2009

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Over-winter Survival of Northern Bobwhite in Relation to Landscape Composition and Structure

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The conceptualization of security of bobwhite during winter has been predicated on the assumption that winter ranges differ in quality, based on habitat structure, composition, or interspersion. Although some studies have qualitatively related habitat composition to survival, no studies have quantitatively linked habitat or landscape characteristics to winter survival and the specific structural or compositional characteristics that influence quality are unknown. To quantify winter habitat quality, we modeled hazards as a function of habitat characteristics in relation to winter survival of radio-marked bobwhite (2000, n = 118 in 16 coveys; 2001, n = 49 in 7 coveys) in a managed agricultural landscape in Mississippi, as a function of landscape structure and composition at 2 spatial scales (daily and seasonal ranges). For each spatial scale we constructed *a priori* models that estimated year-specific winter survival as a function of unique combinations of variables that characterized landscape composition and structure and had previously been identified as relevant to bobwhite ecology. At the spatial scale of winter ranges, the *a priori* model containing % of landscape, mean patch size, and edge density of linear herbaceous was the best approximating model and suggested a negative effect of linear herbaceous cover on survival. In retrospective analyses, models containing variables describing quantity and structure of linear herbaceous cover and cropland indicated that as these elements increased, risk of mortality increased. At the spatial scale of daily activity, metrics describing landscape structure and composition were poor predictors of survival. During this study, the quantity, patch size, amount of edge, or interspersion of patch types within the winter range or surrounding daily activity locations did not measurably influence the hazard function, suggesting that seasonal ranges can have different composition and structure, yet produce similar survival rates for the birds that inhabit each range.

Introduction

Many studies of animal ecology focus on habitat use relative to availability under the presumption that selective use reflects greater habitat quality or relative value (Garshelis 2000.). These studies often use statistical tests (e.g. chi-square tests, compositional analysis, etc.) to detect disproportionate or non-random use for the purpose of making inferences about habitat preference (Dixon et al. 1996). Although this approach may reflect habitat selection, it does not necessary reflect habitat quality as measured by fitness (Van Horne 1983). Inferences regarding habitat quality require knowledge of relationships among habitat composition, structure, and fitness components (e.g. survival, reproduction).

Habitat has been characterized as the sum of the specific resources, consistent with the behavioral, physiological, and morphological adaptations of a species, required by the individual for reproduction and survival. For bobwhite, habitat quality has been conceptualized under 2 competing models, the quality continuum model (Schroeder 1985, Taylor et al. 1999*b*) and the binary response or usable space model (Guthery 1997). Under the quality continuum model, habitat quality varies from poor to excellent in a continuous fashion. Characteristics of habitat such as thermoregulatory value, energetic resources, or security from predators might

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be expected to vary in a continuous fashion. Under the binary response model, a point within the landscape is either entirely usable or not. That is, some region around a point location provides essential resources required by an individual for survival and reproduction, and thus is usable, or not. Under this model, habitat quality is characterized as the proportion of the landscape usable through time (Guthery 1997). Guthery (1997) suggests that bobwhite density can only be increased by increasing usable space through time and management activities should focus on increasing usable space. In contrast, Taylor et al. (1999b) advocated a parameter-based approach to management and suggested that bobwhite management and restoration efforts were likely to be unsuccessful until biologists understood the nature of relationships among management practices, habitat structure, and vital rates that contribute to fitness.

Over-winter survival is an important determinant of bobwhite population performance and may be influenced by the distribution, quantity, and quality of habitats that provide food, thermal cover, and protection from predators. Winter survival has been shown to vary latitudinally (Guthery et al. 2000) and annually in relation to winter weather, snow coverage (Roseberry and Klimstra 1984), harvest rate (Dixon et al. 1996) , ground cover, and predation regimes (Burger et al. 1998). However, despite numerous studies of bobwhite winter habitat use and survival, no studies have linked habitat or landscape characteristics to winter survival. Conroy (1993) suggested that Cox proportional hazard modeling might be used to assess the effects of covariates such as habitat use on fitness measures.

Errington (1935) suggested that as bobwhite populations increased, a greater proportion of individuals occupied marginal ranges and density-dependent mechanisms caused overall population security to decrease. Roseberry and Klimstra (1984) found support for this hypothesis in Illinois in that occupancy rates of winter ranges varied in relation to density. They suggested that high quality ranges were occupied regardless of density, but lower quality ranges were only occupied at high density. Fitness-based, density-dependent habitat selection is predicted by the Fretwell and Lucas (1970) ideal-free habitat selection model. This implies that winter ranges differ in quality, based on habitat structure, composition, or interspersion. However, the specific structural or compositional characteristics that influence quality are unknown.

Some studies have qualitatively related habitat composition to survival (Hines 1987, Klinger et al. 1989, Loegering and Fraser 1995), but few have made quantitative estimations of survival in relation to habitat composition and structure. Landscape structure and composition has been quantitatively related to nesting season (Schmitz and Clark 1999) and winter (Perkins et al. 1997) survival rates for ring-necked pheasants (*Phasianus colchicus*) and nesting season survival for bobwhite (Taylor et al. 1999a). However, we could find no reported data relating landscape structure and composition to over-winter survival of bobwhite. To quantify habitat quality, we estimated the influence of landscape structure and composition at 2 spatial scales (seasonal covey range and daily use) on bobwhite survival during winter.

Study Area

This study was conducted on the Black Prairie Wildlife Management Area (BPWMA), in southern Lowndes County, Mississippi, USA. The BPWMA is approximately 2,300 hectares and is owned by the state of Mississippi and managed by the Mississippi Department of Wildlife, Fisheries and Parks (MDWFP). Land cover/land use on BPWMA during the study included: green ash (*Fraxinus pennsylvanica*) successional areas (2.5%), shrubby/herbaceous 16 m wide cover strips in agricultural fields (0.7%), idle mixed exotic and native grasslands (44%), herbaceous 10 m wide field borders around agricultural fields (1.0%), annual food plots (0.7% in 2000, 2.3% in 2001) consisting of clover, wheat, or sunflowers, improved pasture (0.6%), road right-of-ways (0.6%), agricultural row crops (corn-soybean rotation; 27.5% in 2000, 26.1% in 2001), water (1.0%), woodlands (21.2%), and yard areas (<1.0%) surrounding a few

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Table 1: List and description of metrics generated in Patch Analyst and FRAGSTSATS to assess effects of landscape composition and structure on over-winter survival of radio-marked northern bobwhite on Black Prairie Wildlife Management Area, Mississippi, 2001-2002.

Metric	Description
SDI	Shannon Diversity Index
ED	Overall Edge Density
MPS	Overall Mean Patch Size
LS_GRASS	% of Range in Grass
ED_GRASS	Edge Density of Grass in Range
MPS_GRAS	Mean Patch Size of Grass Patches in Range
LS_WOOD	% of Range in Woods
ED_WOOD	Edge Density of Woods in Range
MPS_WOOD	Mean Patch Size of Woods Patches in Range
LS_LINH	% of Range in Linear Herbaceous Cover
ED_LINH	Edge Density of Linear Herbaceous Cover in Range
MPS_LINH	Mean Patch Size of Linear Herbaceous Cover Patches in Range
LS_RC	% of Range in Row Crops
ED_RC	Edge Density of Row Crops in Range
MPS_RC	Mean Patch Size of Row Crop Patches in Range

houses and equipment storage facilities on the area. Disturbance, including prescribed fire, disking, and herbicide application was used on BPWMA to maintain early successional herbaceous communities.

Methods

The winter season was defined for this study as September 15 to April 14, 2000-2001 and 2001-2002. Bobwhites were captured during spring and fall of each year. Fall capture took place during 2 weeks in September and 2 weeks in November of each year. Spring trapping began in late January and lasted into March each year. Birds were captured in walk-in style wire traps (Stoddard 1931) baited with cracked corn. Traps were checked twice daily during trapping intervals, once in the morning after birds had foraged and returned to loafing cover and once in the evening after birds had foraged and returned to roost sites. After capture, the gender and age of each bird was determined. Bobwhite age was categorically classified as juveniles or adults. Each animal was then weighed, banded on the right leg with a #7 numbered aluminum band, fitted with a 5-6 g necklace style radio transmitter (American Wildlife Enterprises, Monticello, FL), and released at the capture site. Radio transmitters had a 12-hour mortality sensor, a 20 cm antenna, and operated on a unique frequency between 148.000 and 149.999 MHz. Bobwhite that were caught during the evening trap check when the temperature was less than 10° C or when it was raining were held overnight in wooden boxes measuring approximately 60 cm wide by 60 cm long by 30 cm high with a cloth top and a rubber door flap. Bobwhites that were held overnight were released at the capture site the following morning prior to the morning trap check. Additional bobwhites were captured by night netting throughout the study (Truitt and Dailey 2000).

Radio Location

Radio-marked bobwhites were located at least 5 days/week using a programmable scanning receiver and a handheld 3-element Yagi antenna (Advanced Telemetry Systems, Inc., Isanti, MN). The diel pe-

riod was divided into 3 time intervals (sunrise to 4 hours post-sunrise, midday, and 4 hours pre-sunset to sunset) and time of location was systematically rotated through these intervals to ensure representative sampling of habitat use. Birds were located by homing in to ≤25 m of the radio signal and circling the location to pin point the exact location of the animal (White and Garrott 1990). Each daily location was georeferenced using a handheld GPS unit (Trimble Navigation Limited, Inc., Sunnyvale, CA). The distance and azimuth from the georeferenced point to the actual location of the bird was recorded. After the data was downloaded from the GPS unit and differentially corrected, the distance and azimuth were used to estimate the location of each bird. Remains of dead bobwhites were recovered upon receiving a mortality signal.

Land Cover Determination

Aerial photographs were georeferenced and imported into Arcview 3.2. Year-specific, vector-based GIS coverages for BPWMA were developed through heads up digitizing of the georeferenced aerial imagery. Individual polygons that were generated were then classified to land cover and ground truthed.

Population Estimation

Fall population size was estimated by counting early morning covey calls (Wellendorf 2000). As a sampling frame for fall density estimation, 87 500 m X 500 m square grid cells were overlayed on the BPWMA GIS coverage. Eighteen of these cells were randomly selected for sampling. Call counts were conducted during the last week of October and the first week of November during each season. Calling rate probabilities were estimated during 10-day periods before and after the call counts using coveys that contained radio marked individuals. Coveys that contained radio marked individuals were located using radio telemetry techniques approximately 1/2 hour before sunrise. When the covey was located and approached to within approximately 35 m, an observer waited until approximately 1/2 hour after sunrise and listened to determine if the covey made

early morning covey calls. At approximately 1/2 hour after sunrise, the covey was flushed and the number of individual bobwhites in the covey was counted. Calling rate probabilities were estimated as the proportion of marked coveys that called during the 10-day period preceding and following the covey call counts. Mean covey size was determined by calculating the mean number of individuals in all of the coveys that were flushed. During the call counts, 4 observers were assigned to each of the randomly selected blocks. One observer was placed along each outside edge of the block at the midpoint (250 m from a corner) and faced into the block. When a covey call was heard, the observer recorded the azimuth, approximate distance, and time of the call. Covey locations were verified by coordinating the observed calls, times, and azimuths from all 4 observers for a block and triangulating the estimated locations observed by 2 or more observers. Early fall population size was determined by multiplying the average covey size by the total number of covey calls heard within the sampling blocks and dividing that number by the calling rate probability multiplied by the percentage of the grids that were sampled. The same randomly selected blocks were used during all years.

Covey Associations

Individual radio-marked bobwhites were assigned to coveys according to their capture history and association with other radio-marked bobwhite. Winter covey ranges were estimated using one location/covey/day to generate a 95% kernel seasonal range estimate (Worton 1989). Seasonal range estimates were generated for all coveys that had ≥25 unique locations. Locations for different individuals within the same covey at a given location and time were not considered unique for the purposes of generating seasonal range estimates because of lack of independence associated with the coveying behavior of bobwhite.

Home Range Estimation

To determine the minimum number of unique locations necessary to estimate an accurate seasonal

Table 2: Models used to assess effects of landscape composition and structure on over-winter survival of radio-marked northern bobwhite on Black Prairie Wildlife Management Area, Mississippi 2001-2002 in PROC PHREG.

Model	Metrics Used in Model
Shannon Diversity Index	SDI
Overall Edge Density	ED
Overall Mean Patch Size	MPS
Woody Composition and Structure	LS_WOOD, ED_WOOD, MPS_WOOD
Grass Composition and Structure	LS_GRASS, ED_GRASS, MPS_GRAS
Linear Herbaceous Composition and Structure	LS_LINH, ED_LINH, MPS_LINH
Row Crop Composition and Structure	LS_RC, ED_RC, MPS_RC
% of Range Burned Since Last Growing Season	BURN_F, BURN_S
% of Range Burned and Crass Composition	BURN_F, BURN_S, LS_GRASS

range, we used the 5 coveys from each season with the most locations and used the bootstrap method in Animal Movement extension (Hooge and Eichenlaub 1997) in Arcview 3.2 to create seasonal ranges by randomly selecting 5 samples of locations in increments of 5 locations each from 5-50 without replacement within each set and with replacement between sets (i.e., 5 seasonal ranges with 5 locations each, 5 seasonal ranges with 10 locations each,...,5 seasonal ranges with 50 locations each). Mean estimated range size and SD were plotted against estimated home range size for each covey. Ranges based on 5-20 locations were highly variable. Home range estimates based on >25 locations stabilized within 15% of the mean deviation for all other seasonal ranges consisting of 30-50 locations. We used 25 locations as the minimum number required to estimate seasonal ranges in this study and estimated seasonal range for all coveys that had ≥25 locations. Seasonal ranges were generated for 16 coveys containing 118 radio-marked birds during the 2000-2001 season and 7 coveys containing 49 radio-marked birds during the 2001-2002 season.

Landscape Structure And Composition

We examined relationships among landscape structure and composition and survival at 2 spatial scales. At the coarsest spatial scale, we modeled hazards as a function of time-invariate covariates describing the structure and composition of winter ranges. At a finer spatial scale, we modeled hazards as a function of time-varying covariates that described the immediate landscape context in which individual daily locations occurred.

At the home range scale, we associated habitat characteristics with each seasonal range by clipping the covey range boundary to the BPWMA coverage for the corresponding year. Once habitat attributes were added to each seasonal range, landscape metrics were then generated for each seasonal range using the Patch Analyst extension in Arcview 3.2 (Elkie et al. 1999). Researchers commonly acknowledge that habitat types important to bobwhite include woods, brushy areas, agricultural fields, and grasslands (Stoddard 1931, Leopold 1933, Ridley 1952, Stanford 1952, Edminster 1954). Some researchers have suggested that landscape diversity, interspersion, or composition may influence bobwhite densities (Leopold 1933, Baxter and Wolfe 1972, McRae et al. 1979, Schroeder 1985, Brady et al. 1993). We generated values for 3 landscape-level metrics: Shannon Diversity Index, overall mean patch size, and overall edge density. For each of 4 habitat classes presumed to be important to bobwhite (grass, woods, row crop, and linear herba-

ceous cover), we generated 3 landscape metrics; i.e., percentage of the landscape, edge density, and mean patch size. In order to avoid problems associated with multicollinearity, we developed candidate models that, within models, included only a single proportional measure of landscape composition. Linear herbaceous cover was composed of field borders and cover strips pooled into one class (Table 1). Additionally, we calculated percentage of the seasonal range that was burned during the fall (BURN_F) and spring (BURN_S) of each season.

Survival Estimation

After generating covey specific landscape metrics, each individual radio-marked bobwhite that was associated with one of the coveys used to generate the seasonal ranges was assigned the 17 landscape metric values corresponding to that bird's covey as covariates. Seasonal survival rates were estimated using the Kaplan-Meier approach modified for staggered entry (Pollock et al. 1989) within PROC PHREG in SAS (SAS Institute, Inc. 1996). Birds with unknown fates (radio-failure, emigration from study area, mortality attributed to research, or survival past April 14th of each year) were right censored. We assumed that right-censoring mechanisms were independent of the bird's fate, left-censored bobwhite had similar survival distributions to birds that were previously included in the risk set, the sample of bobwhite that we used was a random sample from the population of birds on BPWMA, survival times were independent for all individuals, and capture, handling and marking did not affect survival. We modeled hazards as a function of habitat characteristics in SAS using PROC PHREG (Allison 1995) to estimate effect of landscape metrics described above on survival of radio-marked bobwhite. We constructed 9 *a priori* models that estimated year-specific survival as a function of landscape composition and structure using the covariates listed above (Table 2). Additionally, a model that included no covariates was included in the analysis. We controlled for variation between years using a STRATA statement (Allison 1995). Parameter estimates for each covariate

included in the above models and Akaike's Information Criterion (AIC) values were generated in SAS using PROC PHREG. Then, we conducted an *a posteriori* analysis in which we modeled the composite models listed above along with each class metric individually, while controlling for variation between years. The model from the set of candidate models with the least AIC value was selected as the best approximating model, given the data and the candidate model set (Table 3).

At the finer spatial and temporal resolution, we modeled hazards as a function of landscape characteristics in the immediate vicinity of daily locations. Daily locations simply reflect a discrete snapshot of the habitat space actually used throughout a given day. In order to better capture the landscape structure within the expected range of daily activities, we buffered daily locations by a radius equal to the mean daily movement observed during this study (156 m). Mean daily movement was estimated as the mean distance between consecutive daily locations for same individual, averaged across individuals. Mean daily movement for the 2000-2001 season was 156.92 m and for the 2001-2002 season was 155.49 m. We used 156 m as the mean daily movement for both years. Because locations were taken only once daily, we assumed that the area within a circle with radius equal to the mean daily movement around daily locations would characterize the region most probably used by that bird throughout that day. We recorded 1,417 daily locations for 79 radio-marked bobwhites during the 2000-2001 season and 2,002 locations for 53 radio-marked bobwhites during the 2001-2002 season.

Each daily location was buffered by 156 m generating a circular daily range polygon. The daily range was then clipped to the BPWMA coverage for the corresponding year in ARC/INFO. The corresponding habitat metrics were calculated for each daily range in FRAGSTATS (McGarigal and Marks 1994). After daily locations had been buffered and clipped, the habitat metrics were added to each record as time-varying covariates, the data were analyzed using PROC PHREG in SAS as described above for

Table 3: Habitat models, parameter estimates, AIC values, and hazard ratios for 2000-2002 over-winter seasonal ranges of radio-marked northern bobwhite on Black Prairie Wildlife Management Area, Mississippi.

Model	Variables	Estimate	SE	Hazard Ratio	AIC	Δ AIC
MPS Linear Herbaceous	MPS_LINH	1.8953	0.8509	6.6540	741.5270	0
Linear Herbaceous Composite [a]	LS_LINH	-0.1255	0.0829	0.8820	741.9020	0.375
	ED_LINH	0.0053	0.0028	1.0050		
	MPS_LINH	2.8606	1.2311	17.4730		
ED Rowcrop	ED_RC	0.0019	0.0010	1.0020	742.6960	1.1690
LS Rowcrop	LS_RC	0.0091	0.0046	1.0090	742.7120	1.1850
ED Linear Herbaceous	ED_LINH	0.0018	0.0010	1.0020	743.1470	1.6200
LS Linear Herbaceous	LS_LINH	0.0412	0.0240	1.0420	743.6580	2.1310
ED [a]	ED	0.0010	0.0007	1.0010	744.3780	2.8510
No Covariate Model [a]					744.4680	2.9410
Grass Composite [a]	LS_GRASS	0.0212	0.0109	1.0210	745.2330	3.7060
	ED_GRASS	-0.0034	0.0017	0.9970		
	MPS_GRAS	-0.3522	0.1977	0.7030		
SDI [a]	SDI	0.4499	0.4131	1.5680	745.2530	3.7260
ED Grass	ED_GRASS	-0.0012	0.0011	0.9990	745.3050	3.7780
MPS [a]	MPS	-0.3362	0.3322	0.7140	745.3920	3.8650
ED Wood	ED_WOOD	-0.0017	0.0020	0.9980	745.7250	4.1980
MPS Grass	MPS_GRAS	-0.0978	0.1209	0.9070	745.7930	4.2660
Rowcrop Composite [a]	LS_RC	0.0090	0.0117	1.0090	746.0110	4.4840
	ED_RC	0.0005	0.0021	1.0010		
	MPS_RC	-0.0439	0.1070	0.9570		
MPS Rowcrop	MPS_RC	0.0314	0.0629	1.0320	746.2260	4.6990
Burn Spring	BURN_S	0.0023	0.0053	1.0020	746.2800	4.7530
MPS Wood	MPS_WOOD	-0.1021	0.2598	0.9030	746.3090	4.7820
Burn Fall	BURN_F	-0.0152	0.0530	0.9850	746.3830	4.8560
LS Grass	LS_GRASS	-0.0004	0.0054	1	746.4610	4.9340
LS Wood	LS_WOOD	0.0006	0.0107	1.0010	746.4640	4.9370
Woody Composite [a]	LS_WOOD	0.0283	0.0218	1.0290	747.7300	6.2030
	ED_WOOD	-0.0033	0.0023	0.9970		
	MPS_WOOD	-0.7497	0.5515	0.4730		
Burn Composite [a]	BURN_F	-0.0089	0.0558	0.9910	748.2540	6.7270
	BURN_S	0.0020	0.0056	1.0020		
Grass + Burn Composite [a]	LS_GRASS	-0.0017	0.0067	0.9980	750.1890	8.6620
	BURN_F	-0.0026	0.0611	0.9970		
	BURN_S	0.0029	0.0067	1.0030		

[a] *a priori* models

seasonal ranges (Table 4). Models that included covariates related to burning were excluded from daily range analysis because they composed a very small portion of each daily range. For this analysis, each location was considered to be an independent observation. Each bird was introduced to the risk set each day with the set of covariates calculated for that day. If the bird survived past that day, it was censored

and brought back into the risk set as a new observation on the following day, with a new set of covariates corresponding to the landscape metrics associated with that daily location. If the bird died between that day and the next, it was considered a mortality on that day and that day's landscape metrics were associated with the mortality event.

Mortality Locations

To identify landscape metrics that may have been associated with mortality events, we compared landscape characteristics at locations where dead birds were recovered to known live locations. Mortality and live locations were buffered by 156 m and clipped to land cover layers as described for daily locations. Insofar as recovery sites of dead birds reflect a mixture of actual mortality sites and locations to which depredated birds were translocated and consumed by predators, we did not assume that the location of bird remains was necessarily the location where the mortality occurred. We paired each mortality location with a randomly selected live location for the same bird during the 14 days prior to the recovery of the bird's remains. We used a mixed model ANOVA in SAS using PROC MIXED to compare the habitat composition and structure between live locations and mortality recovery locations. We treated bird ID as a random blocking effect and year and type of location (live or dead) as fixed effects. We compared the 3 landscape metrics, 4 groups of class metrics, and all class metrics individually listed above between live and dead locations.

Results

Population Estimate

The early fall population size on Black Prairie Wildlife Management Area was estimated as 1,849 (SE = 1,170.9) individuals for the 2000-2001 season and 891 (SE = 1,140.4) individuals for the 2001-2002 season. Of the estimated early fall population, we radio-marked 9.1% (n = 169) during the 2000-2001 season and 7.9% (n = 70) during the 2001-2002 season.

Winter Survival

Over-winter survival differed dramatically between years. Survival from 15 September-14 April was 0.060 (SE = 0.019) during the 2000-2001 season and 0.465 (SE = 0.110) during the 2001-2002 season. During the 2000 growing season, this study site experienced a severe drought and ground cover conditions were poor going into winter (Holt 2003). During the 2000-2001 winter season this population experienced high avian cause-specific mortality (Holt 2003).

Covey Range Size

Covey range sizes also differed between years. Mean winter covey range size was 22.46 ha (n = 16, SE = 14.4) during the 2000-2001 season and 44.13 ha (n = 7, SE = 45.1) during the 2001-2002 season. The combined area occupied by radio-marked coveys was 320.23 ha during the 2000-2001 season and 275.44 ha during the 2001-2002 season. Thus radio-marked coveys occupied approximately 13.9% of the total study area during the 2000-2001 season and 12.0% during the 2001-2002 season. The area of the overlapping portion between seasons was 67.01 ha. Twenty-one percent of the 2000-2001 cumulative range was used by radio-marked bobwhite during the 2001-2002 season, and 24% of the 2001-2002 range had been used by radio-marked bobwhite during the 2000-2001 season. Thus, radio-marked bobwhite occupied similar proportions, but different regions, of the total study area between years. Insofar as the entire study area was systematically trapped in both years, differences in occupied areas more likely reflect annual differences in space use rather than spatial distribution of sampling effort.

Covey Range Landscape Metrics

Of the 10 *a priori* models, the linear herbaceous composite model was selected as the best approximating model with an AIC 2.476 less than the next best model (ED model) and 2.566 less than the no covariates model (Table 3). The linear herbaceous model included variables describing % of the landscape in linear herbaceous cover (LS_LINH, β = -0.00192, SE = 0.08292), edge density of linear herba-

Table 4: Habitat models, parameter estimates, AIC values, and hazard ratios for 2000-2002 over-winter daily ranges of radio-marked northern bobwhite on Black Prairie Wildlife Management Area, Mississippi.

Model	Variable	Estimate	SE	Hazard Ratio	AIC	Δ AIC
LS Linear Hebaceous Cover	LS_LINH	0.0373	0.0218	1.0380	356.5160	0
MPS Linear Herbaceous Cover	MPS_LINH	0.6485	0.3770	1.9130	356.6920	0.1760
No covariates [a]					357.1380	0.6220
ED Linear Herbaceous Cover	ED_LINH	0.0030	0.0022	1.0030	357.2920	0.7760
SDI [a]	SDI	-0.4251	0.3678	0.6540	357.8150	1.2990
Distance to Woody Cover	DIS_WOOD	0.0019	0.0021	1.0020	358.3530	1.8370
ED Rowcrop	ED_RC	0.0013	0.0018	1.0010	358.6050	2.0890
LS Rowcrop	LS_RC	0.0032	0.0045	1.0030	358.6390	2.1230
ED Rowcrop	ED_WOOD	-0.0013	0.0021	0.9990	358.7160	2.2000
ED [a]	ED	0.0006	0.0016	1.0010	358.9950	2.4790
MPS Grass	MPS_GRAS	0.0253	0.0759	1.0260	359.0280	2.5120
LS Wood	LS_WOOD	0.0023	0.0087	1.0020	359.0660	2.5500
LS Grass	LS_GRASS	0.0011	0.0046	1.0010	359.0840	2.5680
MPS [a]	MPS	0.0285	0.1469	1.0290	359.1010	2.5850
MPS Wood	MPS_WOOD	0.0234	0.1280	1.0240	359.1050	2.5890
ED Grass	ED_GRASS	-0.0001	0.0017	1	359.1370	2.6210
MPS Rowcrop	MPS_RC	0.0010	0.0988	1.0010	359.1380	2.6220
Linear Herbaceous Composite [a]	LS_LINH	0.0610	0.1146	1.0630	360.3160	3.8000
	ED_LINH	-0.0026	0.0075	0.9970	360.3160	
	MPS_LINH	0.0147	1.1081	1.0150	360.3160	
RowCrop Composite [a]	LS_RC	0.0088	0.0120	1.0090	361.9220	5.4060
	ED_RC	-0.0004	0.0036	1	361.9220	
	MPS_RC	-0.1405	0.1765	0.8690	361.9220	
Woody Composite [a]	LS_WOOD	0.0101	0.0176	1.0100	362.3180	5.8020
	ED_WOOD	-0.0020	0.0023	0.9980	362.3180	
	MPS_WOOD	-0.0861	0.2480	0.9180	362.3180	
Grass Composite [a]	LS_GRASS	0.0002	0.0103	1	363.0250	6.5090
	ED_GRASS	-0.0001	0.0025	1	363.0250	
	MPS_GRAS	0.0232	0.1450	1.0230	363.0250	

[a] *a priori* models

ceous cover (ED_LINH, β = 0.00525, SE = 0.00284), and mean patch size of linear herbaceous cover (MPS_LINH, β = 2.86064, SE = 1.23112). The confidence intervals on the parameter estimates for LS_LINH and ED_LINH included 0, and the sign suggested a weak positive and negative effect, respectively, of these variables on winter survival. The confidence intervals on mean patch size of linear herbaceous cover did not include 0 and the sign and

hazard ratio indicated that as mean patch size of linear herbaceous cover in the range increased, risk of mortality increased. In retrospective analyses that included all 10 *a priori* models + 14 single variable models, 5 models, including the linear herbaceous composite model, had ΔAIC < 2 and therefore were considered as competing models (Table 3). Single variable models that included mean patch size of linear herbaceous cover, edge density of rowcrop, %

of landscape in rowcrop, and edge density of linear herbaceous cover all indicated that as the landscape metric increased, risk of mortality increased (Table 3).

Daily Location Landscape Metrics

Of the 8 *a priori* models estimating survival as a function of characteristics of daily ranges, the no covariates models had the lowest AIC, however, 3 other models (SDI, ED, MPS) were within 2 ΔAIC of the best approximating model, suggesting considerable model uncertainty (Table 4). Additionally, confidence intervals on parameter estimates included 0 for all competing models, providing little evidence for substantive effect on survival of landscape structure and composition within daily activity regions. In the retrospective candidate model set, the percentage of landscape in linear herbaceous cover was the best approximating model, but 5 other models, including the no covariates model, were competing (ΔAIC < 2). Confidence intervals for coefficients of all variables in all competing models included 0.

Mortality Recovery Locations

Live locations did not differ ($P > 0.05$) from mortality locations, regarding overall mean patch size, overall edge density, percentage of the landscape in linear herbaceous cover, percentage of the landscape in grass, edge density of woods, edge density of linear herbaceous cover, edge density of grass, mean patch size of woods, mean patch size of linear herbaceous cover, mean patch size of grass, mean patch size of row crop, or distance to wooded edge. We observed a year by location type interaction for Shannon diversity index ($F_{1,68} = 9.66$, $P = 0.0027$), percentage of the landscape in wooded cover ($F_{1,68} = 4.23$, $P = 0.0437$), percentage of the landscape in row crop ($F_{1,68} = 4.24$, $P = 0.0433$), and edge density of row crops ($F_{1,68} = 9.67$, $P = 0.0027$). During the second season, Shannon diversity index differed between mortality and live locations ($F_{1,68} = 9.56$, $P = 0.0029$), with mortality locations occurring in more diverse landscapes (SDI = 1.0592, SE = 0.09025) than live locations (SDI = 0.8015, SE = 0.09025). Shannon diversity index at mortality lo-

cations differed between years ($F_{1,68} = 4.00$, $P = 0.0494$), with less diverse locations during the 2000-2001 season (SDI = 0.8591, SE = 0.04310) than during the 2001-2002 season (SDI = 1.0592, SE = 0.09025). During the 2000-2001 season, mean percentage of the landscape in wooded cover differed ($F_{1,68} = 4.10$, $P = 0.0468$) between mortality (20.65%, SE = 2.04) and live locations (15.06%, SE = 2.4309). The percentage of the landscape in row crop differed ($F_{1,68} = 4.35$, $P = 0.0407$) between live (15.47%, SE = 8.2988) and mortality (31.83%, SE = 8.2988) locations during the 2001-2002 season. Similarly, during the 2001-2002 season, mortality locations had greater ($F_{1,68} = 9.15$, $P = 0.0035$) edge density of row crops (96.02 m rowcrop/100 ha, SE = 21.4984) than live locations (37.87 m of row crop edge/100 ha, SE = 21.4984).

Discussion

Roseberry and Klimstra (1984) observed that, in Illinois, annual occupancy rates of specific winter ranges differed among ranges and varied from 27-80%. They suggested that these differences might be a function of varying habitat quality, or in the terms of Errington and Hamerstrom (1936), "security". It has commonly been assumed that habitat quality, or security, does vary among covey ranges, with high occupancy reflecting high quality ranges. It follows that only the most optimal ranges will be occupied at low densities and as density increases, increasingly marginal ranges will become occupied. If winter ranges differ in quality, and bobwhite exhibit ideal free habitat selection (Fretwell and Lucas 1970), then at high population densities, a greater proportion of coveys must inhabit ranges of poorer quality than they would at lesser population densities. If so, this provides a natural mechanism for density-dependent winter mortality observed by Roseberry and Klimstra (1984) on their Illinois study site. Negative correlations between percentage of ranges occupied and population densities have been taken as evidence to support the hypothesis "that individual and collective security declines as population density increases" (Roseberry and Klimstra 1984, p. 30). This hypothesis is predicated on the assumption that

survival varies among covey ranges and that security within a covey range (range-specific survival rate) is a function of habitat characteristics.

We studied a bobwhite population in Mississippi during 2 years with dramatically differing density and winter survival. Under the Roseberry and Klimstra (1984) hypothesis, we would predict that a high proportion of the ranges occupied during the low density year (2001-2002) would have been occupied in the high density year (2000-2002) and a low proportion of the ranges occupied during the high density year would be occupied during the low density year. However, we observed that only 24% of the range used during the low density year (2001-2002) had been occupied during the high density year (2000-2001) and a similar proportion (21%) of the area occupied during low density year was occupied at high density. Therefore, in regard to occupancy and density relationships, our observations did not support the quality/security/density hypothesis.

A second prediction of the quality/security hypothesis is that ranges differ in habitat quality, presumably attributable to differences in vegetation structure, patch characteristics, landscape composition, or landscape structure. We found only weak evidence to support the hypothesis that variation in survival of individual birds was related to variation in landscape structure or composition of winter ranges or that survival varies between covey ranges in relation to landscape structure. Finally, our study was conducted at a relatively southern latitude, whereas Roseberry and Klimstra's work was conducted at a more northern latitude with more severe winter weather. If factors that vary among winter ranges, and influence quality, relate to thermal cover or vegetation structure in the presence of snow and ice, differences in response between northern and southern landscapes would be expected. However, we did not find support for dramatic range-specific differences in landscape structure and composition that contribute to variation in winter survival. Several essential habitat components of winter covey ranges have been identified by various researchers. A brushy or woody "headquarters" area

for midday loafing, escape cover, and foul weather roosting seems to be an essential habitat component of winter ranges (Stoddard 1931, Roseberry 1964, Bartholomew 1967, Yoho and Dimmick 1972, Roseberry and Klimstra 1984). An adequate and accessible food resource, including cultivated crops and annual weeds associated with cultivation, is essential and the availability or distribution may affect over-winter survival (Roseberry and Klimstra 1984, p. 31). Various early successional stages of grassy or weedy vegetation may provide essential early season roosting and feeding habitats. The importance of quality, quantity, and distribution of these cover types has been recognized (Edminster 1954, Schroeder 1985, Roseberry and Klimstra 1984). The essential nature of interspersion and juxtaposition of these resources to allow simultaneous access to habitat components that meet daily requirements has been recognized (Stoddard 1931, Leopold 1933, Roseberry and Klimstra 1984) and measures of interspersion have been used to quantify "habitat quality" (Baxter and Wolfe 1972, Schroeder 1985). However, relationships among habitat quantity, spatial distribution, and over-winter survival have not been examined for bobwhite. During our study, we observed no consistent relationships among landscape composition/structure and survival at either the spatial scale of the winter range or daily location. Specifically, the quantity, patch size, amount of edge, or interspersion of patch types within the winter range or surrounding daily activity locations did not measurably influence the hazard function, suggesting that seasonal ranges can have different composition and structure, yet show similar survival rates for the birds that inhabit each range. There was no strong evidence to suggest that seasonal ranges differed quantitatively in their survival benefits in relation to the composition or structure of the habitat within them.

Guthery (1999) defined usable space within different arrangements of the habitat as slack and gave 3 reasons why this may occur: (1) bobwhite are adapted to a range of habitats, (2) bobwhite may change the time that they spend on different activi-

ties, and (3) different types of patches may serve similar functions. Our observations are consistent with predictions of the Guthery (1999) slack hypothesis, that is different configurations of patch types result in comparable fitness. Guthery et al. (2001) similarly concluded that landscape composition was more important in determining bobwhite abundance than configuration.

Covey range models that best explained survival included all models that used linear herbaceous components, in the composite model and individually. The grassy composite model also was included in the top covey range models. This would suggest that linear herbaceous cover and grass composition and structure may influence bobwhite over-winter survival. In general, there is weak evidence to suggest that some components of linear herbaceous cover have a negative influence on bobwhite over-winter survival. However, due to the placement of cover strips and field borders, this may be an effect of row crops closely associated with these components of the landscape. The row crops at this time of year are harvested and the ground is generally bare or sparsely vegetated for a large portion of the season. Thus, birds occupying covey ranges with significant amounts of linear herbaceous cover might spend a disproportionate amount of time foraging in a high risk environment.

Guthery (1997) proposed the concept of space-time saturation in habitat management for bobwhite. He suggested that a point on the landscape is either usable or not, and as such, managers should strive to provide usable points at all locations at all times throughout the year. The data presented here would lend support to this hypothesis as well. Each point that was recorded for a radio-marked bobwhite was compared to all other points taken for radio-marked bobwhite. There was no strong evidence to indicate that the composition or structure of the habitat surrounding those points strongly influenced survival of bobwhite.

At the point scale, models that best explained survival in relation to habitat composition and structure were ones that included linear herbaceous cover, grass cover, and woody cover individually. Shannon Diversity index was also included in the top daily habitat models. The only individual woody cover model that was not included in the top models (ΔAIC < 2) was mean patch size of woody cover (ΔAIC = 2.018). However, the confidence intervals on coefficients included 0, providing relatively weak evidence for influence on survival. This would lend support to the theory that all of the points where data were collected were in usable space at the time they were collected. However, because this data were taken using radio locations of marked bobwhite, one would expect that the points used in this analysis were all at usable locations. Through radio tracking data, we can only see points that are used. Points not used will not be included because a non-usable point will not have a radio location associated with it.

Even though there was weak evidence to suggest influence of these habitat components on survival (i.e. confidence intervals on coefficients included 0), the individual linear herbaceous cover models showed negative influence on survival in the same pattern as those for covey ranges. Once again, as mentioned above, this may be an artifact of the close association of linear herbaceous cover and row crops during this time of year. Similarly, all individual grassy cover models showed weak negative influence on survival. As the percentage of landscape in woody cover and the mean patch size of woody cover increased, there was weak evidence for a decrease in survival. Also, there was a small increase in survival associated with an increase in the edge density of woody cover and a small decrease in survival as distance to woods increased. This would suggest that bobwhite require some woods in the landscape to provide escape cover, but not large blocks of woods.

Although composition and structure within winter ranges and at daily locations were poor predictors of survival, landscape context did differ between live locations and presumed mortality locations. Most notably, during the season with greater survival (2001-2002), mortality locations occurred in

landscapes with more row crop (31.83%) than that surrounding live locations (15.47%) and greater row crop edge density (96.06 m/100 ha vs. 37.87 m/100 ha, respectively). Previous research has found that bobwhite use row crop fields less than other types of habitat in their range during winter (Yoho 1970). During winter, row crop fields are usually harvested and provide little to no overhead or vertical cover to protect bobwhite against predation. If row crop fields and in particular edges within row crop fields are used as travel lanes for predators, the predator may go out into other areas to catch prey and then return with the carcass to a spot that it normally uses to consume its prey.

We have attempted to assess habitat quality in this study with a demographic design. It has been suggested that the demographic approach to habitat quality studies is superior to other designs (Garshelis 2000., Garton et al. 2001). We found no strong evidence to suggest that the habitat composition or structure strongly influences bobwhite survival at either the level of the seasonal range or the daily range. This could occur on an area that has already reached space-time saturation (Guthery 1997). This may not be the case on BPWMA and without having unusable points in time and space to compare to usable points, it is impossible to quantify all points on the area. What may be necessary is a synthesis of the demographic design and a more traditional used point versus random point comparison. This could be accomplished by taking all points that were used, buffering them by the mean daily movement, combining the buffered areas, and removing the resulting area from the GIS coverage as usable space, then an equal number of random points could be placed on the remaining coverage and analyzed in the same fashion as the used points. This would give a way to quantify used versus unused portions of the area.

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