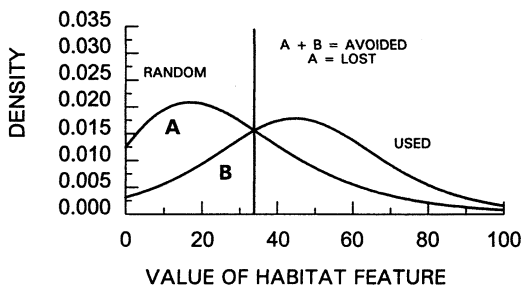


Fig. 1. Probability density (density) functions for used (bobwhite occurrence) and random points for a hypothetical habitat feature sampled in space through time. The areas A and B are used to estimate the proportion of random space-time that is avoided ( $A + B$ ) and the proportion that is lost (A).

season (a month earlier in Texas than in Sonora and Arizona), and vegetation physiognomy (mesquite [*Prosopis* spp.] rangeland with variable degrees of shrub encroachment). The

study areas differed primarily in land use (cattle grazing in Texas and Sonora, no grazing in Arizona) and quantity of annual precipitation (Texas total 1.5–2 times that of Sonora and Arizona). Because of higher elevations (<1,400 m) on the Arizona area, winter temperatures were colder and growing seasons shorter than in the Texas and Sonora areas.

### Texas Bobwhite Sites

The southern Texas study area consisted of 6 sites totaling 18,531 ha in 5 counties (Duval, Kleberg, Jim Wells, San Patricio, and Brooks). The sites had a diversity of vegetation types on sandy to clayey soils. Vegetation types included open prairie, old fields, low- to high-density mixed brush, and closed-canopy live oak (*Quercus virginiana*) forest. Annual precipitation ranged between 66 and 81 cm, depending on

Table 1. Properties of habitat at used and random points for bobwhites in Texas, Sonora, and Arizona, 1994–96.

Variable, class, and point type	Texas			Sonora			Arizona		
	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE
Canopy coverage of woody vegetation (%)									
Used	405	31.3	1.5	379	17.0	0.6	152	17.5	1.3
Random	606	16.7	1.1	416	10.3	0.6	201	12.7	1.0
Visual obstruction (%)									
of vertical strata (cm)									
0–15									
Used	400	53.4	1.5	379	68.8	1.1	155	58.1	1.8
Random	606	35.9	1.1	416	30.3	1.5	204	42.9	2.1
>15–50									
Used	400	40.8	1.4	379	44.1	1.1	155	33.2	1.7
Random	606	20.5	0.9	416	16.5	0.8	204	20.4	1.4
>50–100									
Used	400	32.7	1.4	379	29.6	1.5	155	16.1	1.4
Random	606	12.3	0.8	416	9.2	0.5	204	7.3	0.9
>100–200									
Used	400	27.5	1.4	379	24.7	1.3	155	12.9	1.3
Random	606	8.7	0.7	416	6.7	0.3	204	5.3	0.9
Disc of vulnerability ( $\text{m}^2 \times 10^{-1}$ )									
Used	398	52.3	4.4	379	38.8	5.1	154	74.9	16.0
Random	589	79.2	5.5	416	256.2	19.6	203	77.8	8.4
Cone of vulnerability ( $\text{m}^3 \times 10^{-4}$ )									
Used	405	45.6	2.6	317	49.3	2.7	153	52.6	3.4
Random	606	85.3	2.1	411	132.5	2.8	204	88.8	2.8
Exposure of bare ground (%)									
Used	400	48.7	1.2	379	16.0	0.8	153	10.4	0.7
Random	606	51.1	1.1	416	27.9	1.1	198	14.1	1.1
Canopy coverage of herbaceous vegetation (%)									
Used	400	29.4	1.0	379	46.0	1.3	154	24.7	1.4
Random	606	34.5	1.0	416	27.4	1.1	187	26.5	1.6
Dry mass of herbaceous vegetation ( $\text{kg/ha} \times 10^{-1}$ )									
Used	397	74.4	3.5	371	47.8	1.6	75	141.3	13.5
Random	596	93.2	4.0	410	29.5	2.0	133	115.9	11.0
Operative temperature ( $^{\circ}\text{C}$ )									
Used	405	30.1	0.3	289	25.6	0.5	142	24.1	0.8
Random	606	33.0	0.3	416	32.2	0.5	203	30.2	0.6

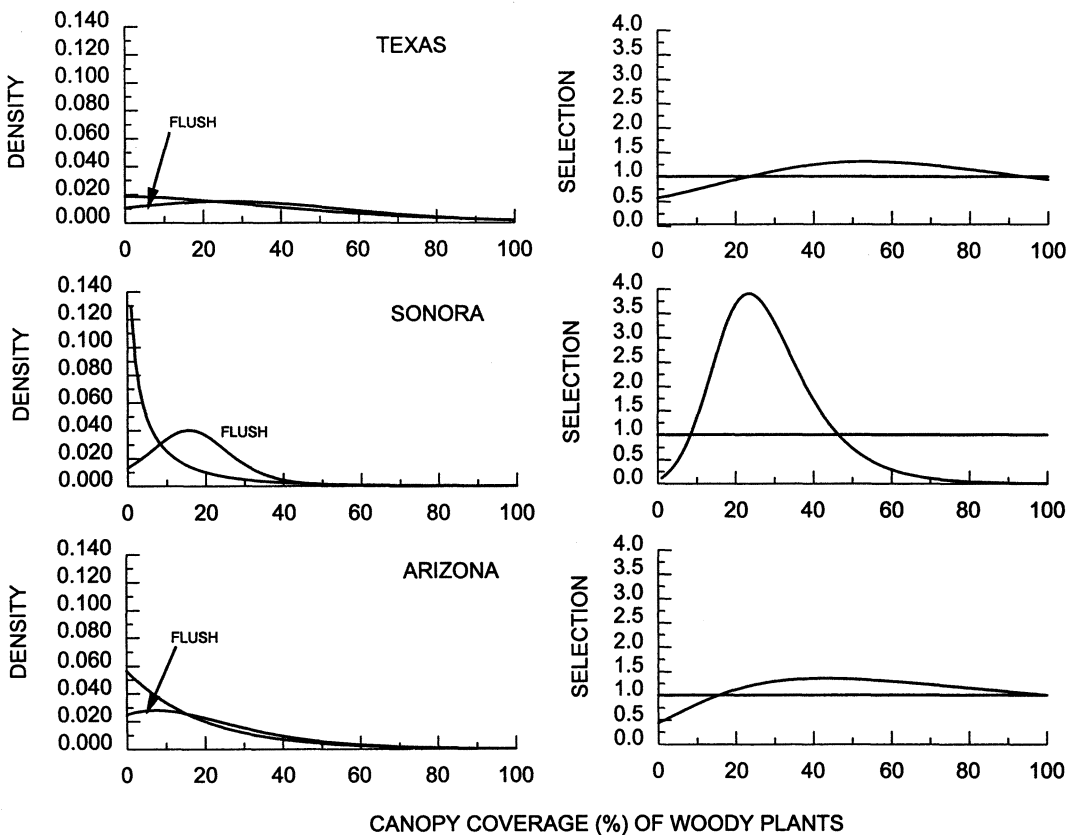


Fig. 2. Probability density (density) functions (left) and selection functions (right) for canopy coverage of woody vegetation at used (flush) and random points for bobwhites in Texas, Sonora, and Arizona, 1994–96. Models for the cumulative distributions, from which density functions were derived, were significant ( $P < 0.001$ ) for Texas (used  $r^2 = 0.96$ , random  $r^2 = 0.94$ ), Sonora (used  $r^2 = 0.99$ , random  $r^2 = 0.98$ ), and Arizona (used  $r^2 = 0.99$ , random  $r^2 = 0.99$ ). Selection is indicated when the selection function is  $>1$  (horizontal line on right); avoidance is indicated when the selection function is  $<1$ .

location. Peak monthly totals occur in May or June (Gould 1975). Average annual temperature is 22–23°C.

### Masked Bobwhite Sites

Sampling in Sonora took place on Rancho El Carrizo, located about 100 km north of Hermosillo. El Carrizo is a private cattle ranch of about 32,000 ha. Soils were sands, sandy loams, and gravels with a sandy loam or loam base on those portions of the ranch occupied by masked bobwhites. The vegetation is classified as subtropical, summer-active savanna grassland within dry-tropic scrub (U.S. Fish and Wildlife Service 1995). Long-term records (1956–94) maintained on Rancho El Carrizo indicate average annual rainfall of 37.1 cm (Camou et al. 1998). About 54% of average annual rainfall occurs during July and August. Temperatures near the study area average 34°C and typically exceed

40°C during June–August (Martin et al. 1995). Typical temperatures are about 8°C at night during winter.

Buenos Aires National Wildlife Refuge, located 97 km southwest of Tucson, was the study area in Arizona. Buenos Aires consists of 48,000 ha with loamy and rocky soils. These soils support semidesert grassland with remnants of Sonora savanna grassland (Brown et al. 1979). Annual rainfall averages 40 cm with 40% occurring during July and August (U.S. Fish and Wildlife Service 1995). The mean annual temperature is 15°C, with temperatures ranging from –11°C in winter to 41°C in summer.

### METHODS

#### Field Sampling

We obtained data from southern Texas during June 1994–August 1995, Sonora during June

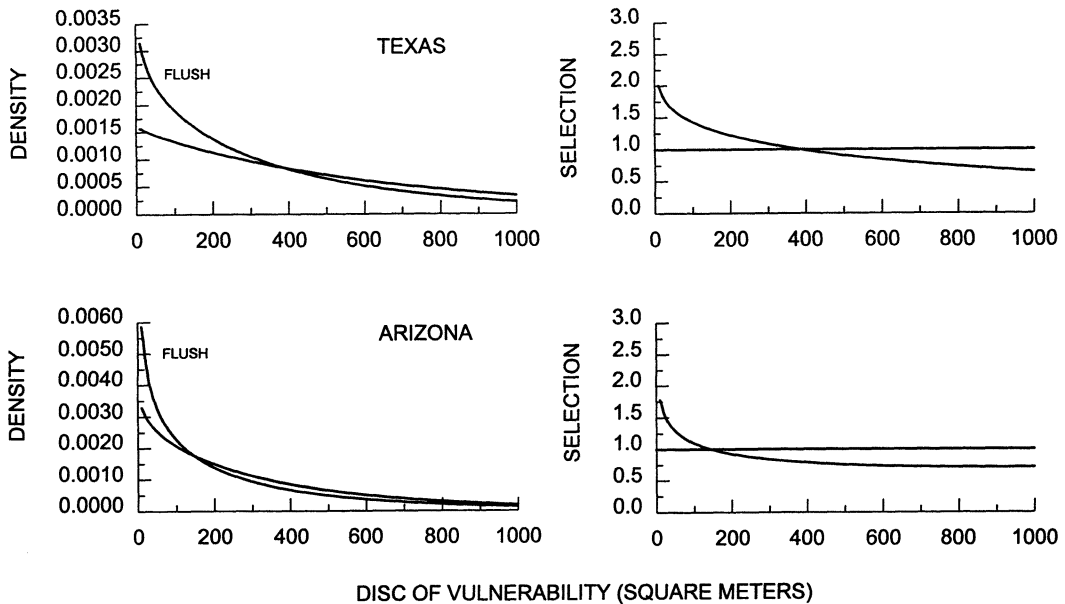


Fig. 3. Probability density (density) functions (left) and selection functions (right) for the disc of vulnerability at used (flush) and random points for bobwhites in Texas, Sonora, and Arizona, 1994–96. Models for the cumulative distributions, from which density functions were derived, were significant ( $P < 0.001$ ) for Texas (used  $r^2 = 0.95$ , random  $r^2 = 0.92$ ) and Arizona (used  $r^2 = 0.99$ , random  $r^2 = 0.98$ ). Selection is indicated when the selection function is  $>1$  (horizontal line on right); avoidance is indicated when the selection function is  $<1$ .

1994–November 1995, and Arizona during October 1994–September 1996. Our study populations consisted of wild bobwhites in Texas and Mexico and reintroduced bobwhites in Arizona. The breeding program for reintroduced birds was conducted to maintain maximal genetic diversity, and thus, no selection occurred in captivity. The reintroduction program previously used wild-trapped males of Texas bobwhites as foster parents for masked bobwhite chicks (Carpenter et al. 1991). Since 1995, masked bobwhite chicks, hatched in rearing facilities on Buenos Aires Refuge, are raised to  $>8$  weeks of age before release with adult masked bobwhites in September and October (Gall et al. 1999).

Kopp et al. (1998) and Forrester et al. (1998) described the sampling procedures used for our work. We present modified and truncated versions of some of their results (selection functions) for Texas bobwhites for comparative purposes. Also, we present original data on the vertical structure of habitat used by Texas bobwhites.

We used organism-centered and randomly located patches (Brennan et al. 1986) to analyze the habitat ecology of masked bobwhites. This approach represents analysis of third-order selection (sites within home ranges; Johnson

1980) under Design 1 of Thomas and Taylor (1990). Our goal was to sample randomly in space and systematically in time to determine the nature of the random environment available to bobwhites for preference–avoidance behavior. Biologists working in Texas met with biologists working in Sonora and Arizona in August 1994 to insure that sampling protocols were similar and to standardize sampling equipment.

The locations of random points governed the locations of searches for bobwhites in the field (searches radiated outwards from random points). This protocol worked well in Texas, where bobwhites were relatively abundant, but it worked poorly in Sonora and Arizona, where bobwhites were relatively rare. Therefore, we analyzed habitat properties at sign (tracks, droppings) as well as at actual observations of masked bobwhites in Sonora. We used locations of radiotagged bobwhites released in Arizona for analysis of habitat features at used points (King 1998). At least 3 quail in each group of 20–40 quail released on Buenos Aires Refuge were fitted with a radiotransmitter (5 g, collar-type harness) that had a mortality sensor. Signals on released birds were monitored for the first 3 consecutive days after release, but these individuals were not approached (flushed) un-

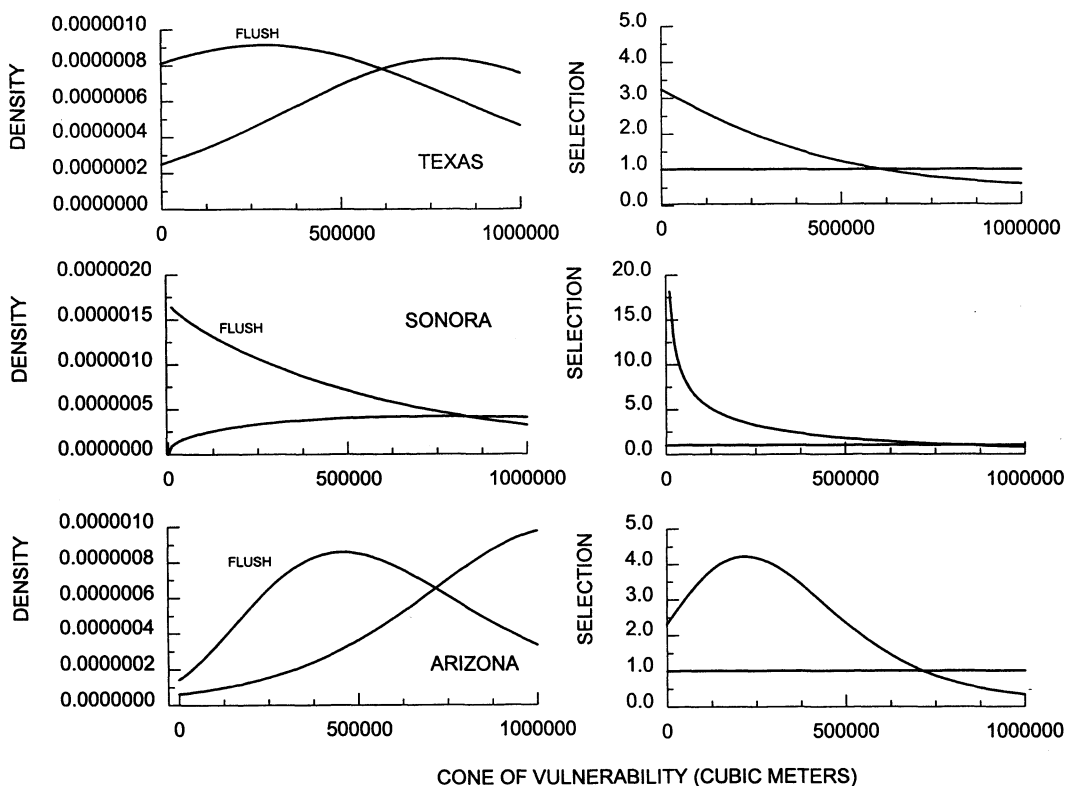


Fig. 4. Probability density (density) functions (left) and selection functions (right) for the cone of vulnerability at used (flush) and random points for bobwhites in Texas, Sonora, and Arizona, 1994–96. Models for the cumulative distributions, from which density functions were derived, were significant ( $P < 0.001$ ) for Texas (used  $r^2 = 0.95$ , random  $r^2 = 0.95$ ), Sonora (used  $r^2 = 0.99$ , random  $r^2 = 0.87$ ), and Arizona (used  $r^2 = 0.99$ , random  $r^2 = 0.98$ ). Selection is indicated when the selection function is  $>1$  (horizontal line on right); avoidance is indicated when the selection function is  $<1$ .

less a mortality signal was detected. After the third day, radioed birds were located at least once a week during a randomly selected time period. We also used bird dogs to assist in locating and flushing groups of masked bobwhites during the covey season (Oct–Mar) in Arizona. Finally, we observed masked bobwhites during line-transect surveys and incidentally in Arizona.

We measured 10 habitat variables and 1 microclimate variable at each used (organism-centered) and random point. Because we could not be certain of the precise location where a bobwhite responded to the presence of an observer, we considered a point to be centered within a patch (small area of habitat). We subsampled (King 1998, Kopp *et al.* 1998) within these patches to derive information on the mean properties of habitat near points.

Kopp *et al.* (1998) described sampling procedures for estimating canopy coverage of woody vegetation (%), visual obstruction dis-

tance (m), visual obstruction angle ( $^{\circ}$ ), dry mass of herbaceous vegetation (kg/ha), canopy coverage of herbaceous vegetation (%), and exposure of bare ground (%). Visual obstruction angles were used to estimate exposure to aerial predators (cone of vulnerability; see Fig. 1 in Kopp *et al.* 1998) and the disappearance distances were used to estimate exposure to ground predators (disc of vulnerability; Kopp *et al.* 1998). We used a profile pole (Nudds 1977) constructed of 2.5-cm-diameter PVC pipe that was separated into 4 strata (0–15, >15–50, >50–100, and >100–200 cm) to index the vertical structure of screening cover along 8 compass radii (N, NE, E, ...). The percentage screening of each stratum was estimated by a kneeling observer (about 1 m height) at a distance of 4 m from the point and mean values for each stratum were calculated. We followed the procedures of Forrester *et al.* (1998) in estimating operative temperature ( $^{\circ}\text{C}$ ) at used and random points (15 cm aboveground). Operative

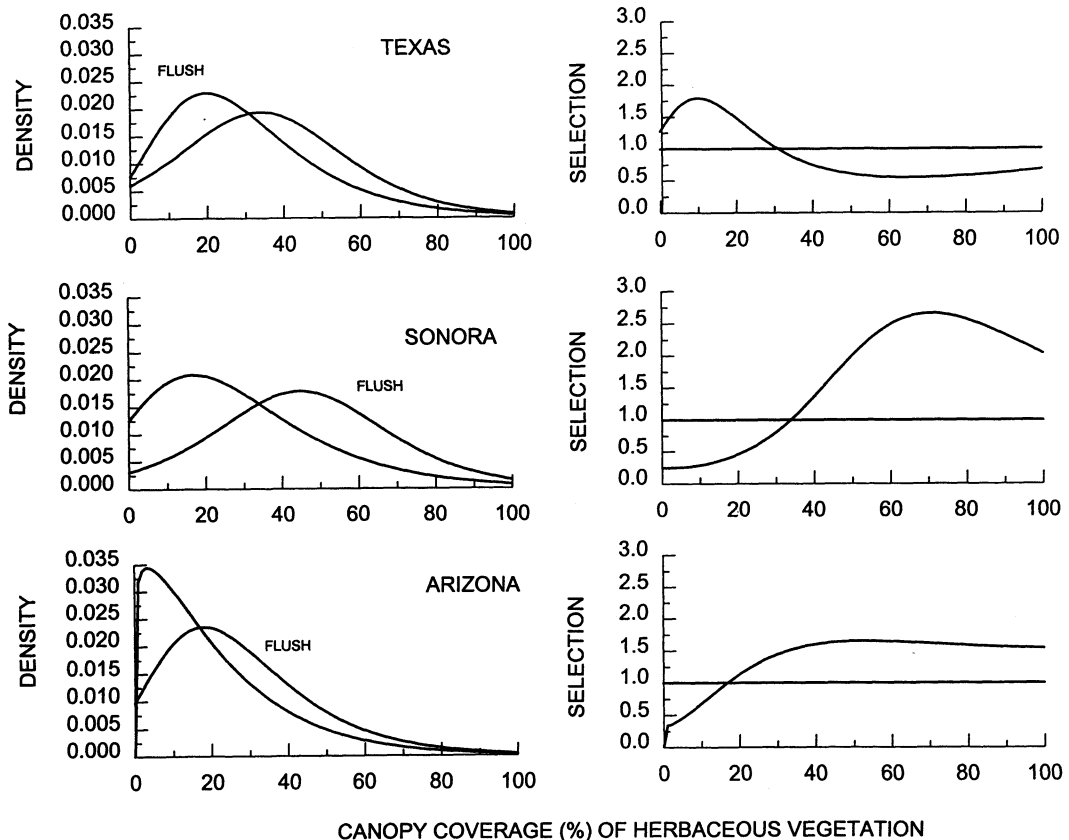


Fig. 5. Probability density (density) functions (left) and selection functions (right) for canopy coverage of herbaceous vegetation at used (flush) and random points for bobwhites in Texas, Sonora, and Arizona, 1994–96. Models for the cumulative distributions, from which density functions were derived, were significant ( $P < 0.001$ ) for Texas (used  $r^2 = 0.99$ , random  $r^2 = 0.98$ ), Sonora (used  $r^2 = 0.97$ , random  $r^2 = 0.99$ ), and Arizona (used  $r^2 = 0.98$ , random  $r^2 = 0.99$ ). Selection is indicated when the selection function is  $>1$  (horizontal line on right); avoidance is indicated when the selection function is  $<1$ .

temperature provides a better measure than air temperature of the thermal environment of wild animals. Operative temperature adds the heating effects of sunlight to air temperature and usually deducts the cooling effects of air movement. Air movement can add to heating effects if air temperature exceeds body temperature of the organism under study.

### Statistical Analysis and Interpretation

We analyzed data pooled over the sampling period for each study area. Pooling of the data generally resulted in large samples and small standard errors for virtually all means presented (Table 1). All comparisons of means were significant ( $P < 0.05$ ) unless otherwise indicated.

We interpreted the strength (adaptive significance) of a variable in the habitat ecology of bobwhites by analyzing the variability of means for the feature over regions. The genus *Colinus* sep-

arated from other quails about 7 million years before present (Gutiérrez 1993). We assumed the evolutionary history of the genus would lead to a niche that was similar amongst widely separated populations. If this assumption is correct, then habitat variables of the highest adaptive significance should show the greatest consistency amongst populations. Conversely, habitat variables of lower adaptive significance should show less consistency among populations. In short, we assumed that the adaptive significance of a habitat feature varied inversely with variability in the feature amongst populations.

We analyzed preference–avoidance behavior for single habitat features with selection functions. Guthery (1997) introduced selection function modeling and Kopp et al. (1998) provided detail on the models and procedures we applied. A continuous selection function,  $u(x)$ , was estimated as

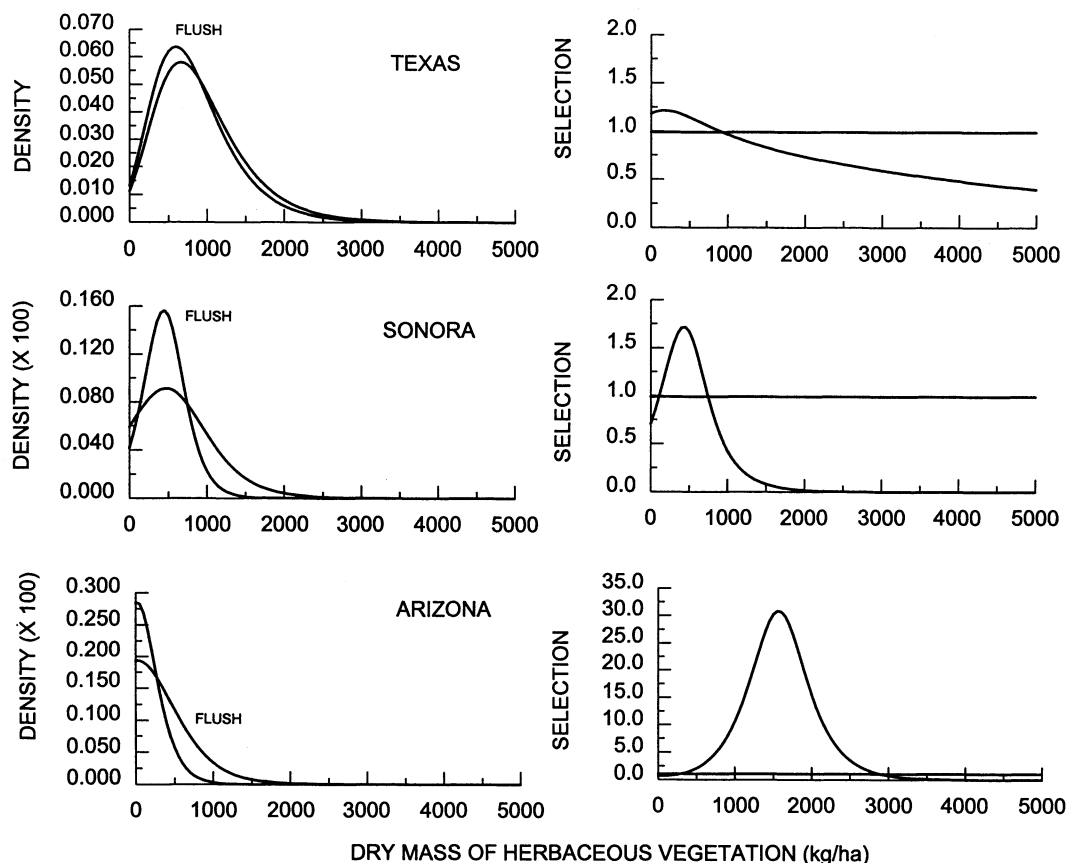


Fig. 6. Probability density (density) functions (left) and selection functions (right) for dry mass of herbaceous vegetation at used (flush) and random points for bobwhites in Texas, Sonora, and Arizona, 1994–96. Models for the cumulative distributions, from which density functions were derived, were significant ( $P < 0.001$ ) for Texas (used  $r^2 = 0.99$ , random  $r^2 = 0.99$ ), Sonora (used  $r^2 = 0.99$ , random  $r^2 = 0.99$ ), and Arizona (used  $r^2 = 0.85$ , random  $r^2 = 0.88$ ). Selection is indicated when the selection function is  $>1$  (horizontal line on right); avoidance is indicated when the selection function is  $<1$ .

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

where  $f(x)$  is the probability distribution for a habitat feature at used points and  $g(x)$  is the probability distribution at random points. Interpretation of a selection function is homologous to the interpretation of discrete selection ratios (proportional use/proportional availability within discrete classes). If  $u(x)$  is  $>1$ , preference is indicated, whereas if  $u(x)$  is  $<1$ , avoidance is indicated. The area under the availability distribution where  $u(x)$  is  $<1$  provides an estimate of the proportion of habitat space–time that is avoided because of a particular habitat feature (Fig. 1). Space–time (ha–days) is the product or integral of usable space (area with suitable habitat) over time; maximization of space–time on a defined area is a goal of habitat management for bobwhites (Guthery 1997). See also Guthery

(1999) for further elaboration of the concept, space–time.

The proportion of space–time lost (avoided and not used) also is estimatable from the density functions,  $g(x)$  and  $f(x)$  (Fig. 1). We used the proportion of space–time avoided and lost to rank habitat deficiencies at the univariate level. A habitat deficiency was defined as a condition that led to the loss or avoidance of space–time. We assumed the most serious habitat deficiency was the one associated with the highest proportional avoidance and loss of space–time.

Finally, the selection function,  $u(x)$ , provides an unscaled image of the ideal probability distribution of a habitat feature in space–time (Kopp *et al.* 1998). The image must be scaled such that the area under the curve equals 1.0 to become a probability distribution (scaling



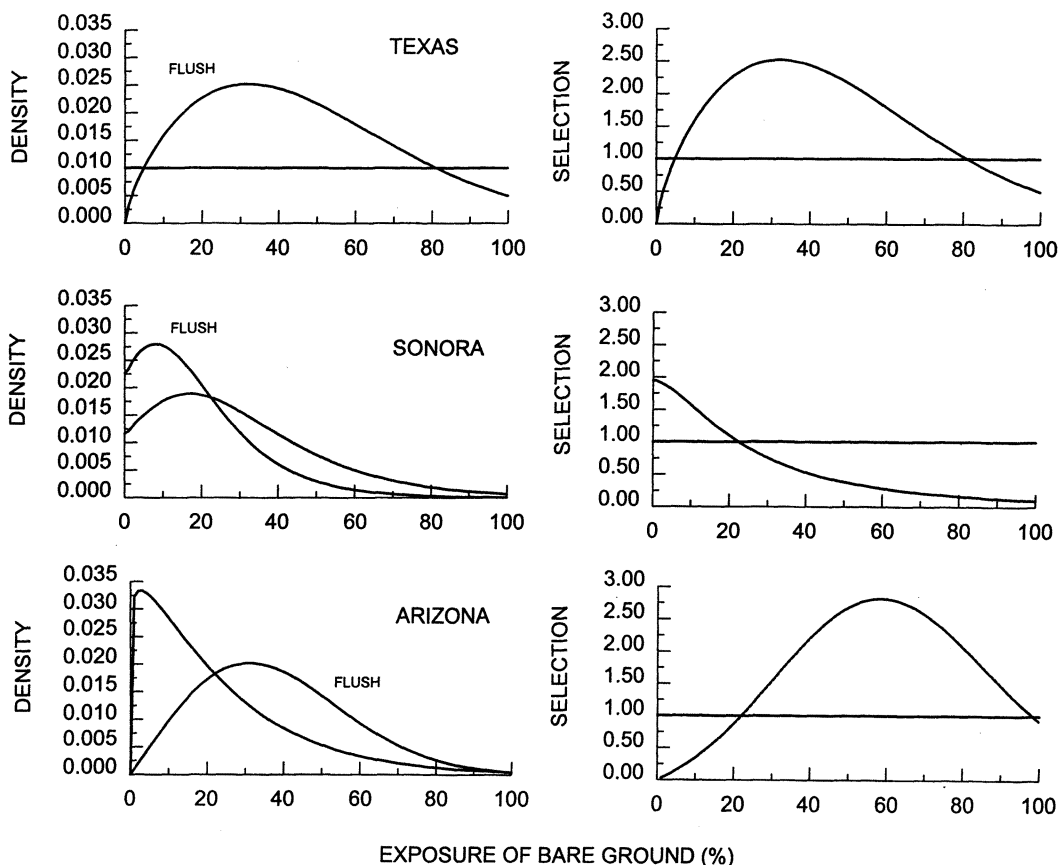


Fig. 7. Probability density (density) functions (left) and selection functions (right) for exposure of bare ground at used (flush) and random points for bobwhites in Texas, Sonora, and Arizona, 1994–96. Models for the cumulative distributions, from which density functions were derived, were significant ( $P < 0.001$ ) for Texas (used  $r^2 = 0.98$ , random  $r^2 = 0.99$ ), Sonora (used  $r^2 = 0.99$ , random  $r^2 = 0.98$ ), and Arizona (used  $r^2 = 0.93$ , random  $r^2 = 0.99$ ). Selection is indicated when the selection function is  $>1$  (horizontal line on right); avoidance is indicated when the selection function is  $<1$ .

changes the shape relatively). Put in different words, the selection function provides an image of how a habitat feature should be distributed in space and time to provide optimum conditions (to permit unconstrained use of space through time [Guthery 1997]) with respect to that habitat feature. Time is invoked because it is a dimension of all events in history (Silver 1998:433), including landscapes. For example, time alters the nature of habitat through the cover effects associated with leaf fall from deciduous plants (Errington and Hamerstrom 1936). The probability distributions we display collapse 3 dimensions (2 space, 1 time) into 1 dimension (value of a habitat feature over space and through time).

## RESULTS

We obtained data at  $\leq 405$  used and  $\leq 606$  random points in Texas,  $\leq 379$  used and  $\leq 416$

random points in Sonora, and  $\leq 155$  used and  $\leq 204$  random points in Arizona (Table 1). The inequalities appear because not all variables were measured at all points.

## Habitat Properties at Used Points

Bobwhites did not seem sensitive to the exposure of bare ground and the biomass of herbaceous vegetation; CVs for these variables were  $>54\%$  across areas. The birds appeared moderately sensitive to the disc of vulnerability, visual screening at 50–100 cm and  $>100$ –200 cm aboveground, canopy coverage of herbaceous vegetation, and canopy coverage of woody vegetation (CVs  $>32.9\%$ ). The highest degree of commonality (Spears et al. 1993) in the features of used habitat included visual screening at 0–15 cm and  $>15$ –50 cm, operative temperature, and the cone of vulnerability

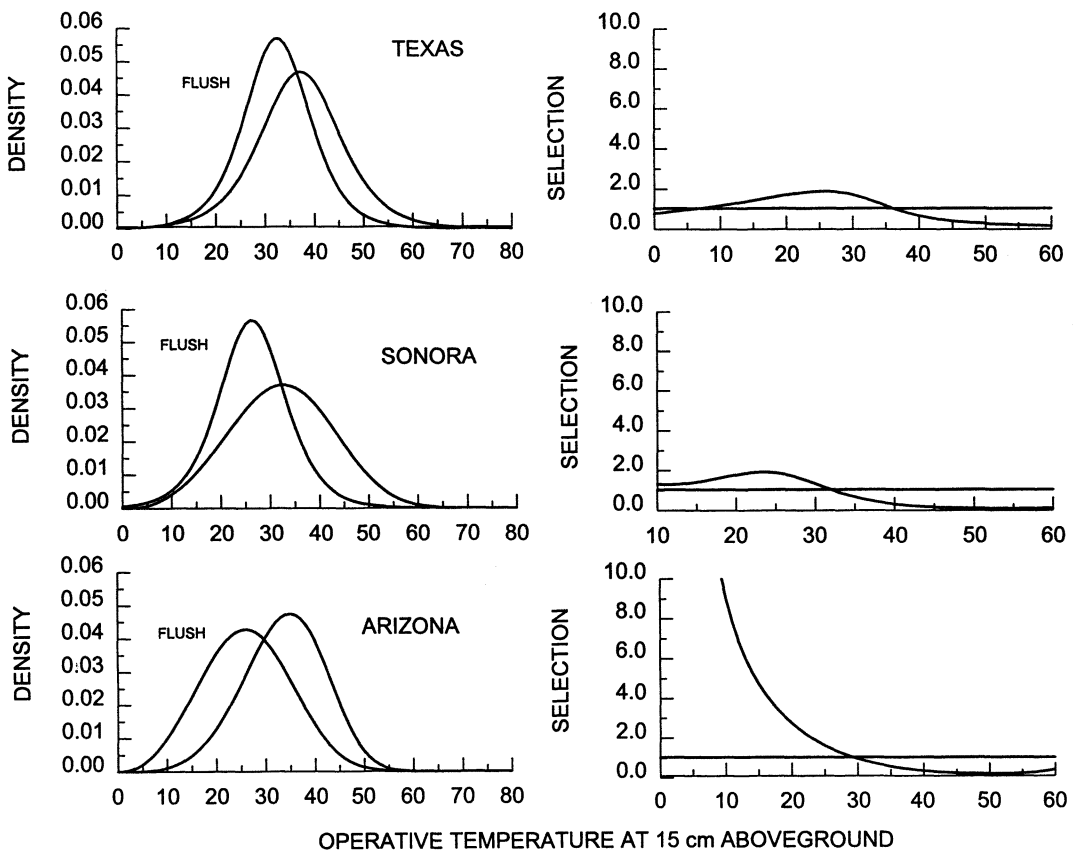


Fig. 8. Probability density (density) functions (left) and selection functions (right) for operative temperature ( $^{\circ}\text{C}$ ) at used (flush) and random points for bobwhites in Texas, Sonora, and Arizona, 1994–96. Models for the cumulative distributions, from which density functions were derived, were significant ( $P < 0.001$ ) for Texas (used  $r^2 = 0.99$ , random  $r^2 = 0.99$ ), Sonora (used  $r^2 = 0.75$ , random  $r^2 = 0.99$ ), and Arizona (used  $r^2 = 0.99$ , random  $r^2 = 0.99$ ). Selection is indicated when the selection function is  $>1$  (horizontal line on right); avoidance is indicated when the selection function is  $<1$ .

(CVs  $<14.2\%$ ). The mean cone of vulnerability, in particular, was remarkably similar among areas (Table 1).

### Habitat Selection Modeling

Bobwhites in all areas exhibited preferential use of patches with higher canopy coverage of woody vegetation than was randomly available (Table 1, Fig. 2). The domain of selection (range of  $x$  where  $u[x]$  was  $>1$ ) was broader in Texas and Arizona (20–100% coverage) than in Sonora (9–46% coverage).

We could not calculate probability distributions for the disc of vulnerability in Sonora. However, the mean disc at random points was 7.6 times larger than that at used points (Table 1), indicating preferential use. Selection modeling indicated preference for discs  $<380 \text{ m}^2$  in Texas and  $<140 \text{ m}^2$  in Arizona (Fig. 3). However, the probability distributions for discs at

used and random points were similar in Arizona, the selection function was near 1.0 for all values of the disc, and the mean values at used and random points were similar (Table 1). The results suggested bobwhites were sensitive to the disc based on behavior in Texas and Sonora; the random availability of discs in Arizona may have approached the ideal distribution, in which case preference–avoidance behavior would not be demonstrable, even if the disc is meaningful from an adaptive standpoint.

Evidence for selection behavior for the cone of vulnerability was present on all study areas (Table 1, Fig. 4). The domain of selection was  $<620,000 \text{ m}^3$  in Texas,  $<830,000 \text{ m}^3$  in Sonora, and  $<710,000 \text{ m}^3$  in Arizona. The volume of a hemisphere (a special case of a cone) with a radius of 100 m, which represents the volume of a cone when screening cover is absent, is  $2,094,395 \text{ m}^3$ . Bobwhites exhibited preferences

Table 2. The effects of habitat variables on the proportion of habitat space–time avoided and lost based on selection function modeling for bobwhites in Texas (TX), Sonora (SO), and Arizona (AZ), 1994–96.

Habitat variable	Avoided			Lost		
	TX	SO	AZ	TX	SO	AZ
Canopy coverage of woody vegetation (%)	0.76	0.66	0.61	0.48	0.48	0.29
Disc of vulnerability (m <sup>2</sup> )	0.56		0.66	0.16		0.12
Cone of vulnerability (m <sup>3</sup> )	0.63	0.71	0.80	0.32	0.44	0.54
Canopy coverage of herbaceous vegetation (%)	0.57	0.66	0.51	0.22	0.44	0.22
Dry mass of herbaceous vegetation (%)	0.34	0.59	0.84	0.05	0.36	0.62
Exposure of bare ground (%)	0.24	0.54	0.61	0.02	0.24	0.13
Operative temperature (°C) at 15 cm aboveground	0.55	0.51	0.72	0.24	0.30	0.35

for cover that exposed them to direct attack from raptors in <40% of potential air space (based on the maximum figure from Sonora). Bobwhites in Texas and Sonora exhibited maximum preference for total concealment from raptors (cone = 0 m<sup>3</sup>), whereas the maximum preference in Arizona was 200,000–225,000 m<sup>3</sup> (vulnerable within about 10% of potential air space).

Although bobwhites exhibited preferential use with respect to canopy coverage of herbaceous vegetation, the nature of the preference varied among areas (Table 1, Fig. 5). The domain of selection for quail in Texas was 0–30% and the mean value at random points exceeded that at used points. Conversely, the domains were 34–100 in Sonora and 17–100 in Arizona. The mean value at used points exceeded that at random points in Sonora, whereas the mean values were similar at used and random points in Arizona (Table 1).

Likewise, preference–avoidance responses to dry mass of herbaceous vegetation differed among areas. The probability distributions for used and random points were similar in Texas, leading to a selection function near 1.0 for dry mass values between 0 and 2,000 kg/ha (>90% of values; Fig. 6). However, mean values differed between used and random points in Sonora (Table 1). The mean at used points in Sonora was 1.6 times that at random points and the Mexico birds showed strong avoidance for values >1,000 kg/ha. Means were similar at used and random points in Arizona (Table 1), although relatively strong preference was indicated for 1,500 kg/ha. This inconsistent result probably occurred because of a small sample

size for biomass at used points in Arizona (Table 1).

Exposure of bare ground was similar at used and random points for bobwhites in Texas (Table 1). The random availability of bare ground in Texas was best modeled as a uniform distribution, so the density curve for used points was similar to the selection curve (Fig. 7). Bobwhites in Mexico exhibited preference for less bare ground than was randomly available (the domain of selection was <20%), and showed strong avoidance for higher exposure of bare ground (>60%). Although the mean value for bare ground exposure was higher at random than at used points in Arizona (Table 1), the statistical difference does not seem to be meaningful (the statistical effect had no biological meaning). Arizona bobwhites exhibited preference for bare ground exposure in the domain 23–98%.

The probability distributions for operative temperature at used and random points were similar on all study areas (Fig. 8). Likewise, mean values at random points exceeded mean values at used points on all areas (Table 1). The domain of selection was <39°C in Texas (Forrester *et al.* 1998), <32°C in Sonora, and <29°C in Arizona.

### Habitat Deficiencies

Based on the proportion of space–time lost, the most severe habitat deficiency in Texas and Sonora was canopy coverage of woody vegetation (Table 2). Dry mass of herbaceous vegetation and the cone of vulnerability were the most severe deficiencies in Arizona, followed by operative temperature at 15 cm aboveground and

canopy coverage of woody vegetation. The cone of vulnerability was the second most severe deficiency in Texas and Sonora; canopy coverage and dry mass of herbaceous vegetation also contributed markedly to lost space–time in Sonora. The general implication from this analysis was that habitat deficiencies of some type contributed to the loss of about 50% of potential space–time on each study area.

## DISCUSSION

### Data Pooling Effects

Habitat use by bobwhites may change among periods within a day and among seasons within a year. Generally, the mean values for habitat features at points used by bobwhites changed more within periods of the day than among seasons. Bobwhites on all study areas used patches with higher canopy coverage of brush during midday (loafing) than during morning–evening (feeding) periods. Accordingly, the cone of vulnerability was smaller during midday than during morning–evening periods.

There was a tendency for bobwhites to use patches with lower canopy coverage of woody vegetation during fall–winter than during spring–summer. This behavior may reflect heat-avoidance during spring–summer, when bobwhites in semiarid environments loaf in patches of taller, denser woody cover than during other seasons (Johnson and Guthery 1988). Otherwise, seasonal effects on habitat use were weak; i.e., the mean values of habitat features, pooled over period of the day, tended to be similar among seasons.

Relative constancy in seasonal habitat use, however, must be viewed from the perspective of seasonal variation in the biotic and physical environment within which bobwhites occur. Functional space–time, which contributes to the number in a population, may be only slightly larger than the minimum quantity occurring on any day of a year multiplied by the days in the year (Guthery 1997). In other words, the proportion of habitat space that is usable varies with time and populations tend to be governed by the minimum proportion usable on an annual basis. Forrester *et al.* (1998) estimated, for example, that the proportion of habitat space–time avoided ranged between 0.52 during cooler seasons and 0.74 during warmer seasons, despite apparent preference for thermoneutral temperatures (30–35°C) during all seasons.

### Selection Modeling

Differences in the preference–avoidance behavior of bobwhites among regions (Figs. 2–8) may be attributed to variation among observers (Block *et al.* 1987), the effects of sampling procedures, the validity of a model selected to describe probability distributions at used and random points, the strength of a habitat feature in the habitat selection process, and differences in adaptations or learned behaviors among regional populations of bobwhites. We attribute some differences to each of these sources.

Although the observers in this study coordinated sampling and measurement protocols, some variables used had subjective elements. The canopy coverage method of estimating the coverage of herbaceous vegetation and the exposure of bare ground involves some subjectivity. Accordingly, these results are best viewed as general trends rather than precise descriptions. The variable that was least subject to human interpretation, operative temperature, also showed the strongest similarities among regions with respect to preference–avoidance behavior (Fig. 8).

We identified used points with human encounters in all study areas, sign in Sonora, and radiotelemetry and bird dogs in Arizona. These differences in sampling procedures could have been associated with variation in preference–avoidance behavior among areas. We have no reason to suspect that habitat use would differ according to method of detection for human encounters, sign, or bird dogs. However, radio-transmitters may alter the field behavior of small animals (Percival and Webb 1971). Despite the possible bias imposed by different sampling procedures, the fact remains that exposure to raptors, low-level screening, and operative temperatures at used points were consistent among regions (Table 1).

Generally, the models we used to describe cumulative frequency distributions, from which we derived probability density functions, explained large portions of the variation in cumulative frequency (see legends, Figs. 2–8). However, we regard such models as, at best, good approximations of the probability distributions prevailing on the study areas. In some cases (e.g., herbaceous dry mass in Arizona), we had small and perhaps unreliable samples. Sampling intensity also was insufficient whenever extremes for the probability distribution of ran-

dom points did not equal or bound those of used points (the random distribution must include all possible points in the used distribution). This problem occurred with operative temperatures in Arizona (Fig. 8). The net effect of modeling problems with frequency distributions was uncertainty over the shape of the selection function and the domain of selection. Slight changes in the parameters and form of the random and used density functions can have rather large changes on the selection function. These difficulties could be partially resolved if methods were available to estimate the variance of the selection function. These methods are yet to be developed (Kopp *et al.* 1998). However, the inferences drawn from selection function modeling were similar to those drawn from discrete preference–avoidance analysis (Manly *et al.* 1993) based on data from Texas (Kopp *et al.* 1998).

The variables we measured are generally thought to be diagnostic of bobwhite habitat (Schroeder 1985, Bidwell *et al.* 1991, Rice *et al.* 1993, Kopp *et al.* 1998), but it does not follow that the variables exert equal influence on the adaptive habitat-use decisions made by bobwhites. We suspect variables associated with preference–avoidance behavior that was inconsistent among areas might be less influential than variables associated with consistent behavior. Accordingly, canopy coverage and dry mass of herbaceous vegetation and exposure of bare ground were perhaps less meaningful to quail than canopy coverage of woody vegetation, the cone of vulnerability, and operative temperature. Mean values at used points were consistent among areas for the latter 2 variables (Table 1).

From the standpoint of possible adaptive uniqueness, masked bobwhites seemed to show less affinity for woody cover and a stronger response to herbaceous components of cover than Texas bobwhites. The mean canopy coverage of woody vegetation at points used by Texas bobwhites was about 1.8 times that of masked bobwhites (Table 1). Likewise, Texas bobwhites seemed to select for points with <20% canopy coverage of herbaceous vegetation, whereas masked bobwhites selected for points with >20% canopy coverage. These differences could arise from the interchangeability of cover functions; *i.e.*, woody and herbaceous vegetation may serve interchangeable cover functions (foraging, loafing; Leopold 1933:130, Errington

and Hamerstrom 1936:386, Guthery 1999). The differences could also arise from differences in the composition and abundance of predator populations on the study areas, which could alter preference–avoidance behavior. Despite the differences in selection behavior regarding woody and herbaceous cover, canopy coverage of woody vegetation seemed deficient on all areas (Table 2).

The commonalities (low-level screening, exposure to raptors, and operative temperature) in preference–avoidance behavior and habitat use among areas may reveal key habitat features in the adaptive outlook of bobwhites. Therefore, aspects of the habitat ecology of Texas bobwhites would transfer to masked bobwhites. This conclusion is supported by morphological, physiological, and genetic similarities between Texas and masked bobwhites (Tomlinson 1975, White 1995, White *et al.* 1999). However, the races appear to use different habitat compositions (woody *vs.* herbaceous cover) to effect the commonalities observed. Our results suggest habitat management for masked bobwhites should focus more on herbaceous cover and less on woody cover in comparison with Texas bobwhites.

### Habitat Deficiencies

We regard the high estimated loss of space–time to dry mass of herbaceous vegetation in Arizona (Table 2) as an artifact of sample size. Otherwise, the habitat deficiencies identified through space–time analysis represented a syndrome arising from a suite of related variables. Any combination of effects that increased the canopy coverage of brush or a functional equivalent such as tall, robust herbaceous cover also would reduce exposure to predators and suppress operative temperatures at quail level. These effects would add to the quantity of space–time available in Sonora and Arizona and, accordingly, would be expected to increase populations (Guthery 1997, Roseberry and Suckamp 1998).

### MANAGEMENT IMPLICATIONS

Masked bobwhites may prefer areas with lower canopy coverage of woody vegetation than Texas bobwhites. Otherwise, management information applicable to the well-studied Texas bobwhite would seem to apply to masked bobwhites. The primary habitat deficiency of masked bobwhites in Sonora and Arizona was a

syndrome resulting in increased exposure to aerial predators and unacceptably high operative temperatures at ground level. The syndrome can be addressed by any management technique that increases the density of brush (within limits) and the height and density of herbaceous cover. Because rangeland vegetation enters stable states after decades or centuries of grazing by livestock (Friedel 1991, Laycock 1991), reducing or eliminating grazing pressure will not necessarily result in increased quantities of herbaceous cover. Mechanical treatments that fracture the soil surface and permit infiltration as opposed to runoff of precipitation would foster herbaceous cover (Hanselka et al. date unknown, Fulbright and Guthery 1996, Hall 1998). Our observations on ranches in Mexico, including those occupied by masked bobwhites, indicate discing and aeration improve the quantity and diversity of herbaceous cover. These mechanical treatments must be applied such that ample amounts of mature woody cover remain post-treatment. Grazing is a key issue in the management of cover for masked bobwhites. Grazing probably is not necessary as a management tool. If it is applied, stocking densities should be low and pasture rest should be included to maintain the diversity of herbaceous vegetation.

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## LITERATURE CITED

- BIDWELL, T. G., S. R. TULLY, A. D. PEOPLES, AND R. E. MASTERS. 1991. Habitat appraisal guide for bobwhite quail. Oklahoma Cooperative Extension Service Circular E-904.
- BLOCK, W. M., K. A. WITH, AND M. L. MORRISON. 1987. On measuring bird habitat: influence of observer variability and sample size. *Condor* 89: 241–251.
- BRENNAN, L. A., W. M. BLOCK, AND R. J. GUTIÉRREZ. 1986. Habitat use by mountain quail in northern California. *Condor* 89:66–74.
- BROWN, D. E., C. H. LOWE, AND C. P. PASE. 1979. A digitized classification system for the biotic communities of North America. *Journal of the Arizona-Nevada Academy of Science* 14:1–16.
- CAMOU L., G., W. P. KUVLESKY, JR., AND F. S. GUTHERY. 1998. Rainfall and masked bobwhites in Sonora, Mexico. U.S. Forest Service Proceedings RMRS-P-5:253–260.
- CARPENTER, J. W., R. R. GABEL, AND J. G. GOODWIN, JR. 1991. Captive breeding and reintroduction of the endangered masked bobwhite. *Zoo Biology* 10:439–449.
- ERRINGTON, P. L., AND F. M. HAMERSTROM, JR. 1936. The northern bob-white's winter territory. *Iowa State College of Agriculture and Mechanic Arts Research Bulletin* 201:305–443.
- FORRESTER, N. D., F. S. GUTHERY, S. D. KOPP, AND W. E. COHEN. 1998. Operative temperature reduces habitat space for northern bobwhites. *Journal of Wildlife Management* 62:1505–1510.
- FRIEDEL, M. H. 1991. Range condition assessment and the concept of thresholds: a viewpoint. *Journal of Range Management* 44:422–426.
- FULBRIGHT, T. E., AND F. S. GUTHERY. 1996. Mechanical manipulation of plants. Pages 339–354 in P. R. Krausman, editor. *Rangeland wildlife*. Society for Range Management, Denver, Colorado, USA.
- GALL, S. A., W. P. KUVLESKY, JR., G. GEE, J. C. LEWIS, AND D. STEINBACH. 1999. Releasing captive-reared masked bobwhites: a new strategy. *Proceedings of the National Quail Symposium* 4:In Press.
- GOULD, F. W. 1975. Texas plants: a checklist and ecological summary. Texas Agricultural Experiment Station Miscellaneous Publication 585 (revised).
- GUTHERY, F. S. 1997. A philosophy of habitat management for northern bobwhites. *Journal of Wildlife Management* 61:291–301.
- . 1999. Slack in the configuration of habitat patches for northern bobwhites. *Journal of Wildlife Management* 63:245–250.
- GUTIÉRREZ, R. J. 1993. Taxonomy and biogeography of New World quail. *Proceedings of the National Quail Symposium* 3:8–15.
- HALL, B. W. 1998. Habitat use by sympatric northern bobwhites and scaled quail in the western Rio Grande Plains. Thesis, Texas A&M University-Kingsville, Kingsville, Texas, USA.
- HANSELKA, C. W., S. D. LIVINGSTON, AND D. BADE. [date unknown]. Renovation practices to improve rainfall effectiveness on rangeland and pastures. Texas Agricultural Extension Service Leaflet 5077.
- JOHNSGARD, P. A. 1973. Grouse and quails of North America. University of Nebraska Press, Lincoln, Nebraska, USA.
- JOHNSON, D. B., AND F. S. GUTHERY. 1988. Loafing coverts used by northern bobwhites in subtropical

- environments. *Journal of Wildlife Management* 52:464–469.
- JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- KING, N. M. 1998. Habitat use by endangered masked bobwhites and other quail on the Buenos Aires National Wildlife Refuge, Arizona. Thesis, University of Arizona, Tucson, Arizona, USA.
- KOPP, S. D., F. S. GUTHERY, N. D. FORRESTER, AND W. E. COHEN. 1998. Habitat selection modeling for northern bobwhites on subtropical rangeland. *Journal of Wildlife Management* 62:884–895.
- KUVLESKY, W. P., JR., S. A. GALL, S. J. DOBROTT, S. TOLLEY, F. S. GUTHERY, S. A. DESTEFANO, N. KING, K. R. NOLTE, N. J. SILVY, J. C. LEWIS, G. GEE, R. ENGEL-WILSON, AND G. CAMOULOURDES. 1999. The status of masked bobwhite recovery in the United States and Mexico. *Proceedings of the National Quail Symposium 4*:In Press.
- LAYCOCK, W. A. 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. *Journal of Range Management* 44:427–433.
- LEOPOLD, A. 1933. *Game management*. Charles Scribner's Sons, New York, New York, USA.
- MANLY B. F. J., L. L. McDONALD, AND D. L. THOMAS. 1993. *Resource selection by animals*. Chapman & Hall, New York, New York, USA.
- MARTIN R., M. H., J. R. COX, AND F. IBARRA-F. 1995. Climatic effects on buffelgrass productivity in the Sonoran Desert. *Journal of Range Management* 48:60–63.
- NUDDS, T. J. 1977. Quantifying the vegetative structure of wildlife cover. *Wildlife Society Bulletin* 5:113–117.
- PERCIVAL, H. F., AND L. G. WEBB. 1971. Notes on reproductive success of pen-reared bobwhite quail equipped with radio-telemetric transmitters. *Proceedings of the Southeastern Association of Game and Fish Commissioners* 25:286–289.
- RICE, S. M., F. S. GUTHERY, G. S. SPEARS, S. J. DEMASO, AND B. H. KOERTH. A precipitation-habitat model for northern bobwhites on semi-arid rangeland. *Journal of Wildlife Management* 57:92–102.
- ROSEBERRY, J. L., AND S. D. SUDKAMP. 1998. Assessing the suitability of landscapes for northern bobwhites. *Journal of Wildlife Management* 62:895–902.
- SCHROEDER, R. L. 1985. *Habitat suitability models: northern bobwhite*. U.S. Fish and Wildlife Service Biological Report 82.
- SILVER, B. L. 1998. *The ascent of science*. Oxford University Press, New York, New York, USA.
- SPEARS, G. S., F. S. GUTHERY, S. M. RICE, S. J. DEMASO, AND R. ZAIGLIN. 1993. Optimum seral stage for northern bobwhites as influenced by site productivity. *Journal of Wildlife Management* 57:805–811.
- THOMAS, D. L., AND E. J. TAYLOR. 1990. Study designs and tests for comparing resource use and availability. *Journal of Wildlife Management* 54:322–330.
- TOMLINSON, R. E. 1975. Weights and wing lengths of wild Sonoran masked bobwhites during fall and winter. *Wilson Bulletin* 87:180–186.
- U.S. FISH AND WILDLIFE SERVICE. 1995. *Masked bobwhite recovery plan (second revision)*. U.S. Fish and Wildlife Service, Albuquerque, New Mexico, USA.
- WHITE, S. L. 1995. *Comparative anatomy of Texas and masked bobwhites*. Thesis, Texas A&M University-Kingsville, Kingsville, Texas, USA.
- , K. R. NOLTE, W. P. KUVLESKY, JR., AND F. S. GUTHERY. 1999. Comparative morphology and phylogenetic relatedness among bobwhites in the southern U.S. and Mexico. *Proceedings of the National Quail Symposium 4*:In Press.

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