
2009

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Recommended Citation

Masters, Ronald E.; Guthery, Fred S.; Walsh, W. Russ; Cram, Douglass S.; and Montague, Warren G. (2009) "Usable Space Versus Habitat Quality in Forest Management for Bobwhites," *National Quail Symposium Proceedings*: Vol. 6 , Article 21.

<https://doi.org/10.7290/nqsp06iq8k>

Available at: <https://trace.tennessee.edu/nqsp/vol6/iss1/21>

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Usable Space Versus Habitat Quality in Forest Management for Bobwhites

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We determined whether habitat quality (patch richness and diversity, edge density) or the quantity of usable space (suitable permanent cover) best explained the presence or absence of calling male bobwhites (*Colinus virginianus*) on 50-ha, circular plots ($n = 80$) in the Ouachita National Forest, Arkansas, during 2000 and 2001. Information theoretic analysis of logistic regression models revealed that usable space was predictive of bobwhite occurrence, whereas habitat quality variables were not. A logistic regression model with data pooled over 2 years predicted the presence of calling males if usable space was >26 ha on the 50-ha plots. Creation of usable space on the study area involved removal of mid story and co-dominant shortleaf pine (*Pinus echinata*) and hardwoods (wildlife stand improvement = WSI) followed by February or March (late dormant season) prescribed burns at 3-year intervals. Application of WSI and fire results in an understory mosaic of low woody sprouts, forbs, and grasses of varying heights depending on time since the last burn. Our results were consistent with the hypothesis that predicts bobwhite presence as a function of usable space in time versus the classical principle of edge and other habitat quality indicators.

Citation: Masters RE, Guthery FS, Walsh WR, Cram DS, Montague WG. 2009. Usable space versus habitat quality in forest management for bobwhites. Pages 184 - 192 in Cederbaum SB, Faircloth BC, Terhune TM, Thompson JJ, Carroll JP, eds. Gamebird 2006: Quail VI and Perdix XII. 31 May - 4 June 2006. Warnell School of Forestry and Natural Resources, Athens, GA, USA.

Key words: Arkansas, *Colinus virginianus*, edge, habitat quality, northern bobwhite, pine-bluestem, prescribed burning, usable space, wildlife stand improvement

Introduction

Habitat management for bobwhites may be viewed under 2 competing hypotheses (Guthery 1997). The first hypothesis involves management for bobwhite habitat quality; it operates under the assumption that bobwhite density on a management area increases with quality attributes such as food supplies, floral diversity, cover interspersion, and edge density, among other variables. For example, management to this end would encompass, respectively, adding food plots or supplemental feeding, plantings of various types of cover (woody plantings or warm season grass plantings), and creation of additional edge within a landscape (Guthery et al. 2002). This hypothesis assumes that habitat quality exists on a continuum from low to high and further that increases in the attributes will necessarily increase bobwhite density (Guthery 1997). Leopold

(1933) could be considered the originator of the habitat quality hypothesis.

The second hypothesis involves management for suitable permanent cover (usable space = structurally suitable habitat) across a landscape with less or no regard for habitat quality issues (Guthery 1997, Guthery et al. 2001). Suitable permanent cover for bobwhites is defined as persistent woody cover (<2 m in height) well mixed with herbaceous vegetation (Cram et al. 2002, Guthery et al. 2002). This hypothesis operates under the simple assumption that mean density of bobwhites on an area is proportional to the quantity of usable space on the area. This hypothesis implies that management should create usable space where none exists rather than alter perceived habitat quality in usable space that already exists. The usable space hypothesis has long been recognized (Stoddard 1931, Leopold 1933, Errington

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and Hamerstrom 1936) but perhaps not fully appreciated until more recently (Guthery 1997).

We conducted a study in the Ouachita Mountains of west-central Arkansas to determine whether selected habitat quality variables or usable space at the landscape level best predicted the presence or absence of calling male bobwhites on 50-ha, circular areas similar to Guthery et al. (2001). Landscape indices of habitat quality included edge density and patch diversity and richness. The habitat quality hypothesis predicts a positive response of bobwhites to these variables, again similar to Guthery et al. (2001). Conversely, the usable space hypothesis predicts a positive response to the quantity of suitable permanent cover and a neutral response to habitat quality variables. We examined only edge-related and patch-related aspects of habitat quality because food based aspects of the quality hypothesis and usable space hypotheses may be confounded to some degree and our interest was at a coarser scale, plus we were paralleling study design of Guthery et al. (2001) albeit in a markedly different ecosystem. As well, the creation of usable space may be associated with increased food supplies, especially in thinned and burned mature forests (Guthery 1997, Cram 2001).

Study Area

The study area was within the 60,000-ha shortleaf pine (*P. echinata*)-grassland renewal area on the Poteau Ranger District in the Ouachita National Forest, Scott County, Arkansas and associated private lands (Figure 1). The Ouachita Mountains generally run east-west with long north- and south-facing slopes. Shortleaf pine tends to dominate south-facing slopes and oaks (*Quercus* spp.) dominate north-facing slopes (Foti and Glenn 1991). Soils in the study area, which developed from sandstone and shales, are thin and drought-prone. The climate is subhumid to humid with hot summers and mild winters. The maximum annual precipitation is >150 cm and the minimum annual precipitation is <100 cm (Anonymous 1973).

The pine-grassland renewal area has been man-

aged extensively for red-cockaded woodpeckers (*Picoides borealis*) since 1990 (Masters et al. 1996). Management consisted of wildlife stand improvement (WSI; removal of midstory and codominant pine and hardwood species). Subsequently, dormant season prescribed fire (in Feb or Mar) is applied to WSI stands on a 3-year rotation; this includes thinned and burned regeneration stands (planted or naturally regenerated to shortleaf pine). Available stands also included mature forest not subject to any treatment and unburned and unthinned regeneration stands of varying ages. Cram et al. (2002) and Masters et al. (1996, 2002) provide further details about forest management in the study area.

Our study area encompassed a matrix of unmanaged shortleaf pine-hardwood [primarily oak (*Quercus* spp.) and hickory (*Carya* spp.)] and pine-grassland restoration stands of varying age-classes managed by the U.S. Forest Service and private land. Private land management varied from dense pine-hardwood stands similar to unmanaged control stands (Cram et al. 2002) to cut-over stands and finally to open, domesticated pasture lands dominated by primarily fescue grass with occasional broomsedge bluestem (*Andropogon virginianus*). Essentially none of the private lands used prescribed fire as a management tool.

We randomly selected 80 non-overlapping plots (400-m radius; 50.3 ha) and conducted calling male counts during May-early June of 2000 and 2001 (Figure 2). We generated random coordinates of points within the bounds of our study area and buffered each point to a 400-m radius. Overlapping buffered points were discarded; we continued the process until 80-non-overlapping plots were generated. We selected 400 m as the radius of our plots because it was the same radius as Guthery et al. (2001) and we wanted to be able to draw direct comparisons. Counts involved a 3-minute listening period at plot center followed by broadcasting a female assembly call in cardinal directions at 90 dB, listening for 90 seconds, again broadcasting the call, and listening for another 90 seconds (Cram et al. 2002). The counts took place between 0600 and 1100 hours. Each site

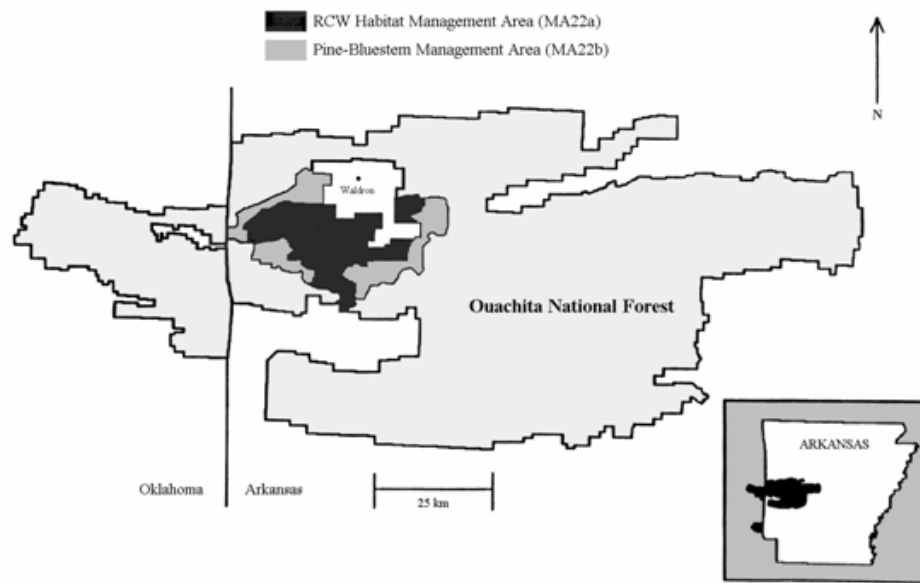


Figure 1: General study site location (MA22a and MA22b) within Ouachita National Forest near Waldron AR.

received 3 counts conducted by a different observer; one count/site was conducted during hours (0600-0800) of peak calling intensity (Hansen and Guthery 2001).

Methods

Measurement of Usable Space

Usable space (suitable habitat) availability (ha) within 400 m of a listening stop was evaluated using ArcView GIS v 3.2 (Environmental System Research Institute, Redlands, California, USA). ArcView coverages with associated stand data were obtained from the U.S. Forest Service office on the Poteau Ranger District. These maps and associated attribute tables provided areas for stand type, composition and age. Private land cover types within a listening stop were delineated from aerial photography, digitized on-screen and verified in the field for type and composition. Usable space was defined as the total area within 400 m of a listening post that consisted of stands (= habitat patch) treated with WSI only, WSI ≤ 3 years post fire, and regeneration stands ≤ 3 years post fire. The stand types defined to be usable space carry the highest density of and receive selective use

from bobwhites on the study area (Cram et al. 2002, Walsh 2004). Fescue pasture was not considered usable space because early listening trials showed no calling activity across multiple years and sites and later telemetry studies (Walsh 2004) showed no use by bobwhites.

Measurement of Habitat Quality

We used FRAGSTATS (McGarigal and Marks 1994) to estimate landscape metrics for the 400 m-radius plots sampled (Table 1). Metrics such as total edge were used as indicators of habitat quality. These metrics were subjected to factor analysis (Afifi and Clark 1984) to reduce the dimensionality of the dataset.

Statistical Procedures

We used logistic regression analysis (Kleinbaum 1994) to test 7 models for predicting the presence or absence of calling male bobwhites on 50-ha areas. The global model $\{u, d, e\}$ included usable space (u ; ha), Shannon diversity (d), and Shannon evenness (e). We also tested the following models: $\{u, d\}$, $\{u, e\}$, $\{d, e\}$, $\{u\}$, $\{d\}$, and $\{e\}$. Model comparisons were based on the small-sample Akaike In-



Figure 2: Listening stop locations (400 m-radius circles, 50.3 ha) on the Poteau Ranger District, Ouachita National Forest and private lands near Waldron AR, May through early June 2000 and 2001.

formation Criterion (AIC_c ; Burnham and Anderson 2002). The data from 2000 were used to generate models and the data from 2001 were used to test the repeatability of the best model from the 2000 data. We also report a model for data pooled over the 2 study years.

Results

Of the 80 listening stops, 26 encompassed at least some private land or were entirely on private land. Our listening stops encompassed a total of 12 different habitat types. Metrics associated with characteristics of discrete habitat patches (quality variables) within a given listening stop (e.g., number of patches, patch density, and patch richness) had a generally wide range about the mean (Table 1). Two factors explained 89% of the variation in the landscape metrics (Table 2). Variables with high loadings (absolute value) on the first factor included patch diversity, patch richness, and total edge, among others. Evenness indices and contagion loaded high on the second factor. These results indicated the landscape metrics evaluated collapsed to essentially 2 variables because of intercorrelation among vari-

ables (variables with high loadings on the same factor are correlated). Therefore, we used Shannon diversity (highest loading on first factor; 0.95) and Shannon evenness (second highest absolute loading on second factor; -0.86) in logistic modeling (variables with high loadings on different factors are not correlated).

During both 2000 and 2001, the average number of calling males/stop was 0.2 ± 0.04 SE ($n = 80$ each year). In 2000 calling males were recorded at 30 of 80 stops, whereas in 2001 they were recorded at 27 of 80 stops. Over the 2 years, 41 listening stops had calling males in ≥ 1 year.

Model selection revealed that any model that contained usable space was plausible ($\Delta AIC_c < 1.4$), whereas any model that did not contain usable space was not plausible ($\Delta AIC_c > 9.4$; Table 3). The Akaike best model contained usable space as the sole variable. Given presence of bobwhites, this model correctly predicted 45% of cases; given absence, it correctly predicted 67% of cases.

The logistic regression model (u only) generated with 2000 data correctly predicted 61% of cases for

Table 1: Mean values for landscape metrics of 50 ha, circular plots ($n = 80$), Ouachita National Forest, Scott County, Arkansas, 2000 and 2001.

Landscape Metric	Mean	Min	Max	Range
Number of patches	10.56	2.00	18.00	16.00
Patch density (no./100 ha)	21.12	4.00	36.00	32.00
Landscape patch index (%)	35.84	15.67	86.89	71.22
Total edge (m)	4879.38	1115.00	8720.00	7605.00
Edge density (m/ha)	97.58	22.30	174.40	152.10
Landscape shape index	2.86	1.53	4.21	2.69
Contagion	57.56	47.50	81.72	34.22
Cohesion	98.82	98.06	99.71	1.65
Patch richness	8.68	2.00	18.00	16.00
Patch richness density (no./100 ha)	17.35	4.00	36.00	32.00
Shannon diversity	1.64	0.59	2.21	1.62
Simpson diversity	0.75	0.24	0.87	0.63
Modified Simpson diversity	1.45	0.28	2.07	1.79
Shannon evenness	0.79	0.33	1.00	0.67
Simpson evenness	0.86	0.29	1.00	0.71
Modified Simpson evenness	0.70	0.15	1.00	0.85

the 2001 data, despite the fact that some stops with calling males in 2000 had no calling males in 2001, and some stops with no calling males in 2000 had calling males in 2001. Given presence of calling males, the model correctly predicted 38% of cases in 2001. Given absence, it correctly predicted 72% of cases.

The logistic regression model for data pooled over years was

$$y = \frac{1}{1 + \exp(1.04 - 0.04x)}$$

where y is the classification score and x is usable space (ha). The 95% CI on the intercept (1.04) and coefficient (0.04) did not contain zero. This model predicts the presence of calling male bobwhites if the quantity of usable space exceeds about 26 ha ($y > 0.5$). Bobwhite occurrence plots ($n = 41$) were associated with an average of 34 ha of usable space (95% CI = 29.7-36.3 ha), whereas non-occurrence plots ($n = 39$) were associated with 21 ha (95% CI = 16.7-25.3 ha). Given presence, the model predicted correctly in 57% of cases, whereas given absence, it

predicted correctly in 55 of cases.

Discussion

As with all field studies, our results have contexts for interpretation and extrapolation. First, the results pertain specifically to calling male bobwhites because we collected no data on other sex-age classes. However, Cram et al. (2002) observed that pine-grassland restoration (WSI, WSI plus burning) provided suitable habitat structure for bobwhites during spring, summer, and fall but may not be adequate during winter. Walsh (2004) observed bobwhite selection for pine-grassland restoration treatments and thinned and burned regeneration stands in both the breeding and covey season. Our listening-stop data also confirmed that domesticated fescue (*Festuca* sp.) pasture was not usable space. Thus, our findings generally were consistent with previous findings on the study area.

Second, our experiment took place in a low-density population. During both 2000 and 2001, the average number of calling males/stop was 0.2 ± 0.04

Table 2: Factor loadings for landscape metrics associated with 50-ha, circular plots ($n = 80$), Ouachita National Forest, Scott County, Arkansas, 2000 and 2001.

Landscape metric	Factor	
	I	II
Number of patches	0.83	0.48
Patch density (no./100 ha)	0.83	0.48
Landscape patch index (%)	-0.85	0.37
Total edge (m)	0.88	0.22
Edge density (m/ha)	0.88	0.22
Landscape shape index	0.88	0.22
Contagion	-0.52	0.82
Cohesion	-0.88	-0.31
Patch richness	0.82	0.43
Patch richness density (no./100 ha)	0.82	0.43
Shannon diversity	0.95	0.01
Simpson diversity	0.91	-0.23
Modified Simpson diversity	0.94	-0.17
Shannon evenness	0.47	-0.86
Simpson evenness	0.65	-0.86
Modified Simpson evenness	0.43	-0.88

SE ($n = 80$ each year). On farms and ranches in central and western Oklahoma, Guthery et al. (2001) observed an average of 4.2 ± 0.43 calling males/stop with a range of 0.1-15.9 males/stop during 1998 and 1999. The apparent low densities we observed could be related to timing of the counts (May-early June). Hansen and Guthery (2001) observed peak calling of bobwhite males in mid June or later in central Oklahoma. Terhune (2004) reported peak calling in June and July in south Georgia and north Florida.

Third, the predictive models developed, though statistically well supported (Table 3), were of relatively low accuracy. For example, the model for data pooled over years correctly predicted 56% of cases overall. We conjecture that the relatively low accuracy occurred for at least 3 reasons. First, population density of calling males might have been too low to fully occupy usable space (more usable space than males available). This situation would have been associated with the absence of males on suit-

able 50-ha circles, thus resulting in modeling score of 0 (absence) in suitable cover. This is plausible because changes in bobwhite density lag somewhat behind creation of suitable habitat because a response is time dependent (Guthery 1997). This was evidenced by comparison of bobwhite abundance just after initiation of the pine-bluestem renewal project by Wilson et al. (1995) and a study a decade later by Masters et al. (2002) within the pine-bluestem renewal area. The amount of treated area on the forest was 1,057 ha in 1993 and 4,970 in 2001; an increase of almost 5 times the usable space. Second, in our study area, bobwhite density in a stand is related to the amount of suitable habitat surrounding the stand (Cram et al. 2002). Our limit of analysis (400 m-radius) did not fully capture this potentiality, which would imply the possible occurrence of calling males in 50 ha plots with low quantities of usable space if larger quantities of usable space were nearby. Third, all treatment types on the study

Table 3: Evaluation of logistic regression models for predicting the presence or absence of calling male bobwhites on 50-ha, circular plots ($n = 80$), Ouachita National Forest, Scott County, Arkansas, 2000 and 2001.

Model ^a	K	AIC _c	Δ AIC _c	Proportion correct
<i>u,d,e</i>	4	100.4	0.50	0.61
<i>u,d</i>	3	100.7	0.80	0.59
<i>u,e</i>	3	101.2	1.34	0.59
<i>d,e</i>	3	110.7	10.81	0.54
<i>u</i>	2	99.9	0.00	0.59
<i>d</i>	2	109.3	9.44	0.54
<i>e</i>	2	109.8	9.98	0.53

^a*u* = usable space (ha), *d* = Shannon diversity, *e* = Shannon evenness

area, including untreated forest, contain at least limited amounts of usable space (Walsh 2004). This would imply usable space as we defined it (WSI, WSI plus burning, and burned and thinned regeneration stands) should be considered an index of the total quantity present. This situation could reduce the accuracy of prediction models.

Given limitations on predictive accuracy, however, the models and other analyses were useful in revealing patterns in the dataset. Factor analysis revealed that several variables presumed indicative of habitat quality measured essentially the same property of experimental plots. The number of patches, total edge, patch richness, and diversity indices all loaded high on Factor I (Table 2). This means the variables were intercorrelated and therefore, at least on our study area, knowing any 1 of them provided information on all the others. Note that landscape metrics expressed as density (e.g., patch density) were scaled versions of the raw homologue (e.g., number of patches) because all areas were 50 ha in our study and thus had factor loadings identical to the homologues.

The pattern revealed by logistic regression models was that male bobwhites responded to the availability of usable space but not to patch diversity and related variables (e.g., total edge; Table 3). This re-

sult supports the usable space hypothesis over the habitat quality hypothesis. Likewise, Guthery et al. (2001) found stronger support for the usable space hypothesis than for the habitat quality hypothesis on farms and ranches in central and western Oklahoma. These authors observed a negative effect of Shannon diversity, patch richness, and density of woody edge on the abundance of calling male bobwhites.

However, the habitat quality and usable space hypotheses are confounded to some degree. For example, the existence of edge between woody cover and prairie implies usable space (Guthery and Bingham 1992) for bobwhites. Within usable space, however, bobwhite density may be independent of the quantity of edge (Guthery 1999, Guthery et al. 2001). Also, the creation of usable space may be associated with increased food supplies, especially in thinned and burned mature forests (Guthery 1997, Cram 2001).

Management Implications

Our results on the presence or absence of calling male bobwhites supported the usable space hypothesis over aspects of the habitat quality hypothesis for management of bobwhite habitat in the Ouachita National Forest, Arkansas; specifically as it relates to patch characteristics of edge. Management that cre-

ates usable space in this setting (mostly contiguous dense forest) implies thinning of young and mature stands of timber to a basal area of at least 13.8 to 18.4 m²/ha, followed by prescribed burning of thinned stands on a ≤ 3 -year rotation (Cram et al. 2002). This reduction in stand basal area results in an increase in understory vegetation composed of a mosaic of low woody sprouts, forbs and grasses of varying heights depending on time since the last burn (Cram et al. 2002, Masters et al. 1996). The increase in understory vegetation also apparently increased food supplies (plant density and thus seed production, plus insect abundance; Cram 2001). Woody vegetation density <2m was an important predictor of bobwhite abundance (Cram et al. 2002). Longer burning rotations than 3-year intervals do not appear acceptable based on other research in this area as rapid understory woody development soon creates unsuitable habitat structure (Cram et al. 2002, Walsh 2004). Further our results provide additional evidence that fescue pasture is not usable space.

Acknowledgments

We thank B. Palmer for reviewing an earlier draft of the manuscript. Financial support came from the U.S. Forest Service, Arkansas Game and Fish Commission, Quail Unlimited, Arkansas Wild Turkey Federation, Bollenbach Endowment, Game Bird Research Fund, Department of Forestry, and Oklahoma Agricultural Experiment Station. D. Wilson, R. Holman, K. Anderson, J. James, and J. Neal assisted with field data collection. The Oklahoma Agricultural Experiment Station approved this paper for publication.

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Bobwhite Management

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