HABITAT AND SPACE USE BY
NORTHERN BOBWHITES
IN NORTH TEXAS

By

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Abstract: My objectives were to describe home ranges and habitat selection behavior of northern bobwhites (*Colinus virginianus*) during the breeding and covey seasons on a High Plains Steppe (Texas Panhandle). I also challenged the usable-space hypothesis, which asserts that usable space-in-time (habitat quantity) governs bobwhite abundance to a stronger degree than habitat quality. Radiotelemetry triangulation was used to locate birds 2–6 times/week and home ranges, constructed from these points, were estimated using the fixed kernel (KHR) and the minimum convex polygon (MCP) estimators. Mean home range estimates ranged from 10.6 ± 0.7 ha using KHR in the 2000–2001 covey season to 47.4 ± 6.2 ha using MCP for annual home ranges. These estimates fell within the ranges reported in the literature. The breeding-season home range of males was 45.8 ± 8.8 ha using KHR (95%) and 46.0 ± 10.4 ha using MCP (100%) whereas that of females was 20.3 ± 3.5 ha using KHR (95%) and 30.1 ± 7.0 ha using MCP (100%). A Geographic Information System was used to create a habitat map for the evaluation of habitat selection behavior. I used the cone of vulnerability to estimate the amount of usable space available to bobwhites in each of 8 habitat types. Selection behavior was evaluated with and without consideration of the amount of usable space available in each habitat type in an attempt to determine the merits of the usable-space hypothesis, which predicts random use of habitats if all are fully usable. The mixed-shrub habitat type was preferred in all seasons, whereas all other habitat types were either avoided or received random use (use in proportion to availability). My results were not consistent with predictions of the usable-space hypothesis because debiting habitats for usable space had little effect on quantified selection behavior.

Key words: bobwhite, *Colinus virginianus,* cone of vulnerability, fixed kernel estimator, habitat, home range, northern bobwhite, telemetry, Texas, usable space.

INTRODUCTION

Intensive studies on northern bobwhites (hereafter, bobwhites) began in the 1920s and have focused on many topics including predation, habitat requirements, home ranges, and responses to habitat management, among others. Bobwhites are among the most popular of America's upland game bird species and are harvested in greater numbers than any other nonmigratory upland game bird in North America (Dimmick 1992). This popularity as a game bird and a research subject is indicated by the bobwhite's presence in the literature; >2,700 publications have accrued on bobwhites since 1822, with >2,500 of those since 1900 (Scott 1985).

Land managers often strive to increase bobwhite abundance on the lands under their management. There are 2 general, competing hypotheses on how abundance can be increased through habitat manipulation. The first hypothesis is to increase the quality of habitat available in an area. Attempts at increasing habitat quality have included such practices as planting food plots, installing feeders, installing supplemental water sources, strip disking, applying herbicides, and conducting prescribed burns. These attempts have largely failed at increasing abundance when relying on the premise that food supplies are a limiting factor for bobwhite populations (Guthery 1997). Instances where abundance increased with the practices outlined above were due to increases of the amount of usable space available to bobwhites, which is the basis of the second hypothesis (Guthery 1997).

The second hypothesis is to increase the amount of usable space available to bobwhites. The usable-space hypothesis (Guthery 1997, 2000, Guthery et al. 2000*a*) suggests that bobwhite abundance is maximized when all points in space are usable at all times. Usability, in this context, is determined by the amount of permanent cover, which consists of a proper mixture of woody and herbaceous species. A reduction in usable space follows the loss of suitable bobwhite habitat. However, the usable-space hypothesis has not been challenged with deductive experimentation to assess its merits in furthering our understanding of bobwhite ecology.

My goals were to describe the general habits and behaviors of bobwhites in a High Plains Steppe and to challenge the usable-space hypothesis. Specifically, my objectives were to 1) obtain descriptive data on the home range size of bobwhites and to quantify the effects of sex and season on home range size, 2) obtain descriptive data on the habitat selection behavior exhibited by bobwhites and to see if this behavior varied with season, and 3) determine if inferences on habitat use vary with the estimated amount of usable space available in different habitat types.

LITERATURE REVIEW

Northern bobwhites occur or formerly occurred throughout virtually all of the eastern United States from the southernmost tip of Maine, southward into Florida, and westward into Texas, New Mexico, Colorado, Nebraska, extreme eastern Wyoming, and South Dakota (Johnsgard 1973, Dimmick 1992). They are also found in eastern and western Mexico, portions of Central America, Cuba, and southeastern Ontario (Johnsgard 1973, Dimmick 1992). There are 21 different subspecies of bobwhites (Johnsgard 1973). Bobwhites are found with scaled quail (*Callipepla squamata*) in western Oklahoma and

Texas, and with scaled quail, Gambel's quail (*C. gambelii*), and Montezuma quail (*Cyrtonyx montezumae*) in Arizona (Dimmick 1992). Taxonomically, bobwhites are in the subfamily Odontophorinae of the family Phasianidae, which includes the partridges and pheasants.

The Annual Cycle of Bobwhites

Bobwhites form social groups called coveys during fall and winter. Coveys range in size from 5 to 26 birds (Dimmick 1992), but mean covey size ranges from 13.4 birds in early November to 9.9 birds in late March in southern Illinois (Roseberry and Klimstra 1984). Coveys begin to break up around April (Rosene 1969), which marks the beginning of the breeding season and the approximate time of formation of mated pairs (Parmalee 1955).

Breeding, nest building, egg laying, and incubation occur during May, June, July, August, September, and possibly October (Stoddard 1931, Klimstra and Roseberry 1975, Lehmann 1984, Dimmick 1992). Upon completion of building a nest, egg laying begins within a few days. Eggs are laid at a rate of approximately 1/day until the clutch is complete; a full clutch consists of an average of 12–16 eggs. The mean incubation period is 23 days, and the chicks can generally fly within 2 of weeks of hatching (Stoddard 1931, Dimmick 1992). Though females are the ones that most commonly incubate the eggs, Stoddard (1931), Klimstra and Roseberry (1975), Dimmick (1992), DeVos and Mueller (1993), and Suchy and Munkel (1993) reported nests that were partially or entirely incubated by males. At the end of the breeding season, coveys begin to reform.

Home Ranges

Bobwhite home ranges reported in the literature vary in time and space (Table 1). The winter home ranges of 5 coveys in western Tennessee varied from 4.0 to 11.7 ha (Dimmick and Yoho 1972). Average home range size for 8 coveys in northeastern Oklahoma was 4.4 ha (Wiseman and Lewis 1981). Urban (1972) reported home ranges of 6.39–16.67 ha during summer in southern Illinois. Summer estimates provided by Puckett et al. (2000) in North Carolina ranged from 53 to 101 ha. Similarly, Taylor et al. (1999*b*) reported summer estimates ranging from 54 to 103 ha in Kansas.

Home Range Estimators

There are numerous methods of estimating home ranges. One popular method of estimating home range size is the MCP estimator. This is the simplest and most commonly used method (White and Garrott 1990, Samuel and Fuller 1994, Powell 2000). The home range area is determined by constructing a convex polygon by connecting the outermost locations of an animal and then determining the area of the polygon (White and Garrott 1990). A major shortcoming of the MCP method is that it uses only the outermost locations of an individual. As a result, it is sensitive to extreme locations and information from interior locations is ignored; it can inflate home range size by including vast areas not used by the animal (Powell 2000).

The utility distribution of locations for an individual is determined from the bivariate probability density function, which gives the probability of finding that animal at a particular location on a plane (Van Winkle 1975). The utility distribution concept was originally used in home range estimation to produce home range estimates with no shape assumptions, no sample size bias, and low deviation from the true distribution of

Table 1. Home ranges of northern bobwhites as reported in the literature.

Source	Location	Season	Estimator used	Size (ha)	SE	*n*
Oakley et al. (2002)	Dorchester County, Maryland	Winter	95% MCP[a]	24.2[b]	2.7	21
Wellendorf et al. (2002)	Tyrrell County, North Carolina	Winter		33.2		10
	Wilson County, North Carolina	Winter		17.4		11
Madison et al. (2000)	Fort Riley, Kansas	Winter	90% adaptive kernel	40.60[c]	5.0	
		Winter	90% adaptive kernel	42.70[d]	4.7	
Puckett et al. (2000)	Dare County, North Carolina	Summer	MCP	101.00	33.0	23
		Summer	Harmonic mean	53.00	11.0	23
Sisson et al. (2000)	Southwest Georgia	Winter	MCP	3.30[e]	1.9	74
		Winter	MCP	8.30[f]	4.0	70
Taylor et al. (1999*b*)	Lyon County, Kansas	Summer	95% kernel	65.00[g]	9.0	33
		Summer	95% kernel	75.00[h]	15	42
		Summer	95% kernel	103.00[i]	11.0	49
		Summer	95% kernel	54.00[j]	16.0	20
Taylor et al. (2000)	Lyon County, Kansas	Summer	95% kernel	14.00[k]	3.0	12

Table 1. Conitnued.

Source	Location	Season	Estimator used	Size (ha)	SE	*n*
Dixon et al. (1996)	Coastal plain of South Carolina	Winter	Harmonic mean	11.10	2.1	15
Wiseman and Lewis (1981)	Rogers County, Oklahoma	Winter	Other[l]	4.40	0.6	16
Urban (1972)	Jackson County, Illinois	Summer	MCP	7.57[m]	1.5	11
		Summer	MCP	16.67[n]	3.2	9
		Summer	MCP	6.39[o]	1.7	5
		Summer	MCP	15.58[p]	4.6	4
Yoho and Dimmick (1972)	Fayette County, Tennessee	Winter		6.76		5

[a] MCP = minimum convex polygon.

[b] Study used released, pen-raised birds.

[c] Birds situated near food plots; size estimates did not vary with season.

[d] Birds in non-food plot areas; size estimates did not vary with season.

[e] Minimum reported by Sisson et al. (2000).

[f] Maximum reported by Sisson et al. (2000).

[g] Males in cropland-dominated area.

[h] Females in cropland-dominated area.

Table 1. Conitnued.

[i] Males in rangeland-dominated area.

[j] Females in rangeland-dominated area.

[k] Study based on brood rearing adults during 21 days posthatch.

[l] Description of technique used given in Marchinton and Jeter (1966).

[m] Study based on mated males.

[n] Study based on unmated males.

[o] Study based on nesting females.

[p] Study based on post-nesting females.

the animal (Anderson 1982). A simple, discrete way to envision a utility distribution is to think of it as a grid lying across a plane with the grid cells representing areas on the plane; as animal locations accumulate in different grid cells, peaks are created above the plane's surface. The more locations that accumulate in a given cell, the higher the peak will be. Higher peaks across the plane indicate areas of more intense use (higher probability of use) with respect to the remainder of the plane.

Powell (2000) argued that kernel density estimators are better for estimating home range sizes and utility distributions than other techniques. Kernel methods for home range estimation are nonparametric; thus, they avoid any shape assumptions (Worton 1989, Seaman and Powell 1996, Powell 2000). The researcher determines the smoothness of the utility distribution by choosing the desired smoothing parameter, h. This parameter controls the amount of variation in each component of the home range estimate. Smaller h values reveal details in location data, whereas larger h values show the most obvious features of the data. When h is too small, results may be too variable, whereas they may be too biased when h is too large (Worton 1989, Worton 1995, Seaman and Powell 1996).

Two different methods of kernel estimators have been developed: the fixed and adaptive methods. With the fixed kernel method, h is held constant for the entire data set, whereas h varies with location density when using the adaptive kernel method. In using the adaptive kernel method, h is smaller in areas of more dense utilization and larger in areas of less dense utilization (Worton 1989, Powell 2000). Worton (1989) evaluated both methods and reported that the adaptive kernel estimate produced the best results when using least-squares cross-validation (LSCV) to choose the smoothing parameter, h.

Worton (1995) later reported that the fixed kernel method produced the least biased results in the evaluation of brush rabbit (*Sylvilagus bachmani*) telemetry locations. Seaman and Powell (1996) found the fixed kernel method, again using LSCV, gave better results than the adaptive kernel method when using simulated data and data from radio telemetry of black bears (*Ursus americanus*). Seaman et al. (1999) also reported that the fixed kernel estimator using LSCV produced the least-biased estimates of home range area on simulated location data.

There are some shortcomings of kernel home range estimators. The time sequence of animal locations is ignored, as with most estimators; thus, one must assume that animal locations are independent and time sequence information is irrelevant. Also, because kernel estimators are based on the probability that an animal will be located in a particular area of its home range, they may produce islands of use not connected to the main portion of a home range, thus producing 95% home range outlines with complicated shapes (Powell 2000). These convoluted home range shapes and islands of use would include areas that were used by an individual but may not include all areas the individual used as part of its home range.

Habitat Requirements of Bobwhites

Due to the vast geographical range of bobwhites, composition of habitat in occupied areas varies greatly. Stoddard (1931:12) stated, "It will be noted from the foregoing discussion of types of quail country that food and cover are fundamental requirements, and that where both are found in satisfactory quantities, the birds thrive over the whole country, regardless of geological and climatic differences." However, some of the habitat requirements remain consistent across their range, including the presence of grassy or herbaceous cover for nesting, cultivated crops or a natural source of plant food, and brushy or woody cover. Some amount of interspersion among these types might also be beneficial (Bidwell et al. 1991), although abundance may be independent of interspersion in many settings (Guthery 1999).

Due to the vast geographical range of bobwhites, it is evident they are adaptable birds. Guthery (1999) emphasized the adaptability of bobwhites with his comparison of different configurations of habitat patches. He indicated that there is "slack" in the configuration of habitat patches that may be usable by bobwhites. Slack was defined by pointing out that "...different patch configurations may lead to fully usable space and, hence, optimal habitat conditions" (Guthery 1999:249). Thus, there is no single definition of optimal habitat for bobwhites; rather, a large variety of arrangements of habitat patches are optimal.

Nesting cover often consists of warm-season grasses such as little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), Indiangrass (*Sorghastrum nutans*), or switchgrass (*Panicum virgatum*) (Bidwell et al. 1991). Quail nesting areas may have grasses of ≥15–20 cm tall (Bidwell et al. 1991). Typical heights reported for nest site grasses in other studies include 50 cm (Klimstra and Roseberry 1975), 52 cm (Taylor et al. 1999*a*), and 84 cm (Townsend et al. 2001).

Foraging habitat may seasonally consist of a patch for foraging on invertebrates (Bidwell 1991). Cultivated cropland may also be a valuable food source in areas where it is available (Rosene 1969, Roseberry and Klimstra 1984, Bidwell et al. 1991). Seeds are a staple in the diet of the bobwhite. The seeds of native forbs, grasses, shrubs, and trees are eaten (Bidwell et al. 1991).

Theories of Habitat Management

Guthery's (1997) evaluation of the food and interspersion hypotheses challenged the traditional ideas of habitat quality. It had been assumed that by increasing the availability of food for bobwhites, through the use of feeders, food plots, strip discing, or any other method, you would effectively increase the density of bobwhites. However, as pointed out by Guthery (1997), there is no solid research evidence that has shown food supplies to be limiting bobwhite survival or production, or that increasing food supplies increases bobwhites. An evaluation of the interspersion hypothesis, based on Leopold's (1933) law of interspersion, which states that increasing the density of edge habitat increases bobwhite density, shows that in different situations the 2 variables (edge and bobwhites) may or may not be correlated (Guthery and Bingham 1992, Guthery 1997). Bobwhite density may be positively correlated with increasing amounts of edge only if there is some amount of the area being considered that is not fully usable (Guthery and Bingham 1992). Otherwise, if all space is usable, increasing edge density will not be correlated to bobwhite density and edge will be redundant, or more edge will be available than required to meet the requirements of the population (Guthery and Bingham 1992, Guthery 1997). Upon evaluating the previously mentioned, generally accepted hypotheses for improving wildlife habitat, and noting the limitations of each, Guthery (1997) formulated the usable-space hypothesis.

Space is defined as a collection of points and, "To be fully usable, a point must by definition be associated with habitat compatible with the physical, behavioral, and physiological adaptations of bobwhites in a time-unlimited sense" (Guthery 1997:294). The usable-space hypothesis can be stated mathematically as

$$D = kF$$

where the abundance of quail on an area (D) is proportional to (k) functional space-time (F) available on an area (Guthery 1997, 2000, Guthery et al. 2000*a*).

STUDY AREA

This study was conducted primarily on the Tallahone Pasture on the Mesa Vista Ranch along the south side of the Canadian River, north of Pampa, in Roberts County, Texas, USA. Covering about 11,330 ha, the ranch lies along the Canadian Breaks in the Great Plains physiographic region (Jordan et al. 1984). Although cattle are grazed for about 5 months/year, the main purpose of the ranch is to support a sustainable population of bobwhites for recreational hunting. The grazing system is a modified form of low-intensity, low-frequency grazing with a varying stocking rate. Duration of grazing within a pasture is variable and is determined by the ranch manager based on a visual assessment of the vegetation cover available to bobwhites.

Tallahone Pasture covered about 797 ha. The minimum and maximum elevations were about 775 m and 859 m, with a mean of 808 m. The slope ranged from 0 to 26.3°, with a mean of 2.5°.

The area has a steppe climate. The climate is mesothermal in most years with an occasional microthermal winter (Jordan et al. 1984). The average growing season is about 192 days. Annual rainfall averages 52.6 cm (Odintz 1996), and winters are usually relatively dry (Jordan et al. 1984). Average minimum temperature for the area is –7 °C in January and July's average maximum temperature is 34 °C (Odintz 1996).

Mollisols are the major soil order of the region (Jordan et al. 1984). The major soil association for Tallahone Pasture is the Likes-Lincoln-Tivoli association. Soils in this association are deep, moderately rapidly to rapidly permeable sands that are found on uplands and bottomlands (Wyrick 1981). Roberts County is in the Rolling Plains vegetation area (Odintz 1996) and native plant species included buffalograss (*Buchloe dactyloides*), western wheatgrass (*Agropyron smithii*), switchgrass, little bluestem, big bluestem, western ragweed (*Ambrosia psilostachya*), sand sagebrush (*Artemesia filifolia*), plains yucca (*Yucca glauca*), plains pricklypear (*Opuntia macrorhiza*), sand plum (*Prunus angustifolia*), and skunkbush sumac (*Rhus aromatica*) in uplands. Cottonwood (*Populus deltoides*) and salt-cedar (*Tamarix gallica*) occurred in riparian and bottomland areas.

METHODS

Trapping

Northern bobwhites were trapped during 2 seasons (4 Sep 2000–26 Apr 2001 and 11 Sep 2001–9 Mar 2002). Traps were modified versions of those described by Stoddard (1931) and Schemnitz (1994). Traps had 2 funnel-type entrances and were baited with milo or a mixture of corn and milo and were checked 2 times/day to minimize the time of constraint for captured birds. Traps were placed in areas of the pasture that were accessible by roads and where single birds or coveys had been seen previously or in areas that were deemed suitable habitat.

Some birds of suitable size (>150 g) were fitted with a 6-g necklace-style radio-transmitter (American Wildlife Enterprises, Monticello, Florida, USA). Some transmitters were mortality sensing (more rapid pulse rate when collar does not move for 12 hours) and some were temperature sensing (pulse rate varied with temperature). Transmitters operated in the 148–154 MHz range with a minimum battery life expectancy of 6 months. The transmitter housing was a waterproof epoxy, painted brown to match the body feathers of quail. A Dacron line neck loop held the transmitter on the bird.

Sex and age-class (juv or ad) were determined for each bird captured. The sex was determined by the color of the chin, upper throat, and eye stripe (Stoddard 1931, Johnsgard 1975, Dimmick and Pelton 1994). Age was determined by the coloration of the tips of the primary coverts (Rosene 1969, Dimmick 1992, Dimmick and Pelton 1994). Birds were released at the trap site.

Monitoring

Each bird was located 2–6 times/week using triangulation (White and Garrott 1990). A 3-element, Yagi antenna and portable radio receiver (Model TR-5, Telonics, Incorporated, Mesa, Arizona, USA or Model TRX-2000S, Wildlife Materials, Incorporated, Carbondale, Illinois, USA) were used to monitor birds from points located by a global positioning system (GPS) unit (Trimble Navigation, Sunnyvale, California, USA or GARMIN International Incorporated, Olathe, Kansas, USA). There was some amount of unavoidable location error inherent in the use of a handheld GPS unit. However, this was random error and was minimized by allowing the GPS unit to average location estimates for points taken until the error rate dropped to an acceptable range (generally 3–5 m). Two azimuths were obtained using a mirror-sighting compass for each bird location so that locations could be estimated. Two azimuths were used, instead of three, to reduce the amount of error in location estimates (Nams and Boutin 1991). When possible, there was a difference of 30°–120° between each azimuth. The distance between the investigator and the bird was kept at a minimum (usually 20–50 m) while minimizing the disturbance to the bird to reduce the error of the triangulation (Springer

1979). This method also allowed identification of the habitat type the bird occupied, which was also recorded as each location estimate was obtained.

The 2 researchers responsible for obtaining the majority of radiolocations assessed their accuracy in obtaining radiolocations by taking 40 bearings toward radio transmitters at known locations, as determined with a GPS unit. Both bearing and location accuracy were assessed. Bearing accuracy was estimated by comparing the known location-to-location bearings with the observer's corresponding bearings (White and Garrott 1990) to assure that there was no bias in the methods used to locate individuals. The accuracy of estimated locations was determined by calculating the mean difference between the absolute values of estimated locations and known locations; the resulting value gave the mean error rate within a circular area around the actual location.

Home Range

Individual home ranges were determined from radiolocations. I used both the KHR and MCP (100%) home range estimators. I determined the appropriate smoothing parameter, *h*, for the KHR estimator using the LSCV method (Worton 1989). The home range estimate was considered to be that provided by the 95% CI for the KHR. During all seasons, the 25, 50, and 75% CIs were also calculated using the KHR. I considered the 25% level to be the core area of the home range estimates. All home range estimations were made using the Animal Movement extension v2.04 (Hooge et al. 1999) to ArcView GIS v3.2 with the Spatial Analyst extension (Environmental Systems Research Institute, Incorporated, Redlands, California, USA).

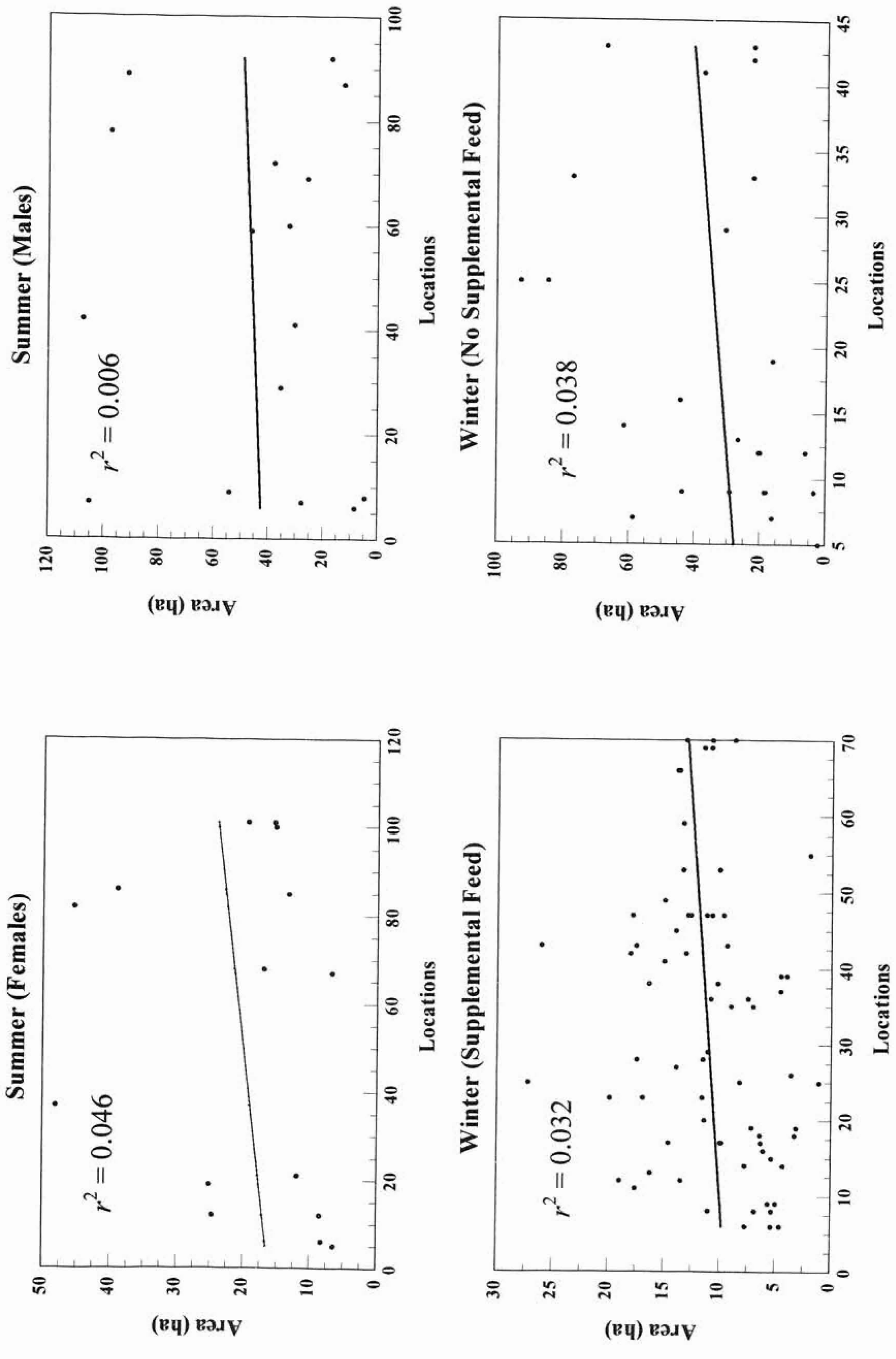
Home range sizes were estimated with respect to season: 2 covey seasons (28 Nov 2000–28 Mar 2001 and 10 Oct 2001–14 Mar 2002), 1 breeding season (19 Apr 2001–18

Sep 2001), and an annual set (28 Nov 2000–14 Mar 2002). The annual or composite set of home range estimates consisted of the home ranges of any individuals that were alive during >1 of the seasons discussed above, and included bird locations obtained throughout the study period. For this, all locations were used for each individual, including the locations that were dropped to account for the transitions in and out of the covey seasons. Mean home range sizes also were compared with historical estimates of bobwhite home range sizes (Table 1).

Supplemental feeding was implemented throughout the study area during the 2000–2001 covey season mentioned above. The study area was divided by Tallahone Creek; there were 20 feeders on the west side and 20 feeders on the east side of the creek. Feeders were located in areas deemed to be good bobwhite habitat and were filled with a mixture of corn and milo. During the 2001–2002 covey season only the feeders on the east side of the study area were filled. Thus, analysis of the 2000–2001 covey season's home ranges was divided to be comparable with the fed and unfed sides during the 2001–2002 season.

Home ranges were calculated for individuals with a minimum of 5 radiolocations. A linear regression was conducted to see how KHR areas varied with the number of radiolocations (Fig. 1). This was done for the KHR because it was the estimator used in the habitat use analyses and it is correlated to the MCP estimator. Although slopes were positive for all regression analyses, the number of radiolocations explained little variation in home range area (Fig. 1). The home ranges used in the regression were chosen to remove confounding effects of pooled home range sets containing males and females or individuals with and without access to supplemental feed.

Fig. 1. Relationship between estimated home range area and number of radiolocations for females ($n = 15$) and males ($n = 16$) in summer 2001, and individuals with ($n = 80$) and without ($n = 27$) access to supplemental feed pooled for winter 2000–2001 and winter 2001–2002 on Mesa Vista Ranch, Roberts County, Texas.



Summer (Females)
$r^2 = 0.046$
Area (ha)
Locations
Summer (Males)
$r^2 = 0.006$
Area (ha)
Locations
Winter (Supplemental Feed)
$r^2 = 0.032$
Area (ha)
Locations
Winter (No Supplemental Feed)
$r^2 = 0.038$
Area (ha)
Locations

Habitat Availability

I evaluated bobwhite preference for habitat types based on the amount of each habitat type that was available and the amount of use it received. Each habitat type was identified and delineated through the use of Geographic Information System (GIS) technology, and the available area of each type was measured. A habitat map was created to facilitate determination of the amount of each habitat type available. Classifications were obtained from a digital aerial photo (1996; 1-m resolution), a false color composite and normalized differential vegetation index generated from an IKONOS satellite image (2001; 4-m resolution), point habitat identifications collected at each radiolocation, 10-m line transect habitat classifications conducted in the summer of 2001, and prior knowledge of the area. The available amount of each classified habitat type was then calculated using GIS routines.

The 9 habitat types considered, and their respective areas (total amount available, percent of total study area) are given with a brief description. Riparian areas (18.3 ha, 2.3%) were low-lying areas, part of which were inundated with water during portions of the year and were primarily covered with cottonwood, willow (*Salix* spp), cattail (*Typha latifolia*), rushes (*Juncus* spp.), and sedges (*Carex* spp.). Grass bottomlands (81.0 ha, 10.2%) were large, open areas consisting of dense grasses including western wheatgrass, switchgrass, tall fescue (*Festuca arundinacea*), Havard panicum (*Panicum havardii*), and alkali sacaton (*Sporobolus airoides*). Grass bottomlands with salt-cedar (44.1 ha, 5.5%) were similar to grass bottomlands with the additional structure provided by salt-cedar. Grass uplands (140.3 ha, 17.6%) were upland areas covered primarily in western ragweed, camphor weed (*Heterotheca pilosa*), western wheatgrass, and little bluestem.

Sand sagebrush (293.8 ha, 36.9%) were large areas covered primarily in sand sagebrush. Mixed shrub (138.7 ha, 17.4%) were areas covered in skunkbrush sumac and sand plum thickets. Other wooded areas (16.7 ha, 2.1%) were wooded areas other than riparian and were covered mostly by hackberry and cottonwood. Hilltop areas (52.7 ha, 6.6%) were hills and slopes that were sparsely vegetated. The classification other (10.9 ha, 1.4%) included any areas that did not fit within the other habitat types as defined, primarily open water, the vegetation in and adjacent to water holes, and roads. Due to overall avoidance of the "hill" habitat class because of its general lack of vegetation structure, this class was not considered during the habitat use analyses.

Usable Space Availability

The proportion of usable space in each habitat type was estimated with the cone of vulnerability, set forth by Kopp et al. (1998:885) as, "a volume of air space within which a raptor would have an unobstructed line of flight to an exposed bobwhite," and as further described by Guthery (2000). During August 2001, starting points were randomly located in each of the habitat types and transects were walked along a random compass bearing and measurements of the cone were taken at 10-m intervals along 100-m transects until 100 estimates were obtained. This process was repeated for each habitat class except for mixed shrub. In the mixed-shrub habitat type, measurements were taken at 5-m intervals along transects of varying length, also until 100 estimates were obtained, due to the smaller patch sizes of this habitat type. Measurements were conducted in the same manner along the same transects during January 2002 in all habitat types except the riparian and grass bottomland classes. During winter sampling, 70 estimates of the cone were obtained in the riparian area because 3 of the summer transects were under water, and 80 estimates were obtained in the grass bottomland, because 2 summer transects had been subjected to prescribed burns before winter sampling.

To estimate the cone of vulnerability, the angle of visual obstruction (Kopp et al. 1998: fig. 1) represented by a line through space that intersects with the top of the object causing the obstruction was measured along each of 8 compass radii (north, northeast, east, southeast, south, southwest, west, and northwest) for each location point. This was done using a 2-m pole with a digital level attached; the pole was placed on the random point and aimed at the top of the object causing the obstruction. The cause of the obstruction also was recorded and frequencies were calculated for each habitat type and season considered (Tables 2 and 3). The mean angle of obstruction for the 8 radii was used to estimate the cone of vulnerability (Kopp et al. 1998).

Using the preferred cone volumes in Kopp et al. (1998) and Guthery et al. (2000*b*), I determined a mean angle of obstruction of ≥35° to be a liberal definition of point usability (this point might be a little too open) and a mean angle of obstruction of ≥45° to be a more conservative estimate of point usability. Upon comparing the estimated proportions of usable space based on the 35° and 45° mean angles of obstruction, I found there to be a minimal difference in these proportions (Table 4). Therefore, I elected to use only the estimated amount of usable space in each habitat type for each season as determined with the mean angle of obstruction ≥45°.

Data Analysis

Home Range Estimates.—My intention was to provide descriptive data regarding estimates of home range size. Therefore, only the mean and SE are reported for the 2 home range estimators used. During the summer of 2001, the pooled mean and the

Table 2. Causes (%) of obstruction for the cone of vulnerability among different habitat types on the Mesa Vista Ranch, Roberts County, Texas, summer 2001.

Category Common name (Genus species)	Habitat type[a, b]							
	R	GB	GS	GU	SS	MS	OW	H
Forbs								
Western ragweed (*Ambrosia psilostachya*)	3.3	2.4	12.1	21.9	4.6	0.0	3.1	5.1
Texas croton (*Croton texensis*)	0.0	0.0	0.5	1.1	0.9	0.3	0.0	2.6
Buckwheat (*Eriogonum annuum*)	0.0	0.0	0.3	6.0	4.5	1.3	0.0	4.5
Indian blanket (*Gaillardia pulchella*)	0.0	0.0	0.0	4.0	3.8	0.0	0.0	1.4
Scarlet gaura (*Gaura coccinea*)	0.0	0.0	0.0	0.1	1.1	0.9	0.0	1.8
Annual broomweed (*Gutierrezia dracunculoides*)	0.0	0.0	0.0	0.4	0.0	0.0	0.0	13.8
Annual sunflower (*Helianthus annuus*)	0.0	0.0	0.1	1.0	0.0	0.0	1.8	0.0
Camphor weed (*Heterotheca pilosa*)	0.0	0.0	0.5	21.0	7.9	0.3	1.4	0.1
Rushes (*Juncus* spp.)	9.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gayfeather (*Liatris punctata*)	0.0	0.0	0.0	0.1	0.1	0.0	0.0	4.1
Beebalm (*Monarda citriodora*)	0.0	0.0	0.0	0.8	0.8	0.6	0.0	0.0
Groundsel (*Senecio* sp.)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	19.3
Silverleaf nightshade (*Solanum elaeagnifolium*)	0.5	0.0	0.0	1.6	0.4	0.0	2.1	0.1
Queen's delight (*Stillingia sylvatica*)	0.0	0.0	0.0	0.8	0.8	0.1	0.0	2.8

Table 2. Continued.

Category Common name (Genus species)	Habitat type[a, b]							
	R	GB	GS	GU	SS	MS	OW	H
Woody								
False indigo (*Amorpha fruticosa*)	4.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sand sagebrush (*Artemesia filifolia*)	0.0	0.0	0.0	5.8	68.6	10.1	2.4	8.0
Hackberry (*Celtis occidentalis*)	0.0	0.1	0.6	0.0	0.0	0.6	65.3	0.0
Buttonbush (*Cephalanthus occidentalis*)	6.5	0.0	0.3	0.0	0.0	0.0	0.0	0.0
Cottonwood (*Populus deltoids*)	7.4	0.1	0.0	0.0	0.0	0.0	10.0	0.0
Sand plum (*Prunus angustifolia*)	0.5	0.0	0.0	0.0	0.0	34.5	0.0	0.1
Skunkbush sumac (*Rhus aromatica*)	4.0	0.0	2.0	1.5	1.4	50.5	7.4	3.0
Sandbar willow (*Salix exigua*)	8.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Prairie willow (*S. humilis*)	4.8	1.0	7.0	0.0	0.0	0.0	0.0	0.0
Black willow (*S. nigra*)	8.6	0.5	0.0	0.1	0.0	0.0	0.0	0.0
Salt-cedar (*Tamarix gallica*)	0.1	0.0	15.6	0.0	0.0	0.0	0.0	0.0
Other woody spp.	0.5	0.0	0.0	0.1	0.1	0.0	2.1	1.4
Hill[c]	0.0	0.0	0.0	0.1	0.0	0.0	0.0	5.6

[a] Habitat types were R = riparian, GB = grass bottomland, GS = grass bottomland with salt-cedar, GU = grass upland, SS = sand sagebrush, MS = mixed shrub, OW = other wooded, H = hill.

Table 2. Continued.

[b] $n = 800$ for all habitat types (100 cone measurements per habitat type and 8 radii for each measurement).

[c] Hill accounts for instances where topography was the obstruction.

Table 3. Causes (%) of obstruction for the cone of vulnerability among different habitat types on the Mesa Vista Ranch, Roberts County, Texas, winter 2001–2002.

Category Common name (Genus species)	Habitat type[a]							
	R[b]	GB[c]	GS[d]	GU[d]	SS[d]	MS[d]	OW[d]	H[d]
Forbs								
Western ragweed (*Ambrosia psilostachya*)	3.2	0.5	5.6	18.0	3.0	0.1	0.5	3.4
Texas croton (*Croton texensis*)	0.0	0.0	0.0	0.4	2.4	0.0	0.0	1.0
Buckwheat (*Eriogonum annuum*)	0.0	0.0	0.5	9.3	5.1	3.0	0.1	5.3
Annual broomweed (*Gutierrezia dracunculoides*)	0.0	0.0	0.0	1.0	0.9	0.0	0.0	14.8
Camphor weed (*Heterotheca pilosa*)	0.9	1.3	0.6	28.6	12.5	2.1	1.5	1.3
Plains yucca (*Yucca glauca*)	0.0	0.0	0.0	0.4	0.0	0.0	0.0	6.9
Groundsel (*Senecio* sp.)	0.0	0.0	0.0	0.0	0.3	0.0	0.0	8.6
Other forb spp.	1.4	0.0	0.6	4.1	0.3	0.0	0.0	3.1
Grasses and grass-like								
Western wheatgrass (*Agropyron smithii*)	3.4	11.9	9.5	10.4	0.0	0.0	2.0	0.4
Annual threeawn (*Aristida oligantha*)	0.0	0.0	0.0	0.6	0.9	0.5	0.0	3.8
Sideoats grama (*Bouteloua curtipendula*)	0.0	0.0	0.0	0.0	0.0	0.1	0.0	5.9
Japanese brome (*Bromus japonicus*)	2.3	4.1	5.3	2.3	0.0	0.0	1.0	0.0
Sedges (*Carex* spp.)	12.5	7.5	0.0	0.0	0.0	0.0	0.0	0.0

Table 3. Continued.

Category Common name (Genus species)	Habitat type[a]							
	R[b]	GB[c]	GS[d]	GU[d]	SS[d]	MS[d]	OW[d]	H[d]
Bermudagrass (*Cynodon dactylon*)	3.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tall fescue (*Festuca arundinacea*)	0.0	3.8	0.0	0.0	0.0	0.0	0.0	0.0
Vine mesquite (*Panicum obtusum*)	0.0	19.5	15.1	4.6	0.0	0.0	1.5	0.0
Havard panicum (*P. havardii*)	0.0	20.2	9.3	0.0	0.0	0.0	0.0	0.0
Switchgrass (*P. virgatum*)	4.8	11.3	7.1	2.3	0.0	0.0	0.0	0.0
Little bluestem (*Schizachyrium scoparium*)	0.7	0.0	4.1	7.4	0.3	0.1	0.0	19.3
Prairie cordgrass (*Spartina pectinata*)	2.1	3.8	0.0	0.0	0.0	0.0	0.0	0.0
Alkali sacaton (*Sporobolus airoides*)	0.0	13.8	17.9	1.0	0.0	0.0	0.0	0.0
Cattail (*Typha latifolia*)	6.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other grass spp.	0.5	0.0	0.0	0.9	0.4	0.0	0.0	1.4
Woody								
Sand sagebrush (*Artemesia filifolia*)	0.0	0.0	2.3	7.5	70.0	14.1	1.4	10.6
Hackberry (*Celtis occidentalis*)	1.6	0.8	0.4	0.4	0.0	0.1	59.8	0.0
Buttonbush (*Cephalanthus occidentalis*)	11.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cottonwood (*Populus deltoids*)	5.5	1.1	0.0	0.0	0.0	0.0	14.9	0.0
Sand plum (*Prunus angustifolia*)	0.0	0.0	0.0	0.0	1.3	34.0	0.0	0.3

Table 3. Continued.

Category Common name (Genus species)	Habitat type[a]							
	R[b]	GB[c]	GS[d]	GU[d]	SS[d]	MS[d]	OW[d]	H[d]
Skunkbush sumac (*Rhus aromatica*)	3.4	0.0	0.4	0.1	2.1	45.8	11.6	0.8
Prairie willow (*Salix humilis*)	10.4	0.0	2.0	0.0	0.0	0.0	0.0	0.0
Black willow (*S. nigra*)	14.5	0.5	0.0	0.0	0.0	0.0	0.0	0.0
Salt-cedar (*Tamarix gallica*)	8.6	0.0	19.4	0.0	0.0	0.0	0.0	0.0
Grape (*Vitis* spp.)	0.0	0.0	0.0	0.0	0.0	0.0	5.8	0.0
Other woody spp.	1.8	0.0	0.0	0.0	0.0	0.0	0.0	1.0
Hill[e]	0.2	0.3	0.0	1.0	0.8	0.0	0.0	12.5

[a] Habitat types were R = riparian, GB = grass bottomland, GS = grass bottomland with salt-cedar, GU = grass upland, SS = sand sagebrush, MS = mixed shrub, OW = other wooded, H = hill.

[b] *n* = 560 (70 cone measurements and 8 radii for each measurement).

[c] *n* = 640 (80 cone measurements and 8 radii for each measurement).

[d] *n* = 800 (100 cone measurements and 8 radii for each measurement).

[e] Hill accounts for instances where topography was the obstruction.

Table 4. Proportion (*P*) of mean angles of obstruction for the cone of vulnerability with minimum angles of 35° and 45° as measured across habitat types and seasons (summer 2001 and winter 2001–2002) on the Mesa Vista Ranch, Roberts County, Texas.

Season	Minimum mean angles of obstruction			
	≥ 35°		≥ 45°	
Habitat class	*P*	SE	*P*	SE
Summer				
Riparian	1.00	0.00	0.97	0.02
Grass bottomland	0.97	0.02	0.95	0.02
Grass bottomland with salt-cedar	1.00	0.00	0.99	0.01
Grass upland	0.71	0.05	0.57	0.05
Sand sagebrush	0.89	0.03	0.79	0.04
Mixed shrub	1.00	0.00	0.98	0.01
Other wooded	1.00	0.00	0.99	0.01
Hill	0.41	0.05	0.28	0.04
Winter				
Riparian	0.89	0.04	0.81	0.05
Grass bottomland	0.90	0.03	0.90	0.03
Grass bottomland with salt-cedar	0.93	0.03	0.87	0.03
Grass upland	0.56	0.05	0.47	0.05
Sand sagebrush	0.68	0.05	0.56	0.05
Mixed shrub	0.94	0.02	0.88	0.03
Other wooded	1.00	0.00	0.98	0.01
Hill	0.16	0.04	0.13	0.03

Table 4. Continued.

Season Habitat class	Minimum mean angles of obstruction			
	≥ 35°		≥ 45°	
	P	SE	*P*	SE
Composite[a]				
Riparian	0.95	0.02	0.89	0.03
Grass bottomland	0.94	0.03	0.93	0.03
Grass bottomland with salt-cedar	0.97	0.01	0.93	0.02
Grass upland	0.64	0.05	0.52	0.05
Sand sagebrush	0.79	0.04	0.68	0.05
Mixed shrub	0.97	0.01	0.93	0.02
Other wooded	1.00	0.00	0.99	0.01
Hill	0.29	0.04	0.21	0.04

[a] Composite angles of obstruction were based on the average of the summer and winter values.

individual means for males and females are reported. Differences in home range size attributable to sex were only considered during the breeding season because bobwhites are in coveys comprised of both sexes during the remainder of the year.

Habitat Selection.— Habitat preference was based upon the proportion of radiolocations for an individual animal that occurred in each habitat type compared with its availability (Neu et al. 1974). Use of habitat resources was measured for individual birds, but habitat availability was measured across the entire pasture and within each home range; these estimates of availability represent study designs II and III, respectively, as discussed by Manly et al. (1993). Evaluation of preference-avoidance behavior at these 2 levels required different analytical approaches.

To determine selection of habitat classes across the entire study area, all bird locations were pooled for each season. From these pooled datasets, I determined the proportion of use for each habitat type within each season. From the habitat map, I obtained the proportion of each habitat type available on the study area. I used Manly et al.'s (1993:42–47) selection ratio (use/availability) and constructed approximate, simultaneous 95% confidence intervals on this ratio using equation 4.15 of Manly et al. (1993:46). Bonferroni's inequality was used to adjust the CIs for multiple comparisons (Manly et al. 1993:47). Selection was assumed when the lower-limit of the CI was >1, avoidance was assumed when the upper-limit of the CI was <1, and random use was assumed when the CIs overlapped 1.

To calculate preference and avoidance of habitat types by individuals inside their home ranges and across different seasons, I used Ivlev's electivity index as the basis for the selection index (I) given as

$$I = (U - A) / (U + A),$$

where U = proportional use of each habitat type by individual birds for a given season and A = the proportional amount of each habitat type available inside the individual's home range (determined by intersecting home ranges with the habitat map in ArcView GIS). This index produced values ranging from −1 to 1. Negative values indicated an avoidance of and positive values indicated a preference for the habitat. Values at or near zero indicated random use or use in proportion to availability. Because the nature of the probability distribution for I values was unknown, I used bootstrapping (Mooney and Duval 1993, Davison and Hinkley 1997) to quantify the degree of selection among cover types. The method used was similar to that described by Suedkamp (2000) and Guthery et al. (2001*a*). Bootstrapping involved random, repeated sampling with replacement from the set of I values for each habitat type within each season and then constructing a sampling distribution (distribution of means). Bootstrapping was conducted using SYSTAT version 8.0 (SPSS 1998); 1,000 samples were drawn for each habitat class and season where n, the number of I values drawn for each bootstrap simulation, was based on the number of home ranges the habitat type occurred in during the respective seasons (not all habitat types occurred in all home ranges; Table 5). I used ProStat version 2.0a (Poly Software International 1999) to generate histograms showing the distribution of bootstrap means. Preference for a habitat type was indicated if ≥95% of the distribution was >0. Likewise, avoidance was indicated if ≥95% of the distribution was <0. Otherwise, random use of the habitat type was assumed. Following methods similar to those presented by Guthery et al. (2001*a*), bootstrap probabilities (P_{boot}) were calculated to support assertions on the preference or avoidance of habitat types. These bootstrap

Table 5. Proportion of home ranges containing each of 8 cover types during different seasons on Mesa Vista Ranch, Roberts County, Texas, 2001-2002 (n = total number of home ranges used in habitat preference-avoidance analysis during each season).

Season Habitat class	P
Summer 2001 (n = 14)	
Riparian	0.29
Grass bottomland	0.79
Grass bottomland with salt-cedar	0.86
Grass upland	1.00
Sand sagebrush	1.00
Mixed shrub	1.00
Other wooded	0.71
Other	1.00
Winter 2000–2001 (n = 36)	
Riparian	0.47
Grass bottomland	0.44
Grass bottomland with salt-cedar	0.56
Grass upland	1.00
Sand sagebrush	1.00
Mixed shrub	1.00
Other wooded	0.69
Other	0.44
Winter 2001–2002 (n = 44)	
Riparian	0.36

Table 5. Continued

Season Habitat class	*P*
Grass bottomland	0.59
Grass bottomland with salt-cedar	0.61
Grass upland	1.00
Sand sagebrush	1.00
Mixed shrub	1.00
Other wooded	0.59
Other	0.59
Composite[a] (n = 19)	
Riparian	0.53
Grass bottomland	0.79
Grass bottomland with salt-cedar	0.84
Grass upland	1.00
Sand sagebrush	1.00
Mixed shrub	1.00
Other wooded	0.79
Other	0.74

[a] Accounts for the home ranges of individuals alive across >1 season.

probabilities give the probability that a statement is true based on the bootstrap simulations (Guthery et al. 2001*a*).

Adjustments for Usable Space.— The usable-space hypothesis predicts random use of available habitat types when all space is usable (Guthery 1997). If the hypothesis is correct, by deducting unusable space I expected the preferred and avoided habitat classes from the initial preference-avoidance analysis would tend more towards random use. I subtracted unusable space based on 2 criteria. (1) If a habitat type was not used, its area was subtracted from usable space. (2) If a habitat type was to some degree usable, the estimated amount unusable was subtracted from the area of that type (proportion unusable times area of type, based on the cone of vulnerability). This was essentially similar to creating a new study area consisting of fully usable space.

The riparian, grass bottomland, other wooded, and other habitat classifications were dropped from consideration with respect to the challenge of the usable-space hypothesis because these cover types are known to represent unusable space. The classification "other" was dropped because the cone of vulnerability could not be used to estimate the amount of usable space because this classification could not be defined specifically. The riparian, grass bottomland, and other wooded classes were dropped because they consist of habitat that does not conform to the general habitat requirements of bobwhites. Guthery et al. (2001*b*) found that increases in mature woodland corresponded with decreases in bobwhite abundance across the landscape as indicated by a call-count index. It is also known that herbaceous vegetation is necessary for forage and near-ground cover (Rosene 1969). To some degree, bare ground is also a necessity in the habitat requirements of bobwhites, as well as woody cover provided by shrubs and trees (Rosene 1969, Kopp et al. 1998, Guthery et al. 2001*a*). The requirements outlined above support the reasoning for dropping the riparian, grass bottomland, and other wooded habitat classes when determining the amount of usable space. Riparian areas were characterized by mature cottonwoods, willows, and an understory of dense grasses and cattails. The grass bottomland was comprised of dense grasses with virtually no bare ground. The other wooded class consisted primarily of hackberry, which shaded out virtually all herbaceous vegetation in the understory.

Cover types remaining after the above deductions included mixed shrub, grass bottomland with salt-cedar, grass upland, and sand sagebrush. The availability of usable space in these cover types was determined by multiplying area times the proportion of points with an obstruction angle ≥45° (see earlier). For example, if 100 ha of the sand sagebrush were available but 80% was usable based on the obstruction angle, then 80 of the 100 ha were deemed usable space.

RESULTS

Trapping Success

During the 2000–2001 trapping season, 395 bobwhites were captured, 304 were banded, 91 were fitted with radio transmitters, and 178 were recaptured. During the 2001–2002 trapping season, 295 individuals were captured, 231 were banded, 77 were fitted with radio transmitters, and 105 were recaptured (including 23 recaptures initially banded during the 2000–2001 trapping season).

Telemetry Accuracy

Accuracy assessment of the radio telemetry methods showed there was no bias in estimated azimuths. The average error in bearing estimates was −1.43° (SE = 2.34, n =

80). Based on the mean of the absolute values of the differences between estimated and actual locations, estimated locations, on average, were within a 360° radius of 8.15 m (SE = 0.84, $n = 40$) from actual locations.

Home Range Estimates

The pooled estimate of home-range size for the breeding season (19 Apr–18 Sep 2001) averaged 33.5 ± 5.3 ha ($n = 31$) using the 95% KHR estimate and 38.3 ± 6.4 ha ($n = 31$) using the MCP estimator. The core-area estimate was 1.6 ± 0.3 ha for the pooled set of breeding season ranges. Home ranges of males during the breeding season averaged 45.8 ± 8.8 ha ($n = 16$) using the 95% KHR estimate and 46.0 ± 10.4 ha ($n = 16$) using the MCP estimator, whereas home ranges of females during the breeding season averaged 20.3 ± 3.5 ha ($n = 15$) using the 95% KHR estimate and 30.1 ± 7.0 ha ($n = 15$) using the MCP estimator. The core area estimates for males and females were 2.2 ± 0.5 ha and 0.9 ± 0.2 ha, respectively.

Mean covey-season home ranges were smaller than mean breeding-season ranges. During the 2000–2001 covey season, estimates of home ranges pooled across the study area averaged 10.6 ± 0.7 ($n = 47$) ha using KHR and 11.4 ± 1.2 ($n = 47$) using MCP, with a mean core area of 0.5 ± 0.03 ha ($n = 47$). The pooled mean of home-range estimates during the 2001–2002 covey season was 21.7 ± 2.5 ha ($n = 64$) using KHR and 14.3 ± 1.6 ha ($n = 64$) using MCP, with a mean core area of 1.3 ± 0.2 ha ($n = 64$).

The means of home range estimates were about equal for all instances where supplemental feeding was implemented during both covey seasons (Table 6). However, during the 2001–2002 covey season, estimates of home range on the west side (the side

Table 6. Mean home range estimates (ha) of northern bobwhites, calculated using fixed kernel (KHR) and minimum convex polygon (MCP) estimators, on the Mesa Vista Ranch, Roberts County, Texas, 2001-2002.

Season		Locations[b]		Days[c]		KHR								MCP (100%)	
classes	n^a	$\bar{x}$	SE	$\bar{x}$	SE	25%	SE	50%	SE	75%	SE	95%	SE	$\bar{x}$	SE
Summer 2001															
Pooled	31	50.2	6.3	82.3	9.6	1.6	0.31	5.3	1.10	13.0	2.57	33.5	5.30	38.3	6.41
Males	16	47.2	8.2	76.3	12.9	2.2	0.52	7.6	1.94	18.3	4.53	45.8	8.77	46.0	10.43
Females	15	53.5	9.9	88.8	14.5	0.9	0.21	2.9	0.53	7.3	1.12	20.3	3.54	30.1	6.96
Winter 2000–2001															
Pooled	47	37.1	3.1	60.7	5.1	0.5	0.03	1.3	0.09	3.6	0.26	10.6	0.68	11.4	1.16
East side[d]	27	37.0	3.7	60.0	6.2	0.4	0.04	1.9	0.12	3.4	0.38	10.6	0.87	10.6	1.51
West side[d]	18	35.9	5.8	59.0	9.6	0.5	0.05	1.4	0.14	3.9	0.35	10.7	1.25	11.6	1.94
Winter 2001–2002															
Pooled	64	24.2	1.7	80.6	6.4	1.3	0.16	4.0	0.52	9.9	1.26	21.7	2.51	14.3	1.59
East side[d]	35	24.8	2.2	77.4	8.6	0.6	0.07	1.7	0.18	4.1	0.40	11.6	1.06	10.2	1.20
West side[e]	27	22.4	2.8	82.4	10.2	2.1	0.31	7.0	0.96	17.2	2.25	33.6	4.72	19.0	3.15

Table 6. Continued.

Season		Locations[b]		Days[c]		KHR								MCP (100%)	
classes	n[a]	$\bar{x}$	SE	$\bar{x}$	SE	25%	SE	50%	SE	75%	SE	95%	SE	$\bar{x}$	SE
Composite															
Pooled[f]	42	78.0	6.6	154.5	12.0	1.6	0.27	5.0	0.79	11.9	1.63	34.5	4.41	47.4	6.16

[a] Number of home ranges estimates.

[b] Number of radio locations used.

[c] Number of days radio collar was active.

[d] Supplemental feed was provided in feeders.

[e] No supplemental feed was available.

[f] Accounts for the home ranges of individuals alive across >1 season.

without supplemental feeding) averaged 2 to 3 times the size of all estimates where supplemental feed had been provided (Table 6).

The overall mean of the composite estimates was 34.5 ± 4.4 ha (n = 42) using KHR and 47.4 ± 6.2 ha (n = 42) using MCP. The mean core area estimate for the composite set was 1.6 ± 0.3 ha (n = 42).

Habitat Use

Study-Area Level.—Analysis of habitat selection behavior at the study area level was conducted with all bird locations pooled for the respective seasons. Based upon all locations obtained during the breeding season (n = 961), the mixed shrub was the only preferred habitat class (95% CI = 2.92–3.43). Avoided habitat classes during this season included grass upland (95% CI = 0.04–0.18), other wooded (95% CI = -0.04–0.64), grass bottomland (95% CI = 0.21–0.55), and sand sagebrush (95% CI = 0.68–0.90). The riparian (95% CI = 0.23–1.23), other (95% CI = 0.23–1.75), and grass-bottomland-with-salt-cedar (95% CI = 0.74–1.52) habitat classes displayed use in proportion to availability during the breeding season.

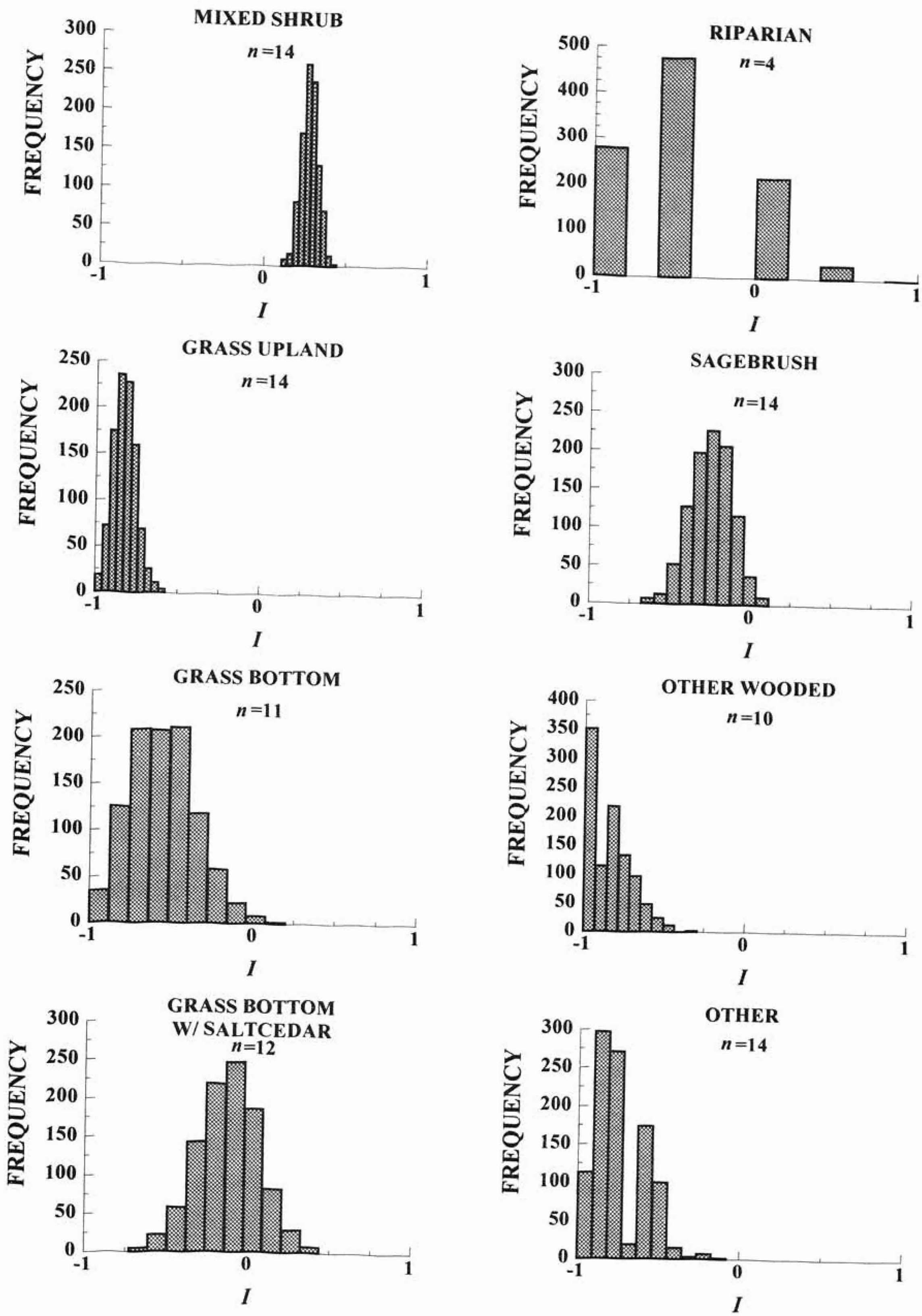
Considering all bird locations obtained during the winters of 2000–2001 (n = 1,513) and 2001–2002 (n = 1,351), the 2 covey seasons followed the same trends of preference, avoidance, and random use of all habitat types. Thus, the CI's for these 2 seasons are expressed together (CI for winter 2000–2001; CI for winter 2001–2002). The mixed-shrub habitat class was the only type displaying preferential use during both seasons (95% CI = 4.54–4.85; 95% CI = 3.66–4.07). Avoided habitat types during the covey seasons were grass upland (95% CI = -0.01–0.04; 95% CI = 0.15–0.32), other (95% CI = -0.09–0.29; 95% CI = -0.08–0.52), grass bottomland (95% CI = 0.04–0.18;

95% CI = 0.17–0.42), sand sagebrush (95% CI = 0.16–0.26; 95% CI = 0.36–0.51), and other wooded (95% CI = 0.04–0.59; no use recorded). No bird locations were obtained in the other wooded habitat class during the second covey season; thus, no CI was reported. Randomly used habitat classes during the covey seasons were the grass-bottomland-with-salt-cedar (95% CI = 0.71–1.30; 95% CI = 0.83–1.50) and riparian (95% CI = 0.58–1.55; 95% CI = 0.58–1.61) classes.

The composite set provided a good summary of habitat-use behaviors for all seasons at the study-area level. With all bird locations (n = 4,141) pooled across all seasons, mixed shrub was the only habitat class that was preferred (95% CI = 3.91–4.14). Avoided habitat classes at the study-area level included grass upland (95% CI = 0.08–0.14), other wooded (95% CI = 0.06–0.31), grass bottomland (95% CI = 0.17–0.30), other (95% CI = 0.13–0.57), and sand sagebrush (95% CI = 0.40–0.49). As during the individual seasons, both the riparian (95% CI = 0.66–1.21) and grass-bottomland-with-salt-cedar (95% CI = 0.90–1.27) habitat classes were used in proportion to the amount available.

Within-Home-Range Level.—At the within-home-range level, all conclusions on habitat preference and avoidance were based on P_{boot} values ranging from 0.97 to 1.0. Interpretation of the distribution of bootstrap means showed that during the breeding season (Fig. 2), avoided habitat classes included grass bottomland, grass upland, sand sagebrush, other wooded, and other. Mixed shrub was the only preferred habitat class, and the grass-bottomland-with-salt-cedar and riparian habitat classes displayed use in proportion to availability.

Fig. 2. Frequency distribution of bootstrap means (1,000 replications of size *n*) for selection index (*I*) values indicating within-home-range preference-avoidance behavior of northern bobwhites for 8 habitat types on Mesa Vista Ranch, Roberts County, Texas, 19 April–18 September 2001. Size *n* refers to the number of home ranges that each habitat type occurred in during this season.


MIXED SHRUB
n=14
RIPARIAN
n=4
GRASS UPLAND
n=14
SAGEBRUSH
n=14
GRASS BOTTOM
n=11
OTHER WOODED
n=10
GRASS BOTTOM
W/ SALTCEDAR
n=12
OTHER
n=14
FREQUENCY
I

During the 2000–2001 covey season (Fig. 3), the mixed-shrub class was the only preferred habitat; all other habitat types were avoided. However, during the 2001–2002 covey season (Fig. 4), both the mixed-shrub and the riparian habitat classes were preferred, and all other habitat classes were avoided.

Habitat selection behavior at the within-home-range level of the composite set (Fig. 5) of home ranges reflected the same trends as the other seasons considered. Mixed shrub was the only habitat class indicating a preference. The composite set also indicated random use of riparian areas and avoidance of all other habitat types

Usable Space

Study-Area Level.—Evaluation at the study-area level showed the mixed-shrub class was consistently preferred during all seasons, but to a lesser degree than when all available habitat was considered (breeding season: 95% CI = 2.07–2.39; first covey season: 95% CI = 2.71–2.86; second covey season: 95% CI = 2.22–2.44; composite: 95% CI = 2.53–2.66). The grass-upland habitat class was avoided across all seasons, though to a slightly lesser degree than when all available habitat was considered (breeding season: 95% CI = 0.05–0.21; first covey season: 95% CI = -0.004–0.04; second covey season: 95% CI = 0.18–0.35; composite: 95% CI = 0.09–0.16). Sand sagebrush was increasingly avoided when compared to the analysis using all available habitat (breeding season: 95% CI = 0.60–0.77; first covey season: 95% CI = 0.15–0.24; second covey season: 95% CI = 0.35–0.48; composite: 95% CI = 0.36–0.43). When considering only usable space, the grass-bottomland-with-salt-cedar habitat class was avoided across all seasons (first covey season: 95% CI = 0.43–0.77; second covey season: 95% CI = 0.52–

Fig. 3. Frequency distribution of bootstrap means (1,000 replications of size *n*) for selection index (*I*) values indicating within-home-range preference-avoidance behavior of northern bobwhites for 8 habitat types on Mesa Vista Ranch, Roberts County, Texas, 28 November 2000–28 March 2001. Size *n* refers to the number of home ranges that each habitat type occurred in during this season.

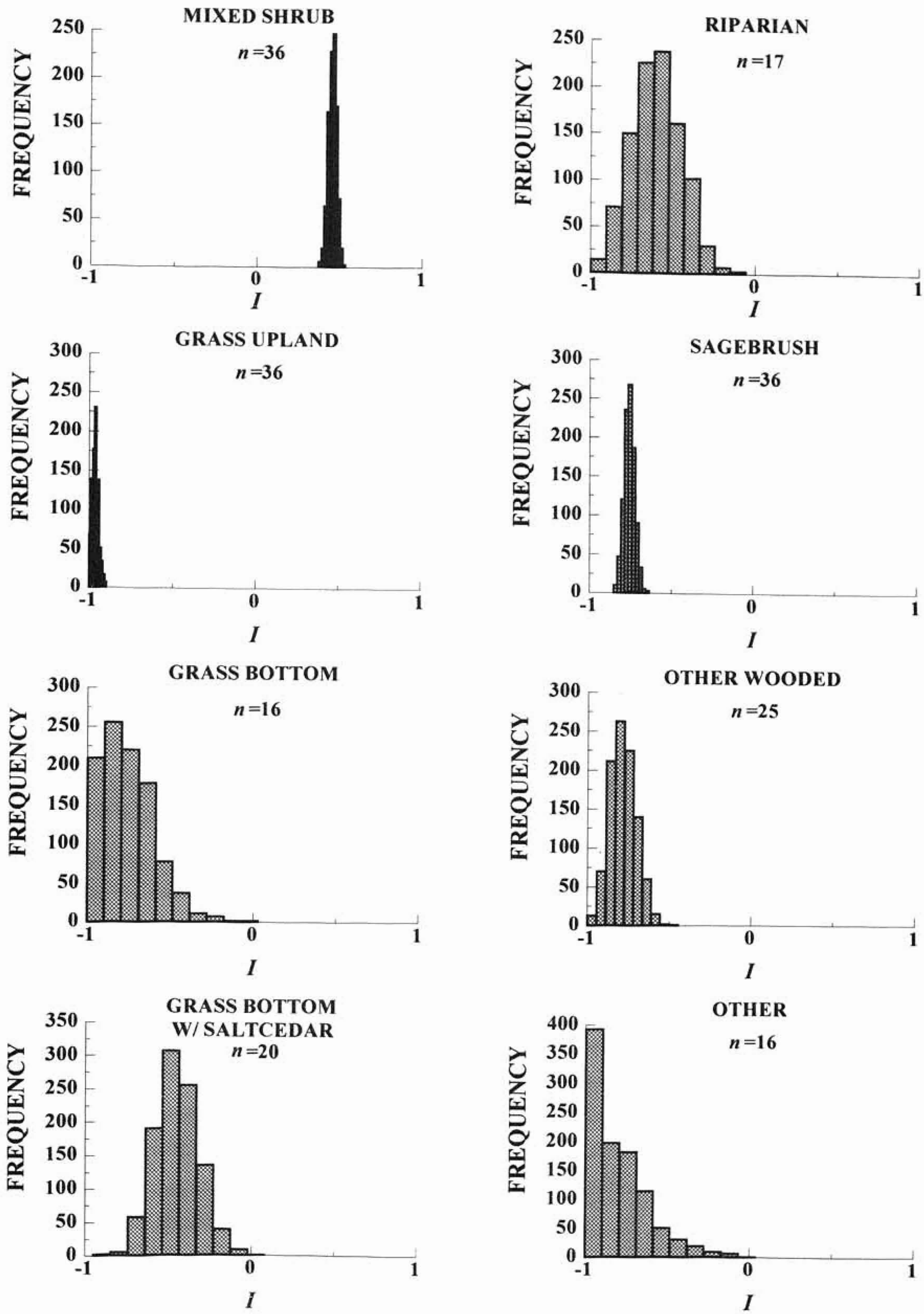

MIXED SHRUB
n =36
RIPARIAN
n =17
GRASS UPLAND
n =36
SAGEBRUSH
n =36
GRASS BOTTOM
n =16
OTHER WOODED
n =25
GRASS BOTTOM
W/ SALTCEDAR
n =20
OTHER
n =16
FREQUENCY
I

Fig. 4. Frequency distribution of bootstrap means (1,000 replications of size *n*) for selection index (*I*) values indicating within-home-range preference-avoidance behavior of northern bobwhites for 8 habitat types on Mesa Vista Ranch, Roberts County, Texas, 10 October 2001–14 March 2002. Size *n* refers to the number of home ranges that each habitat type occurred in during this season.

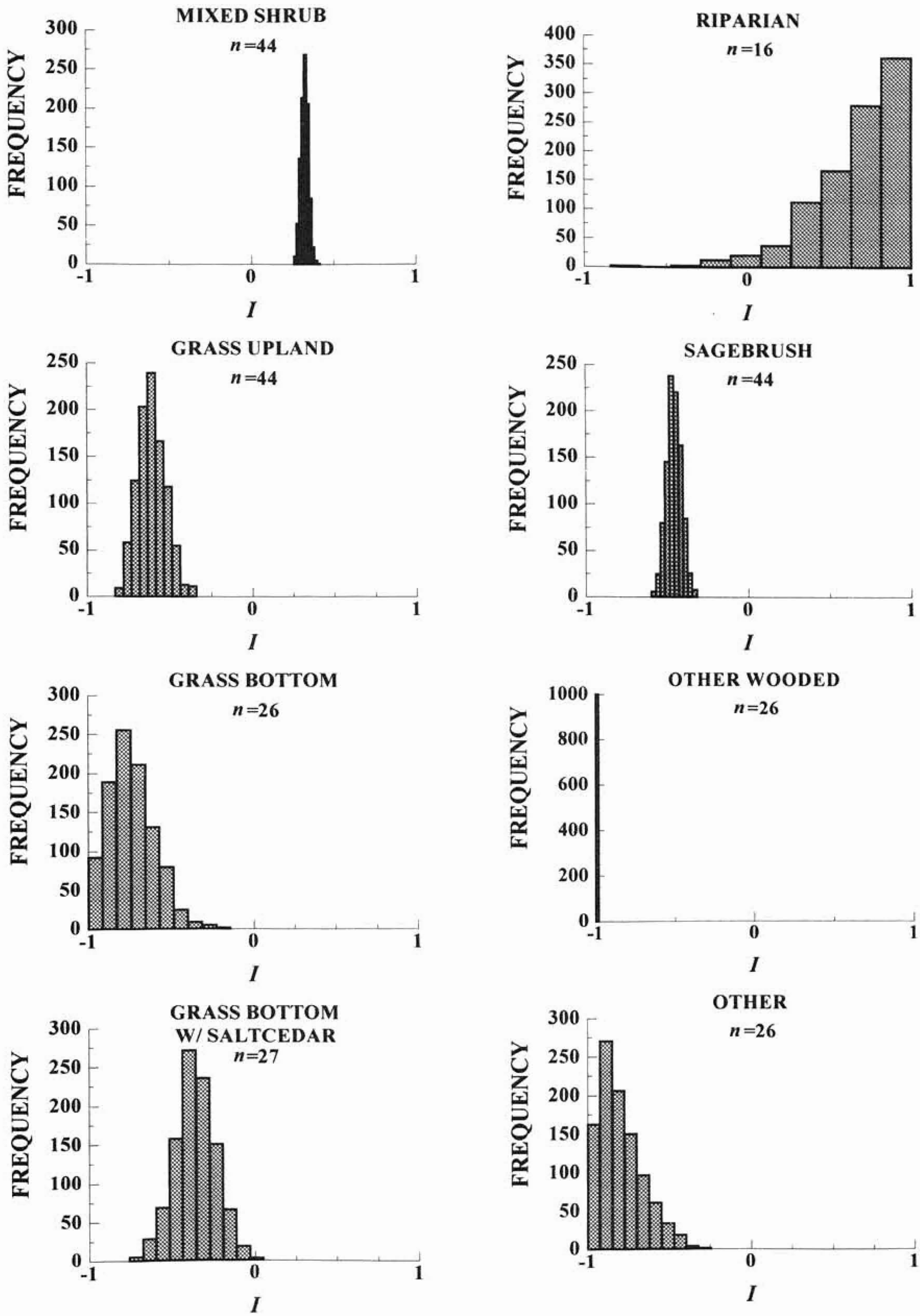
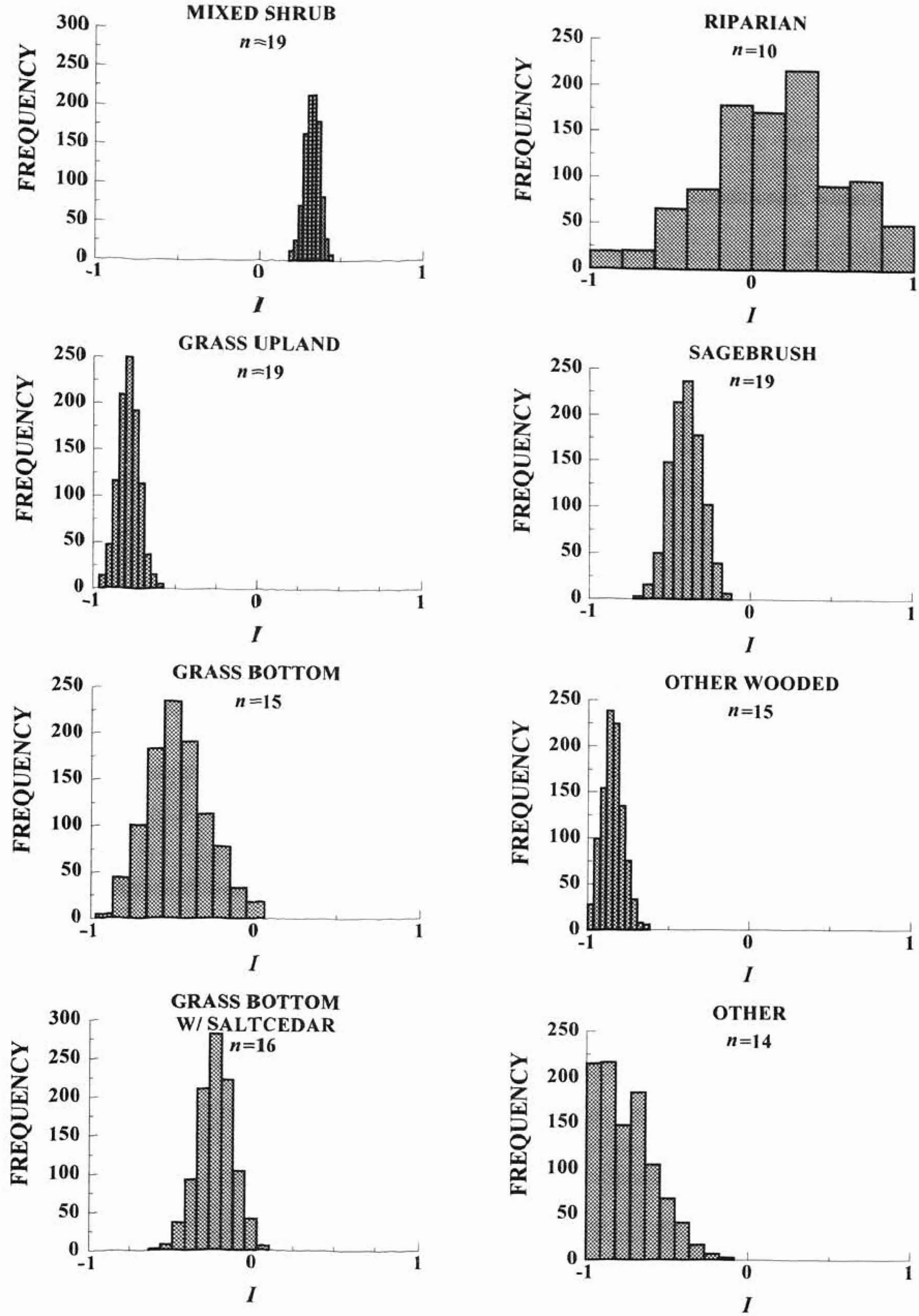

MIXED SHRUB
n=44
RIPARIAN
n=16
GRASS UPLAND
n=44
SAGEBRUSH
n=44
GRASS BOTTOM
n=26
OTHER WOODED
n=26
GRASS BOTTOM W/ SALTCEDAR
n=27
OTHER
n=26
FREQUENCY
I
-1
0
1
0
50
100
150
200
250
300
350
400
200
400
600
800
1000

Fig. 5. Frequency distribution of bootstrap means (1,000 replications of size *n*) for selection index (*I*) values indicating within-home-range preference-avoidance behavior of northern bobwhites for 8 habitat types on Mesa Vista Ranch, Roberts County, Texas, 28 November 2000–14 March 2002. Size *n* refers to the number of home ranges that each habitat type occurred in during this season.


MIXED SHRUB
n=19
RIPARIAN
n=10
GRASS UPLAND
n=19
SAGEBRUSH
n=19
GRASS BOTTOM
n=15
OTHER WOODED
n=15
GRASS BOTTOM W/ SALTCEDAR
n=16
OTHER
n=14
FREQUENCY
I
300
250
200
150
100
50
0
-1
0
1

0.90; composite: 95% CI = 0.59–0.81) except the breeding season (95% CI = 0.53–1.03), which indicated use was in proportion to availability.

Within-Home-Range Level.—Although it was still selected for, the degree of preference for the mixed-shrub class decreased, across all seasons considered, when only usable space was considered (Figs. 6–9). The avoidance of the grass-upland class also decreased across all seasons although it was a negligible difference (Figs. 6–9). The avoidance of sand sagebrush increased negligibly, during the breeding season, when only usable space was considered (Fig. 6), whereas it decreased slightly in avoidance during the 2 covey seasons and for the composite set (Figs. 7–9). The avoidance of the grass-bottomland-with-salt-cedar classification increased across all seasons (Figs. 6–9), although it was still randomly used during the breeding season (Fig. 6).

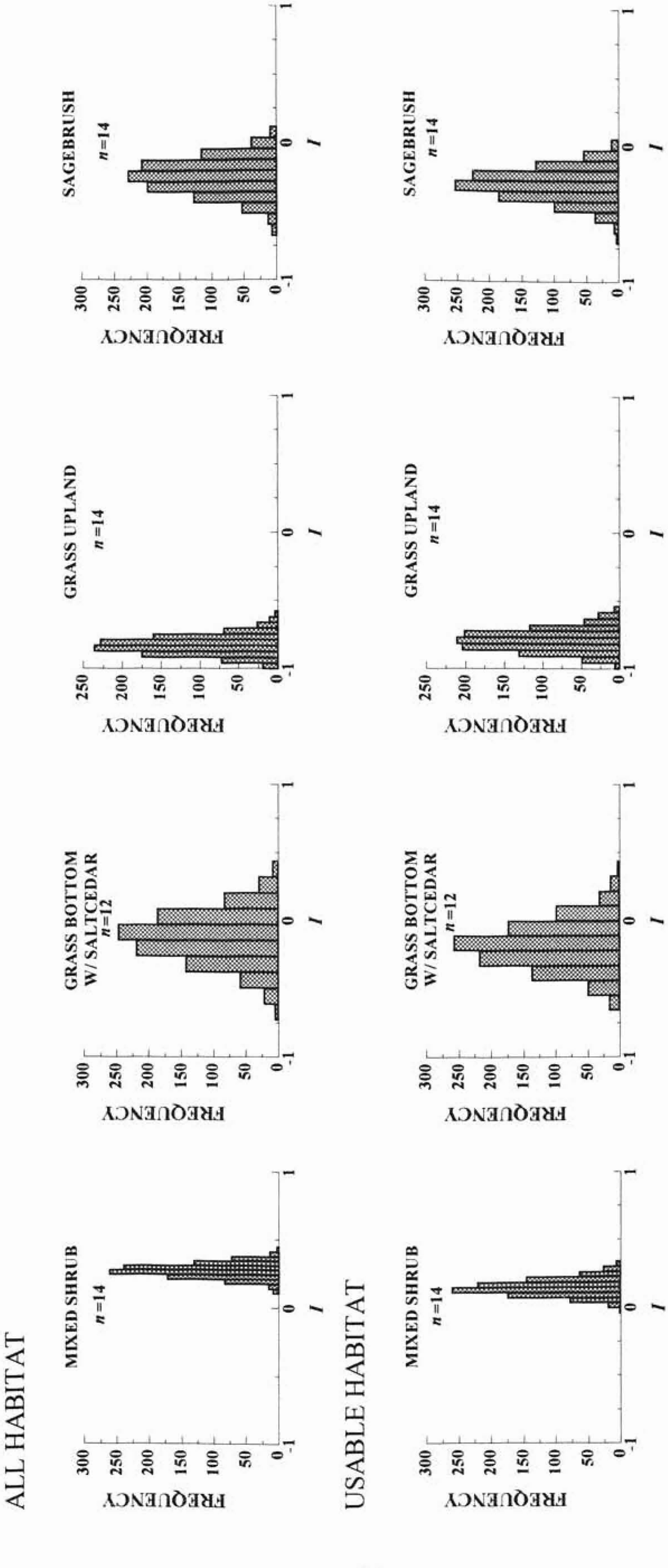
Results at the study area and home range levels did not support a prediction of the usable-space hypothesis: random use in fully usable space. However, there was limited evidence of preference-avoidance adjustments consistent with the prediction.

DISCUSSION

Home Range Estimates

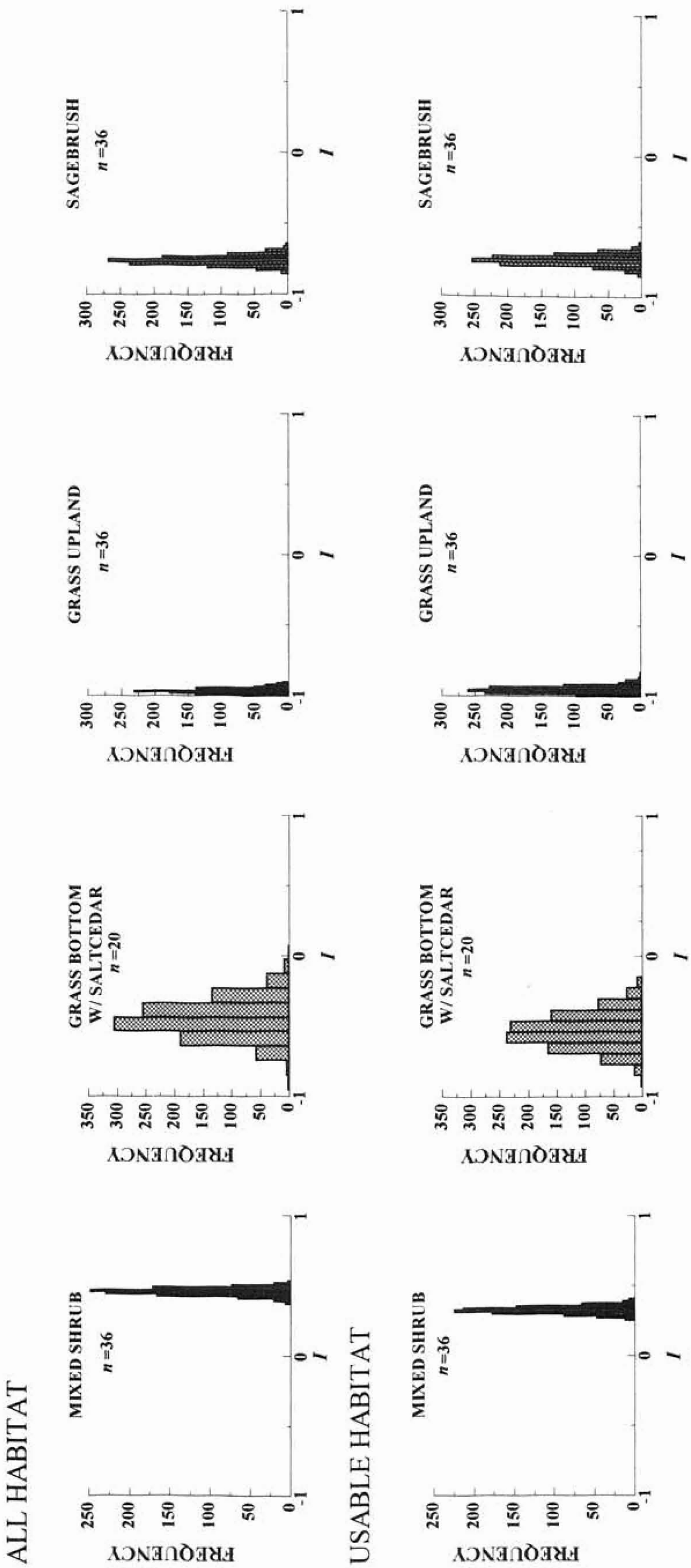
All of the breeding season home range estimates fell within the ranges reported in the literature, which ranged from 6.39 ± 1.7 ha using MCP for nesting females (Urban 1972) to 103.00 ± 11.0 ha using KHR for males in a rangeland-dominated area (Taylor et al. 1999*b*) (Table 1). I expected more movement during the breeding season by males because they play a minor role in the incubation of nests when compared to that of females (Klimstra and Roseberry 1975, Dimmick 1992), thus allowing males more time to move and expand their home range than females. Urban (1972) found the home range

Fig. 6. Comparison of frequency of bootstrap means (1,000 replications of size *n*) of within home range habitat preference-avoidance behavior with and without consideration of the amount of usable space available in each habitat type, as estimated with the cone of vulnerability, on Mesa Vista Ranch, Roberts County, Texas, 19 April–18 September 2001. Size *n* refers to the number of home ranges that each habitat type occurred in during this season.



ALL HABITAT
USABLE HABITAT
MIXED SHRUB
GRASS BOTTOM
W/ SALTCEDAR
GRASS UPLAND
SAGEBRUSH
n=14
n=12
FREQUENCY
I
-1
0
1
50
100
150
200
250
300

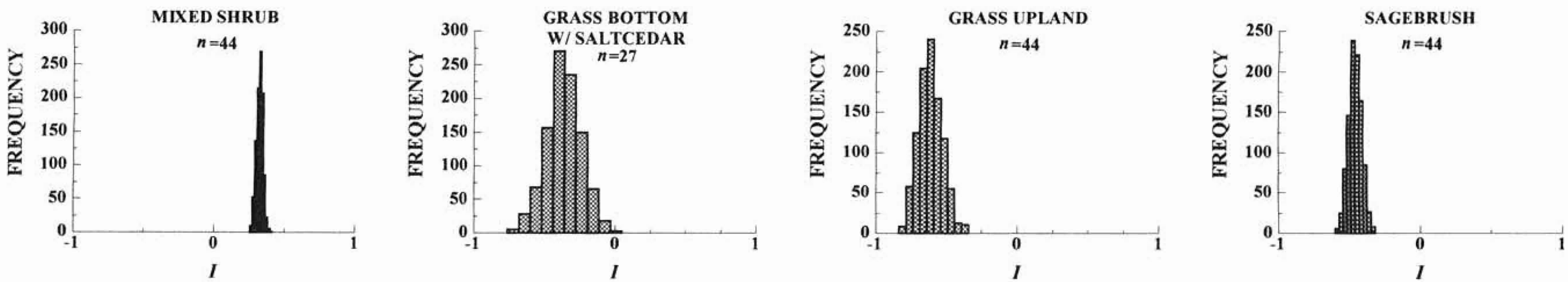
Fig. 7. Comparison of frequency of bootstrap means (1,000 replications of size n) of within home range habitat preference-avoidance behavior with and without consideration of the amount of usable space available in each habitat type, as estimated with the cone of vulnerability, on Mesa Vista Ranch, Roberts County, Texas, 28 November 2000–28 March 2001. Size n refers to the number of home ranges that each habitat type occurred in during this season.



ALL HABITAT
USABLE HABITAT
MIXED SHRUB
n =36
GRASS BOTTOM
W/ SALTCEDAR
n =20
GRASS UPLAND
n =36
SAGEBRUSH
n =36
FREQUENCY
I

Fig. 8. Comparison of frequency of bootstrap means (1,000 replications of size *n*) of within home range habitat preference-avoidance behavior with and without consideration of the amount of usable space available in each habitat type, as estimated with the cone of vulnerability, on Mesa Vista Ranch, Roberts County, Texas, 10 October 2001–14 March 2002. Size *n* refers to the number of home ranges that each habitat type occurred in during this season.

ALL HABITAT



USABLE HABITAT

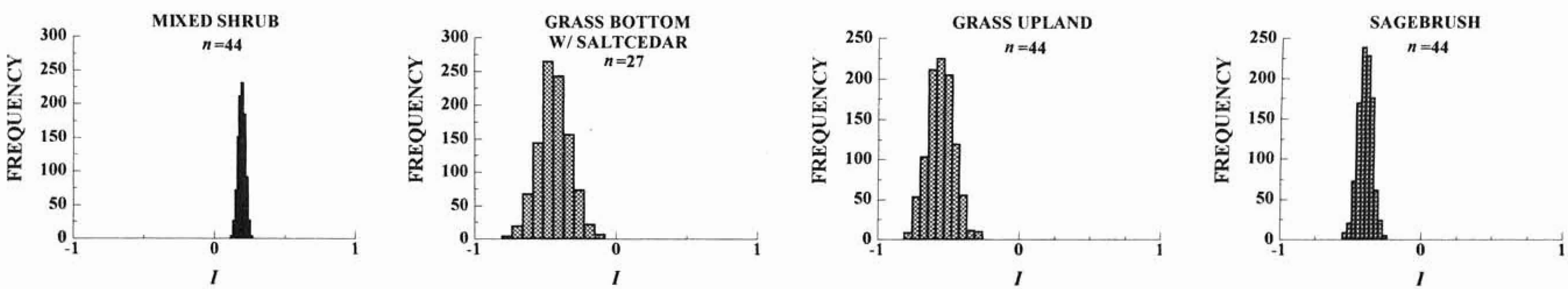
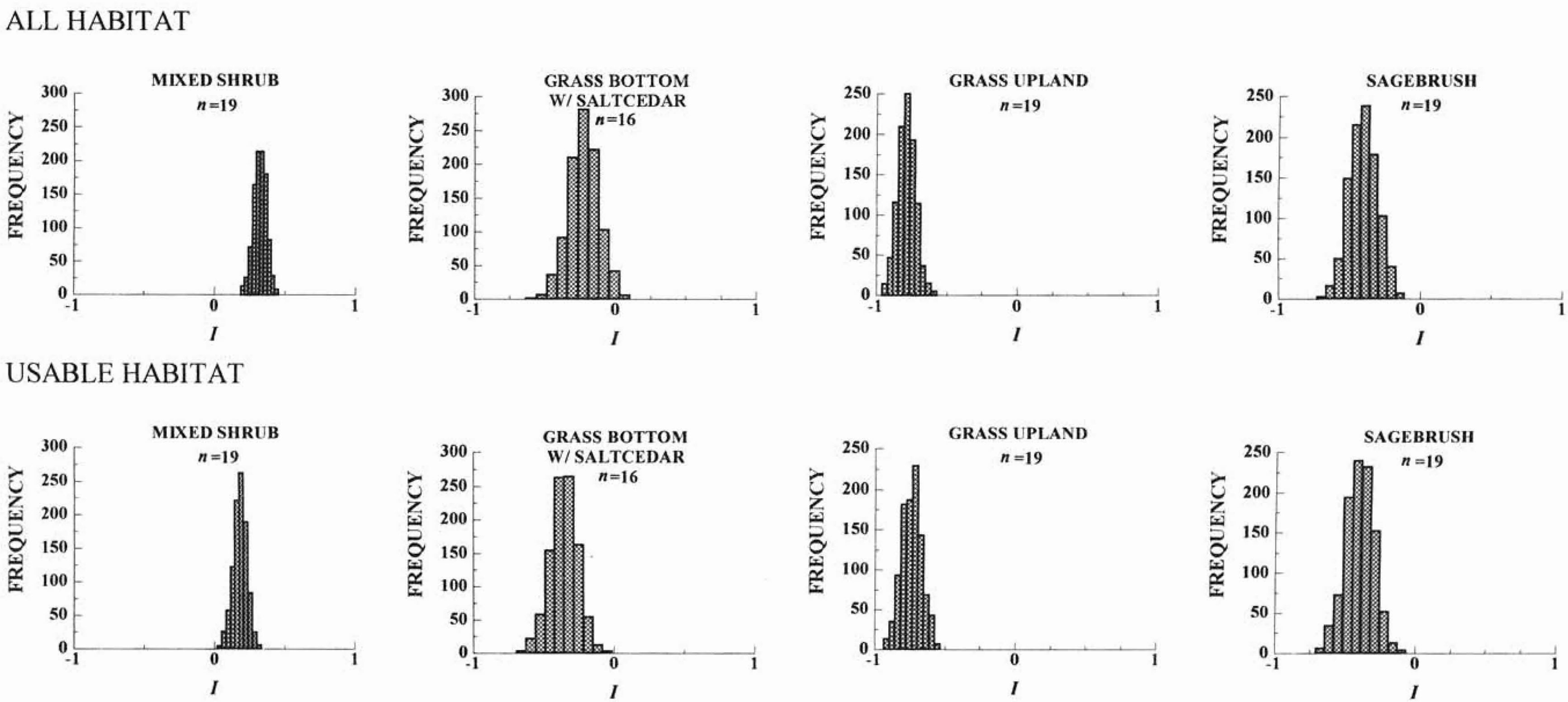


Fig. 9. Comparison of frequency of bootstrap means (1,000 replications of size *n*) of within home range habitat preference-avoidance behavior with and without consideration of the amount of usable space available in each habitat type, as estimated with the cone of vulnerability, on Mesa Vista Ranch, Roberts County, Texas, 28 November 2000–14 March 2002. Size *n* refers to the number of home ranges that each habitat type occurred in during this season.


ALL HABITAT
MIXED SHRUB
n=19
GRASS BOTTOM
W/ SALTCEDAR
n=16
GRASS UPLAND
n=19
SAGEBRUSH
n=19
USABLE HABITAT
MIXED SHRUB
n=19
GRASS BOTTOM
W/ SALTCEDAR
n=16
GRASS UPLAND
n=19
SAGEBRUSH
n=19
FREQUENCY
I

of mated males to be smaller than unmated males and the home range of nesting females to be smaller than that of post-nesting females. Urban's (1972) results also showed that the home range of mated males was similar to that of nesting females and that the ranges of unmated males was similar to that of post-nesting females (Table 1).

Home range estimates during the covey season were smaller than mean breeding season ranges and fell within the range of historical estimates, which ranged from 3.30 ± 1.9 ha using MCP (Sisson et al. 2000) to 33.2 ha (method and SE not given) (Wellendorf et al. 2002) (Table 1). The larger home range estimates of the 2001–2002 covey season can be explained by the supplemental feeding regime across the study area during the covey seasons. During the 2000–2001 covey season, supplemental feed was provided across the entire study area. During the 2001–2002 covey season, however, only the feeders on the east side of the study area contained feed. Home range estimates in areas where supplemental feeding was implemented were similar, whereas the estimates in the area where supplemental feed was not available were 2 to 3 times the size of the ranges where supplemental feed was provided (Table 6). It was evident that the feeders concentrated bobwhites in an area. Though it is not entirely logical to compare the effects of feeders with those of food plots, Madison et al. (2000) found food plots did not affect home range estimates of bobwhites (Table 1).

The composite set of home range estimates (Table 6) also fell within the overall range of previously reported home range estimates (Table 1). However, caution should be exercised when comparing home range estimates from different studies. Different home range estimators will provide different estimates from the same data set (e.g., KHR vs. MCP). Also, home ranges will vary with habitat. Home ranges are likely to be smaller in areas of good habitat or areas with large amounts of usable space, than in areas of poor habitat or with low amounts of usable space. In addition, configuration of habitat patches may affect home range sizes because it determines how much an individual will have to move to meet all of its habitat requirements (Guthery 1999).

Habitat Use

A new method of determining issues of habitat preference-avoidance, using bootstrapping of Ivlev's electivity index values, was presented for analysis at the home-range level. It was not surprising that the mixed-shrub habitat class was consistently preferred during all seasons and at both the home-range and study-area levels. In Rogers County, Oklahoma, Wiseman and Lewis (1981) found tall and short shrubs to be preferred throughout the year. However, it was surprising that the mixed-shrub class was the only habitat class for which bobwhites showed a preference. I expected that the sand sagebrush habitat class would be used to a greater degree than indicated, because it appears to be structurally similar to shrubs. However, according to the cone of vulnerability, areas of sand sagebrush were not as densely covered as areas of mixed-shrub habitat (Table 4).

The other wooded, riparian, grass-bottomland, grass-bottomland-with-salt-cedar, and grass-upland habitat classes were either avoided or were used randomly across all seasons at the home-range and study-area levels. These findings correspond with those of previous studies. Wiseman and Lewis (1981) found woodland to be used in proportion to its availability and large-seeded forb and grassland habitats were used to a lesser degree than if use were random. In Oklahoma, Guthery et al. (2001*c*) found that bobwhite abundance, as indicated with call-count indices, decreased with increasing amounts of mature woodland and increased with increasing amounts of brushy prairie or early successional woodland. Guthery et al. (2001*a*) reported that bobwhites used patches with greater canopy coverage of woody vegetation, primarily velvet mesquite (*Prosopis velutina*), than was available at random patches.

As with home range estimates, caution must be exercised when comparing the findings of different habitat use studies. Due to the vast geographical range that bobwhites occupy, it is evident they are adaptable birds. They have the adaptability to occupy many different types of habitat. Thus, it may not be proper to compare habitat selection behavior indicated by studies conducted in different areas, as habitat types available to and used by bobwhites will vary with geographic region.

Usable Space

My challenge to Guthery's (1997) usable-space hypothesis resulted in data that did not support the hypothesis; i.e., debiting unusable space from habitat availability had a minor effect on inferences from preference-avoidance analysis. Tendencies towards random use after such debits were not observed. The results could indicate the hypothesis or my approach to challenging the hypothesis was flawed.

The usable-space hypothesis is to some degree conceptually trivial because it asserts there will be more bobwhites where there is more area to use. That concept is virtually axiomatic. However, the hypothesis is not trivial from the standpoint of management, because it further asserts that management for habitat quality will be unrewarding in comparison with management for habitat quantity (Guthery 1997).

There exists empirical evidence in support of the usable-space hypothesis. Guthery's (1997) review of the management literature revealed that creation of more permanent cover has been the only method of increasing the abundance of bobwhites on a fixed area; his review also revealed that management for habitat quality (food, edge, interspersion) has not been successful. However, Taylor et al. (1999*b*) obtained ambiguous results regarding the habitat quality versus habitat quantity hypotheses. At the scale of small farms and ranches in Oklahoma, bobwhite abundance increased with usable space in the form of lower successional woodland or brushy prairie (mixed brushland and prairie, including early-successional woodland) and decreased with patch richness, woody edge, and patch diversity (Guthery et al. 2001*c*). Cram (2001) observed that bobwhites in forest settings in Arkansas increased with both foods and usable space; his data suggested that usable space was the more important variable. Guthery (1997) observed that food supplies might increase with increasing usable space, but that food supplies were not necessarily the driving variable. Thus, whereas the usable-space hypothesis remains provisional, it has theoretical and empirical support.

Several possible flaws occur in my challenge to the usable-space hypothesis. First, I assessed usable space with 1 variable, the cone of vulnerability. Although this variable seems to be a key predictor of patch use by bobwhites, it is not the only predictor (Guthery et al. 2000*b*, Guthery et al. 2001*b*). Had I assessed space usability with additional features, such as the disc of vulnerability (Kopp et al. 1998), the estimated quantity of usable space in cover types might have declined further. This change would have had the effect of reducing avoidance in cover types with indications of avoidance by reducing the amount of usable space. Second, it does not necessarily follow that the usability of points is a good index of the usability of space. For example, usable points might have been dispersed among unusable points in a manner that rendered them unusable by bobwhites. To illustrate this concept by way of example, a patch of mixed-shrub habitat in a sea of bottomland grass would not be usable, despite the fact that it would contain usable points based on the cone of vulnerability. If this circumstance held on the study area, the effect would have been an overestimation of space usability in cover types and a failure to support the random-use prediction of the usable-space hypothesis.

Despite the possible flaws mentioned above and perhaps others, I regard the usable-space hypothesis as an incomplete explanation of the behavior of bobwhite populations in the field. The sand sagebrush cover type seemed to provide structurally suitable permanent cover (usable space in time), yet it was strongly avoided by non-nesting birds. During the breeding season of 2001, 21 of 26 nesting attempts on the study area were in sand sagebrush (Steven Smith, Oklahoma State University, unpublished data). The reason for avoidance of sand sagebrush is not embodied in the usable-space hypotheses and I conjecture that some component of habitat quality was involved. Further research will be necessary to elucidate the interplay between habitat quality and habitat quantity as the theoretical basis for bobwhite management.

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VITA 2

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