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Usable Space Versus Food Quantity in Bobwhite Habitat Management

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We studied the response of northern bobwhite (*Colinus virginianus*) foods (plants and invertebrates), usable space, and populations following thinning and burning on the 60,000-ha pine (*Pinus* spp.)-grassland restoration area in the Ouachita National Forest, Arkansas, to examine 2 hypotheses commonly used to manage bobwhite habitat: 1) usable space (suitable permanent cover) and 2) food quantity (an element of habitat quality). We estimated invertebrate food abundance using sweep nets and abundance of food-producing plants using herbaceous and woody stem counts. The disk of vulnerability was used to index usable space. We used whistling-male counts to index population response. Relative abundance, mass, and frequency of occurrence of invertebrate foods and richness, density, and frequency of occurrence of bobwhite food-producing plants increased following thinning and fire. Relative abundance of whistling males was greatest in thinned stands 3 growing seasons post-burn and in thinned but unburned stands. We found food supply was related to usable space following treatment. However, food abundance alone did not explain bobwhite population response, whereas, usable space was predictive for bobwhite response. By comparing treated stands with similar usable space but different food quantity, we observed no differences in bobwhite abundance. Neural models suggested bobwhite population response was less sensitive to changes in food supply relative to changes in usable space. We recommend that managers should seek first to provide usable space (suitable permanent cover in low basal area stands), recognizing that adequate food supply will likely be a side effect of management to this end.

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Key words: Arkansas, *Colinus virginianus*, food quantity, management philosophies, northern bobwhite, Ouachita Highlands, pine-grassland restoration, prescribed fire, usable space

Introduction

Currently, northern bobwhite habitat managers have 2 hypotheses from which to choose when considering management programs. The usable space hypothesis formalized by Guthery (1997) contends as suitable habitat increases on an area of fixed size, mean bobwhite density will increase on the area. Usable space can be defined as suitable permanent cover. The second hypothesis predicts bobwhite density is a function of food quantity (Guthery 1997). This hypothesis contends habitat quality, such as food supply, exists along a continuum ranging from poor to good. Bobwhite management practices such as food plots and food supplementation operate under the quality hypothesis. Any number of habitat variables such as water supply, thermal cover, or habitat-type interspersion could be considered measures of habitat quality. Quality-based management assumes a higher level of habitat quality will support a greater number of bobwhites.

The food quantity hypothesis assumes food is limiting in a given area and increasing the food supply with food plots or supplemental feeding will increase bobwhite densities. We contend managers often focus first on addressing the quantity of the food supply rather than usable space. If food is assumed limiting in a given area, literature reporting on food-increasing management techniques should

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indicate an effect on bobwhite densities commensurate with an increase in food supply (Guthery 1997, 2002). However, the literature suggests management techniques aimed at increasing food supplies are ineffective in terms of increasing fall bobwhite densities (Burger and Linduska 1967, Ellis et al. 1969, Guthery 1997, 2002, Guthery et al. 2004).

Bobwhite populations have responded positively across the southeastern United States in forest stands managed for the endangered red-cockaded woodpecker (*Picoides borealis*) (Brennan 1991, Fuller 1994, Wilson et al. 1995). In Arkansas, bobwhites were found more frequently in thinned and burned stands managed for the red-cockaded woodpecker than in unthinned and unburned control stands (Wilson et al. 1995, Cram et al. 2002). To manage for the red-cockaded woodpecker on the Ouachita National Forest the U.S. Forest Service has delineated a 60,000 ha area for pine-grassland ecosystem restoration. Pine-grassland restoration efforts in the Ouachita National Forest included a program of tree thinning called wildlife stand improvement (WSI) and dormant-season prescribed fire every 3 years. WSI removes <1/3 of the overstory shortleaf pine (*P. echinata*) and >2/3 of the hardwood midstory, and has created stand structure with an open midstory maintained by fire (Wilson et al. 1995, Masters et al. 1998).

Our objective was to investigate the usable-space hypothesis (Guthery 1997, 2002) versus the food quantity-based hypothesis to determine if either or both explained an increase in bobwhite relative abundance. We predicted that food supply, both plant and animal, would increase through the 3 growing seasons following midstory removal and fire, yet would have nominal effects in terms of an increase in relative bobwhite abundance as compared to an increase in usable space (suitable permanent cover). An increase in usable space, as determined by an increase in relative bobwhite abundance, was defined by an increase in forest hectares restored to open pine-grassland conditions following restoration treatment (i.e., WSI and dormant season prescribed fire every 3 years) (Cram et al. 2002).

Study Area

Study sites were in the west-central Ouachita Mountains on the Poteau Ranger District of the Ouachita National Forest, Scott County, Arkansas. All sites were within the 60,000-ha pine-grassland restoration area and under active management for the endangered red-cockaded woodpecker. The Ouachita Mountains cover an area approximately 380 km east to west by 100 km north to south in western Arkansas and southeastern Oklahoma. Mountain ridges typically run east-west with long north-facing and south-facing slopes. The drier south-facing slopes characterized study sites. Elevations range from 100 to 900 m.

The forest is composed of mixed pine-hardwood stands with shortleaf pine dominating drier south-facing slopes, and hardwoods (primarily oaks [*Quercus* spp.] and hickories [*Carya* spp.]) dominating mesic north-facing slopes (Foti and Glenn 1991). Codominant overstory and midstory species included red maple (*Acer rubrum*), mockernut hickory (*C. tomentosa*), pignut hickory (*C. glabra*), flowering dogwood (*Cornus florida*), black cherry (*Prunus serotina*), Mexican plum (*P. mexicana*), southern red oak (*Q. falcata*), blackjack oak (*Q. marilandica*), northern red oak (*Q. rubra*), post oak (*Q. stellata*), and black oak (*Q. velutina*). Post oak, blackjack oak, red maple, and mockernut hickory sprouts <3 m tall dominated the understory in WSI stands 3 years postburn. Woody shrub and vine species included New Jersey tea (*Ceanothus americanus*), blackberry (*Rubus* spp.), Virginia creeper (*Parthenocissus quinquefolia*), winged sumac (*Rhus copallina*), greenbrier (*Smilax bona-nox*), poison ivy (*Toxicodendron radicans*), low-bush huckleberry (*Vaccinium pallidum*), and muscadine (*Vitis rotundifolia*) (Sparks 1996).

Methods

Experimental Design

We used a completely randomized design over 2 years with 4 replications of 5 treatments in 20 stands in 1999 and 2000 for a total of n = 40 stands. Each year 20 stands ≥16 ha ($\bar{x}\pm$ SE; 35 ha ± 2.9) were randomly selected from a list of all suitable stands in the restoration area. Treatment stands in 1999 and 2000 were stratified based on the number of 3-year burning cycles completed (1-7). Treatments (n = 8 for each treatment) were 1) unthinned, unburned control; 2) WSI-no burn (WSI-NB); 3) WSI-burn, first growing season after dormant-season burn (WSI-B1); 4) WSI-burn, second growing season after dormant-season burn (WSI-B2); 5) WSI-burn, third growing season after dormant-season burn (WSI-B3).

Bobwhite Counts

To estimate bobwhite abundance we used whistling-male call counts with playback recordings (Coody 1991) at 1-2 listening points/stand over a 2-week period in May 1999 and 2000. Points were centrally located ≥200 m from stand edge. Each point had an implied 200-m radius of audibility contrary to the standard 400-m radius (Stoddard 1931, p. 102) of rangelands because topography effects on the ONF reduced the distance sound waves could be detected by a human. Whistle counts were repeated 3 times by 3 different individuals between sunrise and 1100 hrs. Whistle counts were stratified during the morning to encompass peak calling periods.

We recorded the number of different whistling males over a 6-min listening period. Playback of an assembly call (Don Scott, Lake Charles, Louisiana, USA) broadcast at 90 dB in the cardinal directions was used twice, once at the 3-min mark and again after the 4.5-min mark (Coody 1991). Relative abundance as indexed by whistle counts is reported by treatment as mean whistling males/point.

Covey-call counts were conducted 3 times by 3 different observers 45 mins before sunrise to 1100 hrs during the first week in October 1999 and 2000. Listening-point locations and assembly-call broadcast methodology were unchanged from whistle-count procedures. The 6-min listening periods were stratified by observer to encompass peak calling times. We recorded the number of different calling coveys and reported relative abundance by treatment as mean coveys/point.

Invertebrate Sampling

To index invertebrate abundance during critical brood-rearing months (June-August) (Stoddard 1931, Rosene 1969, pp. 41 and 59, respectively), we examined the effects WSI and fire had on invertebrate abundance, mass, and frequency of occurrence in untreated pine-hardwood stands as compared to treated stands at various stages of succession following thinning and burning. We collected invertebrates using a standard canvas sweepnet (48-cm handle, 38-cm net hoop diameter, and 76-cm net depth) to estimate relative abundance, mass, and percent frequency of occurrence. Invertebrate sweepnet samples were collected in each stand along 6 randomly located transects 25 m in length on 2 randomly spaced parallel lines (i.e., 3 transects per line), perpendicular to the contour. We used 20 sweepnet strokes/transect line. Transect lines bisected bobwhite whistle-call sampling points. Invertebrates were collected in July 1999 and 2000 between 1000 and 1500 hours when cloud cover was <50% and temperatures were <35° C. Contents of sweepnets were transferred to labeled plastic bags, sealed, and frozen for storage. Invertebrates were sorted to order following Borror et al. (1989), dried at 40° C for 72 hours, and weighed to the nearest 0.001 g. Relative invertebrate abundance and mass were calculated from the 6 transect samples, and reported as mean individuals/sample and mean mg/sample. Percent frequency of occurrence was calculated for the 6 transects.

Sweepnet sampling was selected because of its widespread acceptance as an invertebrate sampling technique (Callahan et al. 1966). Although shortcomings associated with sweepnet sampling are acknowledged (Thompson 1987), sweepnet samples do reflect the taxonomic heterogeneity and magnitude of the invertebrate biomass present in the vegetative canopy of grasslands (Evans et al. 1983). Time and resource constraints precluded the use of vacuum sampling. Vacuum sampling is potentially better suited to trap invertebrates more vulnerable to chick foraging, i.e., invertebrates that are small in size, on the ground, and relatively slow moving

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(compared to aerial invertebrates).

Vegetation Sampling

To examine plant food quantity, we estimated density and frequency of occurrence of known bobwhite food-producing plants based on regional food habit studies (Baumgartner et al. 1952, Masters et al. 1996, Bidwell et al. 1998). To characterize and index bobwhite food-producing plants in each stand, we sampled 30 1-m^2 plots at 30-m intervals on 2-4 randomly spaced parallel lines, perpendicular to the contour over a 2-week period in July 1999 and late-June 2000. We recorded density for each herbaceous species within plots. We recorded density for woody vegetation within 30 fixed-radius plots (radius 3.59 m). We divided woody understory, shrub, and midstory species into 3 height classes: 0-1, >1-3, and >3 m. To further index structure we estimated the disc of vulnerability (Kopp et al. 1998) by measuring the distance at which a 15 X 2.5 cm cylinder disappeared from view of a kneeling observer (height = 1 m) at cardinal radii, then used mean distance to calculate area. A comprehensive list of individual bobwhite food-producing species counted on the Ouachita National Forest was reported in Cram (2001). To avoid bias from surrounding stands, no sampling was conducted within 50 m of stand edge (Mueller-Dombois and Ellenberg 1974, p. 123).

Data Analysis

We calculated species richness of bobwhite food-producing herbaceous and woody vegetation at the stand level. We summarized herbaceous and woody species by mean density and percent frequency of occurrence for each treatment. Differences in means between years and treatments were tested using Kruskal-Wallis nonparametric tests (Steel et al. 1997, p. 177). Stand (year x treatment) Type III mean square was the error term (SAS Institute, Inc. 1985, p. 651). We used multiple comparisons between mean ranks with the Least Significant Difference (LSD) test with P = 0.050 (Steel et al. 1997, p. 178). Stand means were tested for homogeneity of variance among treatments using Levene's test (Snedecor and Cochran 1980). Regression analysis was used to examine relationships among total plant food abundance and invertebrate abundance and mass with whistle-count results.

To further understand nonlinear effects, we modeled mean whistling-male response to habitat variables using artificial neural-network models. Neural Connection software (SPSS Inc., Chicago, Illinois, USA) was used to conduct modeling. We used neural models to detect relationships between mean whistling-male abundance and habitat structure and composition following treatment. Our model used 6 input nodes (independent variables), 1 hidden node, and 1 output node (dependent variable). The *a priori* rationale for choosing 1 hidden node was to prevent overtraining, which would result in models that generalize poorly. The input nodes were year and stand means for forb cover, preferred bobwhite invertebrate abundance, hardwood basal area, conifer basal area, and exposure to ground predators (disc of vulnerability) (Cram et al. 2002). The output node was predicted whistling males/point. The neural model was trained using a randomly drawn data set comprising 80% of the data (n = 32); testing was conducted on the remaining 20% of the data (n = 8).

Results

Population Response

Based on spring whistle counts, the greatest relative abundance of bobwhites occurred in unburned, thinned stands ($\bar{x} = 1.1 \pm 0.32$ [SE]) and in thinned stands in the third growing season following fire ($\bar{x} = 1.54 \pm 0.39$ [SE]) (Cram et al. 2002). Thinned stands in the first (WSI-B1) and second (WSI-B2) growing seasons following fire had similar levels of relative bobwhite abundances ($\bar{x} = 0.4 \pm 0.2$ [SE], $\bar{x} = 0.8 \pm 0.3$ [SE], respectively) (Cram et al. 2002). Control stands had the least measure of bobwhite relative abundance ($\bar{x} = 0.1 \pm 0.1$ [SE]) (Cram et al. 2002). There was no statistically significant difference in mean bobwhite relative abundance between 1999 and 2000 (1999: $\bar{x} = 1.0 \pm 0.2$ [SE], 2000: $\bar{x} = 0.6 \pm 0.2$ [SE], P = 0.157). Based on covey-call counts, relative abundance of covey calls was similar in nature to whistle counts; relative abundance of covey calls was greatest in unburned, thinned stands (WSI-NB) ($\bar{x} = 0.50 \pm 0.27$ [SE]) and in thinned stands 3 growing seasons following fire (WSI-B3) ($\bar{x} = 0.57 \pm 0.30$ [SE]) (Cram et al. 2002). No coveys were detected in control stands using covey-call counts (Cram et al. 2002).

Invertebrate Response

Relative invertebrate abundance (mean invertebrates/sample) and mass (mean mg/sample) increased over control stands following WSI and fire treatment (Table 1). Thinned stands in the third growing season following fire had the greatest total invertebrate abundance and mass as compared to other treatments. Total invertebrate abundance was more than 2-fold greater than controls and total invertebrate mass was more than 3-fold greater than controls in WSI stands 3 growing seasons following fire. Relative to the total number of invertebrate orders identified (12) there were few differences between orders between years in terms of relative abundance (i.e., Araneae, Homoptera, and Lepidoptera differed between years) or mass (i.e., Homoptera, and Lepidoptera differed between years) of individual orders, but no differences between years when total abundance or total mass was considered.

Sweepnet sampling captured invertebrates from 12 different orders (see Cram 2001) with locomotion adaptations ranging from cursorial to saltatorial to aerial. Invertebrates frequently consumed by bobwhite adults and chicks included Coleoptera, Hemiptera, Homoptera, Lepidoptera larvae, and Orthoptera (Stoddard 1931, Hurst 1972, Jackson et al. 1987). Percent frequency of occurrence of these important invertebrate orders increased following thinning and fire (Table 2). Orthoptera had 100% frequency of occurrence in WSI-B3 stands. Araneae, Coleoptera, Homoptera, Lepidoptera larvae, and Orthoptera abundance were all positively related to number of times a stand had been burned (r = 0.32, 0.44, 0.49, 0.63, 0.52, respectively).

Herbaceous and Woody Response

Of 286 different herbaceous and woody species identified using stem counts on the Ouachita National Forest, 52 (18%) herbaceous and 14 (5%) woody species were known to be food-producing plants for bobwhites and used in data analysis. Orthogonal contrasts indicated 22 herbaceous and 5 woody species increased in density following thinning and burning as compared to controls. Herbaceous species richness of bobwhite foods was greatest in thinned and burned stands 1, 2 and 3 growing seasons following fire (Table 3). Total herbaceous stems (stems/m^2) were greatest following fire and decreased 2 and 3 growing seasons following fire (Table 3).

Total panicum species (*Panicum* spp.), a preferred bobwhite food in pine-oak forests (Baumgartner et al. 1952), increased following thinning and maintained higher densities than controls following fire (Table 2). Percent frequency of occurrence of wooly panicum (*P. acuminatum*), Bosc panicum (*P. boscii*), forked panicum (*P. dichotomun*), open-flower panicum (*P. laxiflorum*), and slimleaf panicum (*P. linearifolium*) all increased following thinning and again following burning.

We identified 25 different species of legumes, including 10 species of tick trefoil and 7 species of bush clover. Total legume stems (stems/m^2) increased >3-fold 1, 2, and 3 growing seasons following fire (Table 2). Hog peanut (*Amphicarpaea bracteata*), partridge pea (*Cassia fasciculata*), and downy-milk pea (*Galactia regularis*), preferred legumes by bobwhites (Baumgartner et al. 1952), increased in density in WSI treated stands as compared to control stands. We found 13 legume species increased in percent frequency of occurrence in response to fire alone. Densities of partridge pea (*Cassia fasciculata*), butterfly pea (*Clitoria mariana*), small-leaved trick trefoil (*D. ciliare*), beggar's lice (*D. laevigatum*), panicled trick trefoil (*D. paniculatum*), tick trefoil spp., tick trefoil (*D. viridiflorum*), downy-milk pea (*Galactia regularis*), bicolor lespedeza (*Lespedeza bicolor*), prostrate lespedeza (*L. procumbens*), and reclining lespedeza (*L. repens*) were positively related to number of times

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Table 1: Relative invertebrate mass (mean mg/sample) and invertebrate relative abundance (mean invertebrates/sample) response to wildlife stand improvement and fire on the Ouachita National Forest, Arkansas, July 1999 and 2000.[a]

	Treatment[b]										
Variable	Control	SE	WSI-NB	SE	WSI-B1	SE	WSI-B2	SE	WSI-B3	SE	P > F
Total mass	53.3	19.2 C	79.8	15.6 BC	84.1	21.4 BC	132.4	21.6 AB	166	28.9 A	0.004
Total abundance	11.1	1.9 C	14.6	1.6 C	17.5	3.1 BC	21.2	2.4 AB	26.2	3.6 A	0.004

[a] Row means followed by the same letter or without letters were not significantly different at the 0.05 level (LSD)

[b] Control = unthinned, unburned; WSI-NB = wildlife stand improvement, no burn; WSI-B1 = wildlife stand improvement, second growing season following burn; WSI-B3 = wildlife stand improvement, thrid growing season; n = 8 for each treatment

Table 2: Invertebrate (only orders frequently consumed by northern bobwhites) percent frequency of occurrence response to wildlife stand improvement and fire on the Ouachita National Forest, Arkansas, July 1999 and 2000.[a]

	Treatment[b]										
Invertebrate order	Control	SE	WSI-NB	SE	WSI-B1	SE	WSI-B2	SE	WSI-B3	SE	$P > F$
Coleoptera	43.8	9.9 B	54.2	7.6 B	77.1	8.9 A	81.3	5.8 A	85.7	7.7 A	0.003
Hemiptera	2.1	2.1 B	56.3	8.3 A	62.5	8.8 A	62.5	5.2 A	76.2	8.8 A	< 0.001
Homoptera	18.8	6.6 B	56.3	10.9 A	60.4	10.4 A	66.7	13.7 A	76.2	13.5 A	0.012
Lepidoptera larvae	16.7	5.5 D	35.4	5.8 CD	39.6	8.9 BC	60.4	9.4 AB	64.3	5.7 A	< 0.001
Orthoptera	56.3	8.3 C	83.3	6.3 B	87.5	6.9 AB	97.9	2.1 A	100	0.0 A	< 0.001

[a] Row means followed by the same letter or without letters were not significantly different at the 0.05 level (LSD)

[b] Control = unthinned, unburned; WSI-NB = wildlife stand improvement, no burn; WSI-B1 = wildlife stand improvement, first growing season following burn; WSI-B2 = wildlife stand improvement, second growing season following burn; WSI-B3 = wildlife stand improvement, third growing season following burn; n = 8 for each treatment

Table 3: Herbaceous (stems/m^2) and woody (thousand stems/ha) northern bobwhite food-producing stem category response to midstory thinning and dormant-season prescribed fire on the Ouachita National Forest, Arkansas, July 1999 and 2000.[a]

	Treatment[b]										
Category[c]	Control	SE	WSI-NB	SE	WSI-B1	SE	WSI-B2	SE	WSI-B3	SE	P > F
Total stems											
Grass[d]	0.3	0.2	0.2	0.2	0.6	0.5	0	0	0	0	0.453
Panicum	2.5	0.6 C	18.5	4.2 B	24.9	3.2 AB	26.6	3.1 A	24.9	5.7 AB	< 0.001
Sedge	2.2	0.3 B	8.2	1.4 A	7.8	2.9 A	9	2.1 A	8.2	3.0 A	0.001
Legume	4.3	1.0 B	5.3	0.9 B	25.3	6.1 A	22.3	4.3 A	19	2.2 A	< 0.001
Forb	0.4	0.2 C	2.2	0.5 B	13.5	4.0 A	7.6	1.3 A	7.4	1.4 A	< 0.001
All herbaceous	9.7	1.7 C	34.5	5.2 B	72.1	8.8 A	65.5	6.1 A	59.5	8.5 A	< 0.001
All woody	23.1	3.8	20.7	3.5	36.6	7.7	17	3.7	16.7	3.4	0.125
Species richness											
Herbaceous	16.5	1.5 C	23.1	1.0 B	29.9	1.6 A	28.4	1.4 A	27.6	0.9 A	< 0.001
Woody	10.3	0.3	11.9	0.6	11.6	0.8	10.6	0.8	11.9	0.6	0.079

[a] Row means followed by the same letter or without letters were not significantly different at the 0.05 level (LSD)

[b] Control = unthinned, unburned; WSI-NB = wildlife stand improvement, no burn; WSI-B1 = wildlife stand improvement, first growing season following burn; WSI-B2 = wildlife stand improvement, second growing season following burn; WSI-B3 = wildlife stand improvement, third growing season following burn; n = 8 for each treatment

[c] Food-producing stems only

[d] Not including panicum stems

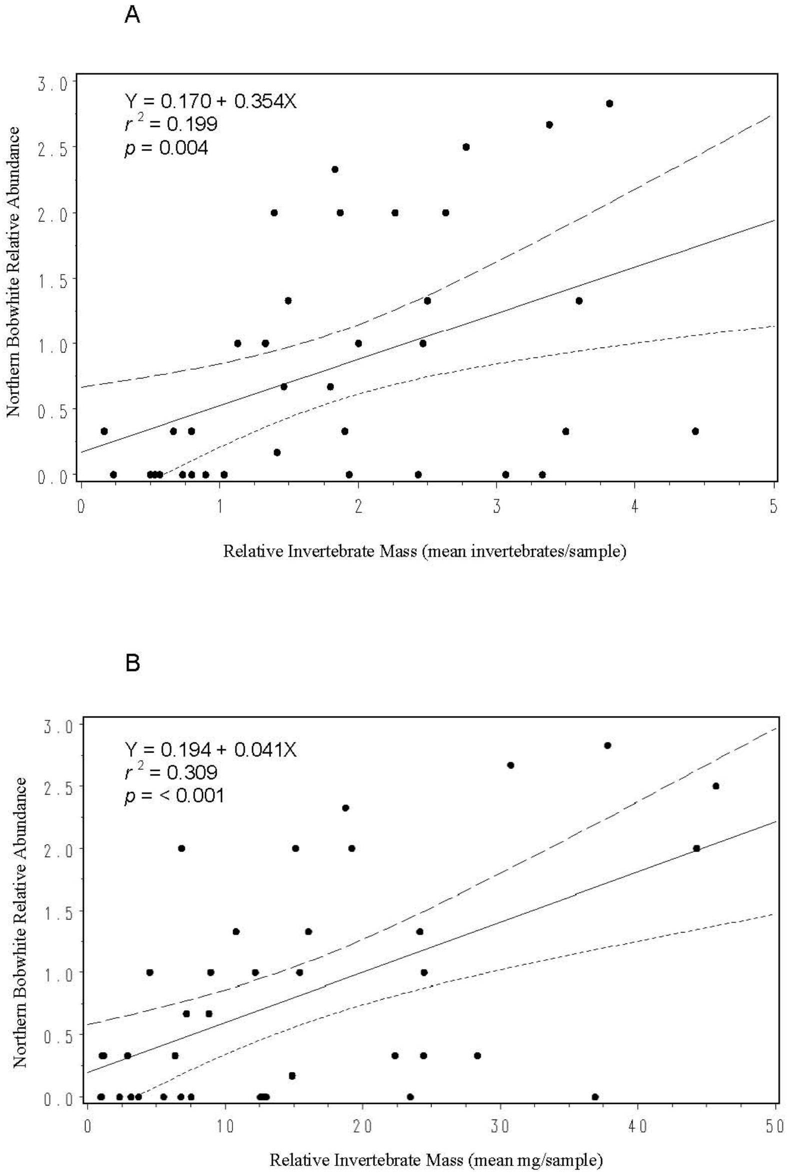

Figure 1: Response of northern bobwhite whistling males (mean whistling males/point) to increasing relative invertebrate abundance (mean invertebrates/sample) (n = 40) of Coleoptera, Hemiptera, Homoptera, Lepidoptera larvae, and Orthoptera (A), and to increasing relative invertebrate mass (mean mg/sample) (n = 40) of Coleoptera, Hemiptera, Homoptera, Lepidoptera larvae, and Orthoptera (B) on the Ouachita National Forest, Arkansas, July 1999 and 2000 (95% confidence intervals shown with dashed lines).

burned ($0.33 < r < 0.70$).

Total forb stem density (stems/m^2) increased also after thinning and again following fire (Table 3). Preferred forbs, common ragweed (*Ambrosia artemisiifolia*), and rough-leaf sunflower (*Helianthus hirsutus*), increased in density following WSI treatment. Three-seeded mercury (*Acalypha gracilens*), plains tickseed (*Coreopsis tinctoria*), rough-leaf sunflower, and black-eyed susan (*Rudbeckia hirta*) increased in percent frequency of occurrence following

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fire treatment.

Total woody stems (stems/m^2) were greatest following fire and decreased 2 and 3 growing seasons following fire (Table 3). Winged sumac, smooth sumac (*R. glabra*), and farkleberry (*Vaccinium arboreum*) increased in density in response to thinning and again in response to fire. Winged sumac, smooth sumac, and blackberry increased in percent frequency of occurrence following WSI.

Bobwhite Response to Food Abundance

We found increases in abundance and mass of frequently consumed invertebrates explained 20% and 31% of the variation in bobwhite relative abundance (Figure 1). No strong relationships were detected between total stems of grass, panicum, legume, or forb with bobwhite relative abundance. Linear regression indicated an increase in total bobwhite food-producing herbaceous stems explained only 15% of the variation in bobwhite relative abundance (Figure 2). The neural model explained 40% of the variation in the training data and 32% of the variation in the validation data. Bobwhite relative abundance appeared more sensitive to a decrease in disc of vulnerability as compared to increases in forb cover or preferred bobwhite invertebrate abundance (Figure 3).

Discussion and Conclusions

Hypothesis Testing

The preeminent dichotomy in bobwhite habitat management remains managing for food quantity or usable space. Guthery et al. (2001) indirectly tested the habitat quantity versus quality hypothesis and found bobwhite abundance increased with usable space on areas of fixed size, and declined with Shannon diversity of patch types, patch richness, and woody edge density (as they defined it). However, >70% of the variation in bobwhite abundance remained unexplained by the usable space hypothesis. In a *post facto* comparison between the 2 philosophies Taylor et al. (1999) also found ambiguous results.

We found the effects of increased food supply (invertebrate abundance and mass, and herbaceous food stems) following thinning and fire on bobwhite relative abundance were ambiguous in terms of supporting either the usable space hypothesis or the food quantity hypothesis. Because bobwhite abundance increased as a function of usable space (Cram et al. 2002) and bobwhite abundance increased somewhat as a function of food supply (Figs. 1, 2), food supply and usable space were confounded; food supply may be a function of the usable space created following pine-grassland restoration. However, food is not a condition of the usable space hypothesis and therefore food abundance cannot create usable space per se (Guthery 1997).

Deductions, however, can be made to separate the correlated effects of usable space and food supply. WSI-NB and WSI-B3 stands had similar amounts of usable space as measured by the mean disc of vulnerability (m^2) ($\bar{x}$ ± SE; 75.8 ± 14.8, 52.0 ± 7.7, respectively) and woody stem density (stems/plot) ($\bar{x}$ ± SE; 126.2 ± 15.7, 161.5 ± 21.9, respectively) and measures of bobwhite relative abundance (bobwhite/ha) ($\bar{x}$ ± SE;1.1 ± 0.3 and 1.5 ± 0.4, respectively), but significantly different food supplies as measured in preferred invertebrate abundance, mass, and herbaceous stem density of food-producing plants (Tables 1, 2, 3). The food quantity hypothesis contends an increase in food supply should result in an increase in bobwhite abundance, while the usable space hypothesis contends a threshold in the food supply has been met and no further increase in food supply will result in an increase in bobwhite abundance. Based on this observation, we deduced bobwhites responded to an increase in usable space rather than an increase in food supply, or conversely, food was not limiting following thinning and burning.

Artificial neural network model predictions were consistent with this deduction. Changes in habitat structure, predominately woody cover <2 m as indexed by the disc of vulnerability, largely predicted whistling male abundance. A threshold region appeared to exist beyond which the addition of increased food resources had a minor effect on bob-

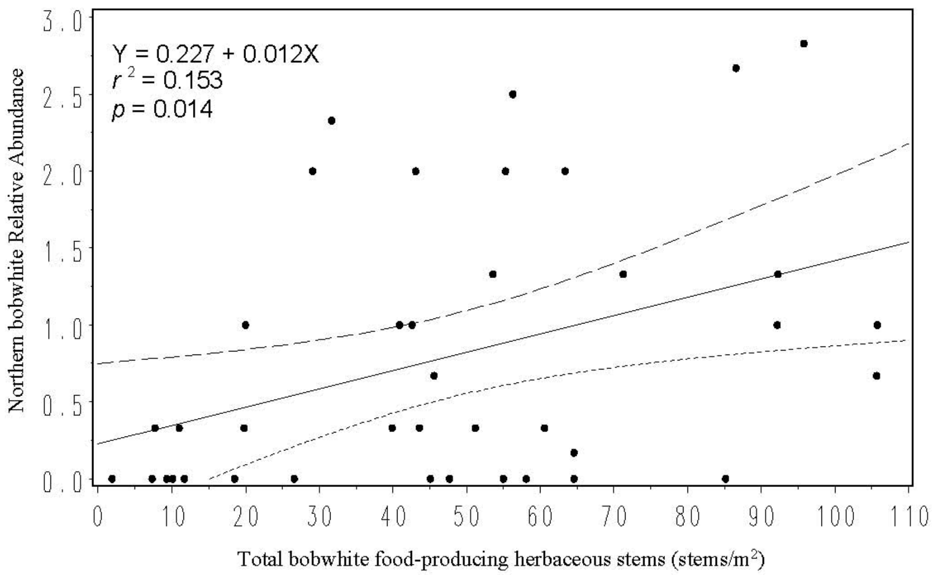

Figure 2: Response of northern bobwhite whistling males (mean whistling males/point) to increasing total bobwhite food-producing herbaceous stems (stems/m^2) ($n = 40$) on the Ouachita National Forest, Arkansas, July 1999 and 2000 (95% confidence intervals shown with dashed lines).

white abundance (Figure 3). Furthermore, Palmer et al. (2001) found greater densities of invertebrates in a defined area did not translate linearly into greater benefits to bobwhite chicks as indexed by foraging rate or a growth index.

Guthery (1999) offered a hypothesis explaining the general circumstance: food supplies as evaluated through energy-based carrying capacity routinely exceed the needs of bobwhite populations. Furthermore, the literature on the effects of food plots and food supplementation has failed to provide unchallengeable evidence an increase in food supply results in positive bobwhite population response as measured by fall densities (Guthery 1997, 2002). It has also been argued (Palmer et al. 2001) that a problem may exist in equating food supply directly to available food. However, an ongoing study of bobwhite food habits on the same study areas in Arkansas (R. E. Masters, unpublished data) suggests that the food supply items measured were consumed and ranked high in preference. Therefore as measured in this study, the increase in frequency of occurrence in herbaceous species and preferred bobwhite invertebrates following thinning and fire suggests an increase in bobwhite food availability. Frequency of occurrence provides an indication of uniformity in distribution (Mueller-Dombois and Ellenberg 1974). Although sweepnets may have missed exclusively cursorial invertebrates important to chick survival, arguably, we assumed these invertebrates responded in similar fashion to habitat change as compared to captured orders. Southwood (1968) and Southwood et al. (1979) reported the most prominent factor influencing invertebrate abundance was structure, arrangement, and floristic diversity of the plant community. Finally, body weights of captured birds from within our study sites were well within the normal range reported by Brennan (1999) and were not significantly different on an annual or seasonal basis (Walsh 2004), also suggesting that food supply was not limiting for bobwhites.

We recommend management efforts in similar mixed shortleaf pine-oak forests aimed at increasing bobwhite densities include thinning to reduce midstory cover and frequent fire to maintain park-like

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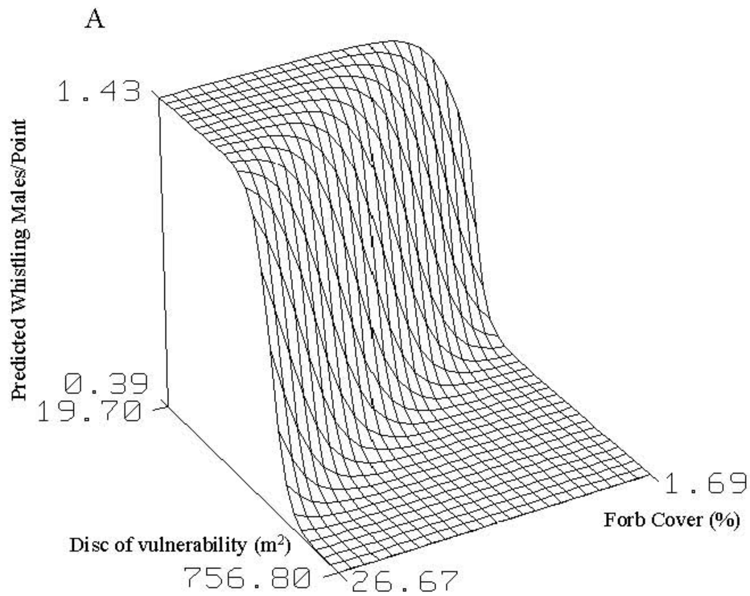

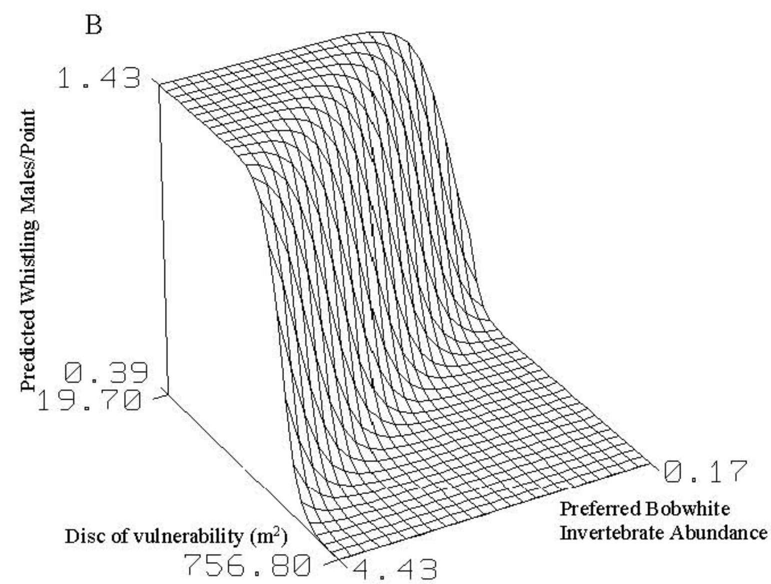

Figure 3: Artificial neural network predictions on the response of northern bobwhite whistling males to percent forb cover (%) and disc of vulnerability (m^2) (A), and to preferred bobwhite invertebrate abundance (mean invertebrates/sample) and disc of vulnerability (m^2) (B) on the Ouachita National Forest, Arkansas, 1999 and 2000.

conditions. Pine-grassland restoration efforts as described here created usable space (permanent understory woody cover in low basal area stands) for bobwhites (Cram et al. 2002). However, Walsh (2004) reported a winter shift in usable space in the same study area from treated stands as described here to thinned stands 2 years following fire and planted with shortleaf pine (regeneration stands). Planting food plots or providing supplemental feed on similar sites following thinning and fire would seem to be unnecessary based on the abundance of invertebrate and plant food items produced by thinning and fire. A final point is that our study area was managed toward ecosystem management goals on a landscape level not specifically for bobwhites. To reconcile the relative importance of the usable space vs. food quantity issue more work is needed.

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