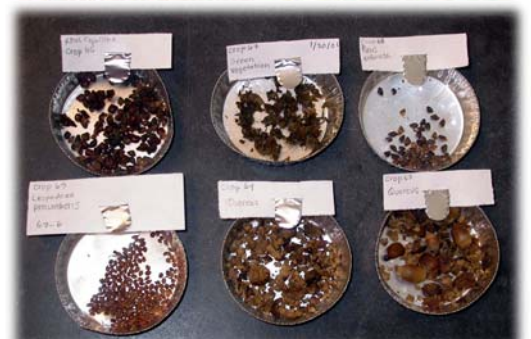


# RESPONSE OF NORTHERN BOBWHITES TO MANAGED FOREST LANDSCAPES



Northern Bobwhite Fall and Winter Food Habits in Restored Pine-bluestem Habitats  
**Final Report 2007**

**Ronald E. Masters**  
Director of Research  
Tall Timbers Research Station



# **Final Report 2007**

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### **Northern Bobwhite Fall and Winter Food Habits in Restored Pine-bluestem Habitats**

To

**U.S. Forest Service  
Poteau Ranger District  
Waldron, Arkansas 74937**

From

**Ronald E. Masters  
Director of Research  
Tall Timbers Research Station**

**TALL TIMBERS RESEARCH STATION  
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**September 19, 2007**



# Northern Bobwhite Fall and Winter Food Habits in Restored Pine-bluestem Habitats

## INTRODUCTION

The Pine-bluestem Renewal Area on the Ouachita National Forest has provided the opportunity to examine Northern bobwhite population response, habitat suitability, food abundance and bobwhite habitat relationships in a forested context along with a host of other species—plant and animal. Previous studies on the ONF documented bobwhite response to a series of five treatments at the stand level that included the following: control, unthinned and unburned; midstory thinning or wildlife stand improvement (WSI)-no burn (WSI-NB); WSI-burn, first growing season after dormant-season burn (WSI-B1); WSI-burn, second growing season after dormant-season burn (WSI-B2); WSI-burn, third growing season after dormant-season burn (WSI-B3) (Wilson et al. 1995, Masters et al. 2002, Cram et al. 2002). These treatments were based on the current management of existing mature stands that were undergoing the restoration treatments of thinning followed by late dormant season prescribed burning at three year intervals. Following work by Cram et al. (2002) and telemetry work by Walsh (2004) it became apparent that other stands in the landscape matrix, specifically thinned and burned regeneration stands and upland drainages, were being utilized and provided usable space on at least a seasonal basis. Therefore habitat structure was characterized for both untreated regeneration stands (unusable space) and thinned and burned regeneration stands (usable space) and upland drainages (usable space) for comparison with Cram et al. (2002) and to have a more complete data series defining usable and unusable space for bobwhites on the pine-bluestem renewal area (See Guthery et al. 2004, Walsh 2004).

The present study on food habits was initiated to add another piece to the puzzle in terms of understanding how restructuring of upland pine-hardwood stands creates usable space for bobwhites and what foods are available in restructured stands. This is the final report for this portion of the project and thus completes the overall project “**Response of Northern Bobwhites to Managed Forest Landscapes.**” The report is formatted for submission to a peer-reviewed journal and is appended on the following pages.

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### **Northern bobwhite fall and winter food habits in restored pine-bluestem habitats**

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**Abstract:** We determined fall and winter food habits of hunter harvested Northern bobwhites (*Colinus virginianus*) ( $n = 267$ ) in restored pine-bluestem (*Pinus-Andropogon- Schizachyrium*) stands on the Ouachita National Forest, Arkansas, from Dec 1998 to Feb 2006. Restoration treatments on the study area involved thinning of midstory hardwoods and midstory and co-dominant shortleaf pine (*Pinus echinata*), a process called wildlife stand improvement (WSI), followed by February or March (late dormant season) prescribed burns at 3-year intervals. Application of WSI and fire resulted in an open mid story with an understory dominated by a mosaic of woody sprouts, forbs, and grasses of varying heights depending on time since the last burn. Shortleaf pine seed, post oak (*Quercus stellata*) acorns and various legume seed

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(*Lespedeza* spp, *Desmodium* spp.) occurred most often of 81 items and were highest in importance. Green vegetation was prevalent in crops and invertebrates also were important parts of fall and winter diets, particularly Orthopterians. Species richness of individual crops varied from 0 to 16. Based on crop contents and movement data from (Walsh 2004) upland drainages dominated by oaks (*Quercus* spp.) are an important constituent of bobwhite habitat in this restored pine-bluestem landscape. Shortleaf pine and post oak mast production appeared to be somewhat compensatory as both were rarely abundant in the same year. Our results provide additional evidence that suggests the usable space hypothesis and habitat quality hypothesis are confounded. Creation of usable space through WSI and use of prescribed fire dramatically increases bobwhite food availability. Our results provide additional evidence that thinning and frequent burning are appropriate management strategies for reversing downward trends of bobwhite populations throughout its range in forested habitats.

**Key words:** Arkansas, *Colinus virginianus*, foods, food habits, habitat quality, northern bobwhite, restoration, pine-bluestem, prescribed burning, wildlife stand improvement

Numerous studies on Northern bobwhite (*Colinus virginianus*) food habits have been conducted since the 1930s in the southeastern U.S. (see Landers and Johnson 1976). Most of these studies were in the context of land use of that time, which has been variously described as small patch agriculture interspersed with woodlots and patch forests. As is often stated, over the last several decades bobwhites have declined precipitously as land use changed (Brennan 1991, 2002). A positive association with small-patch agriculture and bobwhite abundance permeates much of the early literature and persists in recent published compendiums (e.g., Brennan 1999). Much of the recent work related to bobwhite foods and feeding focuses on food supplementation via food plots, feed spreading or feeding stations, metabolizable energy of various domesticated

plants used in a food plot context, implementing practices that seek to manage edge such as field borders, etc., or adding soil disturbance to increase relative abundance of weed seed.

Remarkably few efforts have proven successful at restoring or even documenting an increase in quail numbers (Brennan 2002), but one exception has been Cram et al. (2002) in a study on a pine-bluestem (*Pinus-Andropogon-Schizachyrium*) restoration area on the Ouachita National Forest (ONF), Arkansas. Studies on the ONF documented bobwhite response to restoration treatments of thinning (WSI – wildlife stand improvement) and dormant season prescribed burning on a three-year interval (Wilson et al. 1995, Masters et al. 2002, Cram et al. 2002). Following work by Cram et al. (2002) and telemetry work by Walsh (2004), it became apparent that other stands in the landscape matrix, specifically thinned and burned regeneration stands and upland drainages, were utilized and provided usable space on at least a seasonal basis (Guthery et al. 2005). Cram (2001) and Cram et al. (2007) determined density of plants known to provide food for quail and invertebrate abundance and mass on restoration treatments based on the literature available for bobwhite food habits in similar habitats in the region (Baumgartner et al. 1952; Bidwell et al. 1991, 1998, 2004; Masters et al. 1996a). Further they examined bobwhite abundance as related to summer food plant abundance and usable space through neural network modeling (Cram 2001, Cram et al. 2007). They found a weak positive relationship between summer food plant abundance and spring whistling males (Cram et al. 2007).

Summer food abundance does not equate directly with winter food availability. One index to food availability is to determine the proportion of plant and insect matter in actual diets as bobwhites reportedly select foods based on availability (Errington and Hamerstrom 1936). Bobwhites exhibit preferences for different foods in feeding trials when given specific choices (Ellis 1961, Robel et al. 1979a), but that is decidedly different than opportunistic searching in a wild environment.

No systematic food-habit study has been conducted on the pine-bluestem renewal area to determine which foods were actually selected and the extent of use nor their contribution to meeting nutritional requirements for bobwhites. Although food habits studies have been conducted that incorporated oak-pine habitats of eastern Oklahoma or southern Missouri similar to and some in close proximity to our Arkansas study sites (Bird and Bird 1931, Korschgen 1948, Lee 1948, Wagner 1949, Baumgartner et al. 1952) none have been conducted in Arkansas. Arguably habitats in the Ouachita Highlands have changed considerably since that time with fire suppression and changing land use (see Masters et al. 1995, 2007a). No studies we are aware of, other than Cram et al. (2007) have examined restored habitats in terms of food availability or abundance, much less examined crop contents to determine what foods are being selected in restored habitats or made comparisons with historic food habits studies. Therefore we sought to determine food habitats from crop contents of hunter harvested bobwhites within the pine-bluestem renewal area. Further we wanted to determine if selected foods on a restored area would provide generally adequate nutrition.

## **STUDY AREA**

The study area was in the west-central Ouachita Mountains on the Poteau, Mena, and Cold Springs Ranger Districts of the Ouachita National Forest, Arkansas (approximately 34°54'N, 94°4'W). All sites were within the 60,000-ha pine-bluestem renewal area and mature stands were under active management for the endangered red-cockaded woodpecker (*Picoides borealis*). The area is mountainous with east-west trending ridges and valleys with forests composed of second growth mixed pine-hardwood stands. The pine-grassland stands have been previously described and have been used to monitor northern bobwhite, breeding birds, small mammals, vegetation and forage response to WSI and prescribed fire (Wilson et al. 1995; Masters et al. 1996b, 1998, 2007b; Sparks 1996, Sparks et al. 1998, 1999; Cram 2001, Cram et

al. 2002, 2007; Walsh 2004). Detection rates in spring point-counts suggest a steadily increasing population from spring 1992 to 2000 (Wilson et al. 1995, Cram et al. 2002). Although the density of this population is low compared with other published accounts (Brennan 1999), it has increased dramatically during the past decade (Cram et al. 2002).

The forest matrix 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 in upland drainages 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*) (Sparks 1996, Guthery et al. 2004, Walsh 2004). Post oak, mockernut hickory, shortleaf pine and black oak were prevalent overstory species in upland drainages (Guthery et al. 2004, Walsh 2004).

The understory of untreated regeneration stands was litter dominated and sparsely vegetated with sprouts of post oak, blackjack oak, mockernut hickory, blackberry (*Rubus* spp.), Virginia creeper (*Parthenocissus quinquefolia*), winged sumac (*Rhus copallina*), greenbrier (*Smilax bona-nox*), poison ivy (*Toxicodendron radicans*), and muscadine (*Vitis rotundifolia*) and occasionally other hardwood species. Herbaceous species were generally limited and included scattered panicums (*Panicum* spp. and *Dicanthelium* spp.) and some forbs (Walsh 2004).

The understory of treated regeneration stands in addition to the previously mentioned tree and shrub species was dominated by grasses such as big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), numerous panicum species (*Panicum* spp. and *Dicanthelium* spp.) and numerous forbs (Guthery et al. 2004) similar to restored pine-grassland

stands (Sparks 1996, Sparks et al. 1998). Woody shrub and vine species included New Jersey tea (*Ceanothus americanus*), blackberry, Virginia creeper, winged sumac, greenbrier, poison ivy, low-bush huckleberry (*Vaccinium pallidum*), tree sparkleberry (*Vaccinium arboreum*), and muscadine similar to Sparks (1996).

Wildlife openings are a minor part of this landscape and typically occur around wildlife ponds. They have been planted to a variety of plant materials including: Japanese lespedeza (*Kummerowia striata*), Korean lespedeza (*Kummerowia stipulacea*), bicolor lespedeza (*Lespedeza bicolor*), rye (*Secale cereale*), browntop millet, milo and others. Korean, Japanese and seresia lespedeza (*Lespedeza cuneata*) have been planted in the past along roadsides for ditch stabilization, on old logging roads and on log decks for cover. These species are no longer planted widely across the forest but persist in disturbed areas.

## **METHODS**

### **Food habits**

Bobwhite winter food habits were determined by analyzing crop contents. All crops used in analysis were collected from hunter-harvested birds from November-January in 1998–2006 on the Ouachita National Forest, Arkansas. Time, date, location, and sex were recorded for each harvested bird. Wings from each sample were collected for later age determination (adult/juvenile) following Rosene (1969:44–54) and Anonymous (1992). Following collection, crops and wings were sealed in a labeled plastic bag (stand location, stand description, time, date, and sex) and frozen until crop necropsy. Crops contents were hand sorted and separated into the following categories: debris, rock, green vegetation, invertebrates, and seeds. Seeds were then identified to the lowest taxon possible and verified using the Oklahoma State University, Zoology Department's reference seed collection, Tall Timbers Research Station reference seed collection, and reference manuals by Landers and Johnson (1976), Martin and

Barkley (1961), Rosene and Freeman (1988) and Young and Young (1992). Voucher specimens for most items were deposited in the Tall Timbers Research Station seed collection.

Invertebrates were keyed at least to the nearest order following Borror et al. (1989). Green vegetation was identified to species where possible and debris was identified to said category only. Bird shot that was found in crops was considered as incidental and related to harvest because of the limited quail hunting that has been conducted in this area over the past several decades. Food items were oven-dried for 72 hrs and were weighed to 0.001 g, and volume of total crop contents and individual items measured by water displacement, measured to 0.1 cc, with lesser displacement items listed as a trace.

### **Food Value**

We compiled data from published accounts of gross energy, metabolizable energy, neutral detergent fiber (an index to digestibility), fat, fiber, carbohydrates (Nitrogen-free extract-NFE), crude protein, phosphorous, and calcium of major food items. Similar values were compiled for comparative purposes for items used in food plots and supplemental feeding program (Appendix 2). There is a dearth of information on these plant materials and it is often assumed that domesticated foods have the highest nutritive values. Our interest was in terms of increasing our understanding towards energy-based carrying capacity (Guthery 1999).

### **Relative Abundance – Mast**

We used an average of subjective relative abundance estimates (1-5) from three biologists for three years to assess pine and oak mast production and a published account of mast production for two years equated to our relative abundance scale (Perry and Thill 2003).

### **Data Analysis**

We used descriptive statistics to summarize data about specific food items and other bird related parameters. For each food item we determined mean weight and mean number of items

and ranked items based on said parameters. We also calculated frequency of occurrence, the percent of crops in which an individual food item occurred, and relative volume, the total volume of food item expressed as a percent of the total volume of all foods. We present relative ranks by weight (g) as tiny seeds had insufficient volume to measure. Previous work suggested that both methods achieved comparable results and nutritional studies use weight as a basis for comparison (Jensen and Korschgen 1947).

Food items were ranked according to average frequency within a crop of an individual food item and by total weight averaged across all crops. We also derived an importance value (1-16, 16=highest) after Landers and Johnson (1976) for comparative purposes. We compared ranks to examine possible differences by sex and age. We also used simple correlation to examine the relationship between abundant mast years by pine and oaks and their respective occurrence in quail crops in a given year. We also examined the relative occurrence of one food item against another through time to determine if different food items might be compensatory in occurrence.

## **RESULTS AND DISCUSSION**

We found 81 food categories present in 267 crops collected from late fall and winter harvested birds (Appendix 1). Our samples included 16 crops from 1998-99, 9 from 1999-00, 37 from 2000-01, 1 from 2001-02, 35 from 2002-03, 55 from 2003-04, 108 from 2004-05, and 6 from 2005-06. The maximum weight of crop contents was 16.7 g. The volume (as measured by water displacement) of food items ranged from 0.0 ml to 18.0 ml. Only 2.6% of the crops contained grit similar to that found by Korschgen (1948). Although grit is considered a requirement (McCann 1939) when hard seeds make up a substantial proportion of the diet, it may be unnecessary (Handley 1946, Korschgen 1948). Approximately 13.9% (n=37) of the crops were empty with an average time of death (ATD) of 1381 hours. The range for time of

death of birds with empty crops was 0800 hrs to 1715 hrs. This was somewhat unexpected as one would assume that birds harvested in the late afternoon would have some contents from feeding during the afternoon. Eubanks and Dimmick (1974) reported 6.1% of the crops were empty in their study on Ames Plantation, where land-use is dominated by agriculture.

The sex and age breakdown for quail from which crops were obtained was 38 adult females, 93 juvenile females, 53 adult males, and 82 juvenile males (Figure 1). We found no differences by sex or age in terms of the top food items selected and only minor differences in relative ranks.

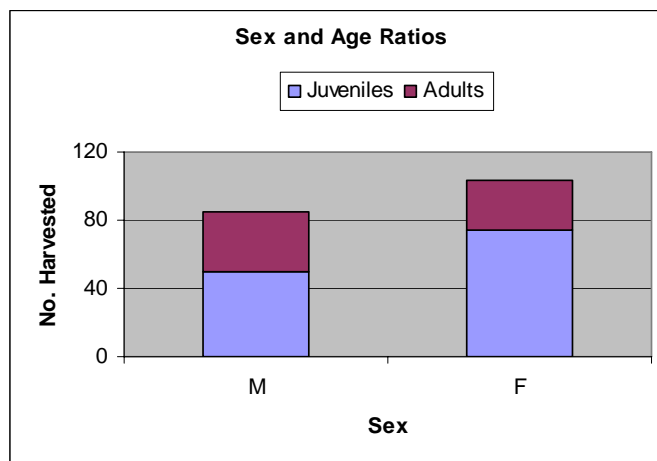


Figure 1. Sex and age ratios of harvested northern bobwhite in the pine-bluestem renewal area from winter 1998-2006, Ouachita National Forest.

Most birds (64.4%) were harvested in restored pine-bluestems stands (WSI, Figure 2). Regeneration areas were next in terms of the habitat that birds were most often harvested in with just under 17% of the birds coming from this habitat type (Figure 2). Miscellaneous openings which included, log decks, fire breaks, openings around ponds or wildlife openings, were the next most prevalent habitat type where birds were harvested (Figure 2).

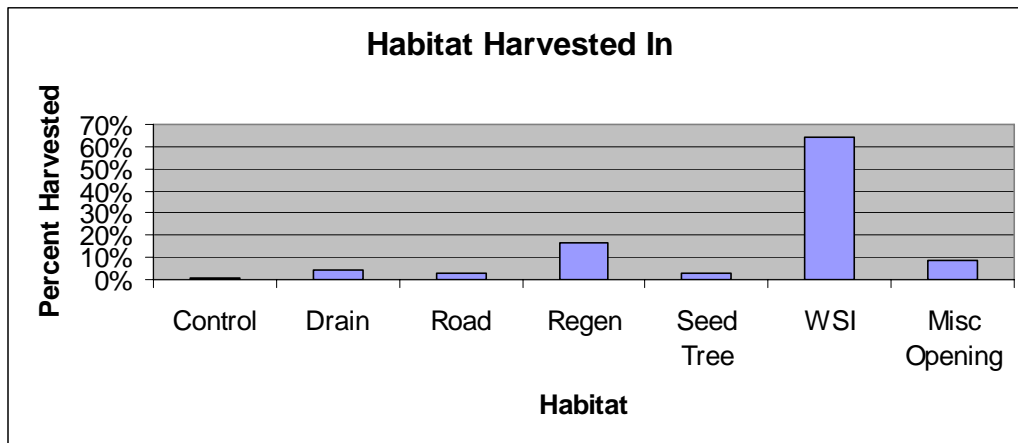


Figure 2. Habitat that northern bobwhite were harvested from during fall and winter 1998-2006 within the pine-bluestem renewal area, Ouachita National Forest, Arkansas.

Shortleaf-pine seed was ranked highest in importance, average frequency (average number of items /category/crop), and by weight across all years. It was also one of the most commonly occurring food items and was found in 46.8% of the crops (Table 1). The greatest number of shortleaf seed observed in a single crop was 564. However, shortleaf pine seed did not occur to any extent in crops in the winters of 1999-2000, 2001-2002 and 2002-2003 possibly the result of a poor seed year (L. Hedrick, USFS, pers. Communication, Figure 3). However, sample size was only 1 crop in winter 2001-2002 which did not include any pine seed and estimates indicated a moderate pine mast crop in that year.

Table 1. Top 10 northern bobwhite foods based on average rank of weight (g), number of items, and importance values (after Landers and Johnson 1976) on the pine-bluestem renewal area of the Ouachita National Forest, Arkansas from November 1998 – February 2006.

Food Items	Average Rank by Weight (g)	Average Rank by number of items	Frequency (% of all crops found in)	Importance Value
<i>Pinus echinata</i>	1	1	46.8%	16
<i>Quercus stellata</i>	2	5	25.8%	15
<i>Lespedeza procumbens</i>	3	2	31.1%	15
<i>Kummerowia striata</i>	4	3	15.7%	10
<i>Rhus copallina</i>	5	11	8.2%	10
Green vegetation	6	4	47.9%	12
<i>Quercus velutina</i>	7	14	2.6%	9
<i>Lespedeza virginicus</i>	8	7	15.4%	10
<i>Desmodium</i> spp.	9	10	10.9%	10
<i>Orthoptera</i>	10	19	11.2%	10

Post oak (*Quercus stellata*) acorns were the 2<sup>nd</sup> ranked food item by weight (Table 1). Post oak acorns were ranked 5<sup>th</sup> by frequency and were found in 25.8% of all crops and had an importance value of 15. Black oak (*Q. velutina*) acorns were ranked 7<sup>th</sup> by weight but only 14<sup>th</sup> by frequency of occurrence (Table 1). In winters 1998-99, 1999-00 and in 2000-01 post oak acorn occurrence was very limited in crops and non-existent in the first two winters. The post oak acorn crop was low in the winter of 1998-99, and only moderate for the winter of 1999-00 (Perry and Thill 2003, Figure 3). The limited occurrence of post oak acorns in crops for the second winter may be a reflection of low sample size and lack of availability (no oaks present) in the stands where birds were harvested (Figure 4). In winter 02-03 when post oak abundance was high, over 80.0% of the crops examined had post oak acorns and 85.7% of all crops ( $n=35$ ) had acorns. These findings suggest that use of pine seed ( $r=0.940$ ) and oak acorns ( $r=0.960$ ) is closely related to their availability. When abundant mast years of either occur, they will be selected. Further, pine and acorn mast appear to be somewhat compensatory in abundance, over the 5 winters that we had estimates of abundance ( $r=-0.490$ ) with one being abundant in off-

years of the other. When examined by monthly occurrence in diets shortleaf seed occurred in from 40–60% of crops between November and February with a slight increasing trend (Figure 5). Shortleaf cones are persistent and may release seed over several months. Acorns were more prevalent in diets in November and declined in the later winter months. This might be expected as acorns are a favored food of many wildlife species and availability would be expected to decline through time from competition for this limited food resource (Kirkpatrick and Pekins 2002).

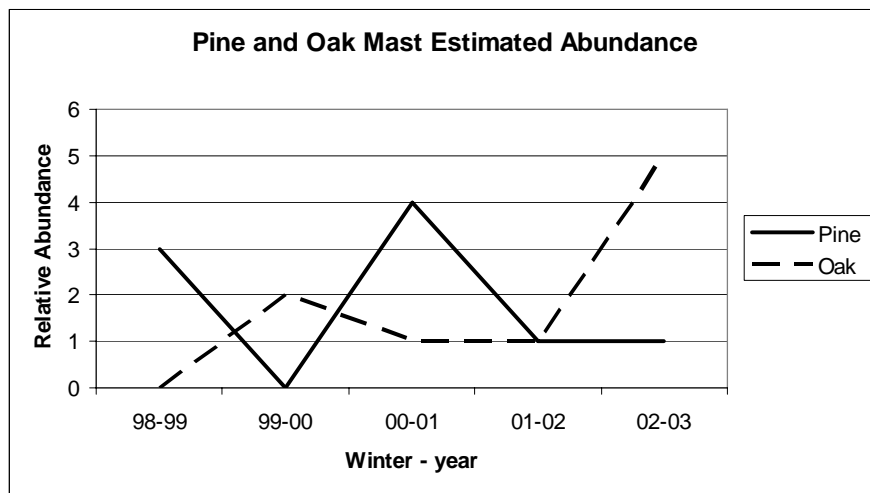


Figure 3. Pine and oak mast relative abundance (Scale = 1-5) based on biologist estimates in three years and published estimates in Perry and Thill (2003) for 2 years from Nov 1998 – Feb 2006 on the Ouachita National Forest, Arkansas.

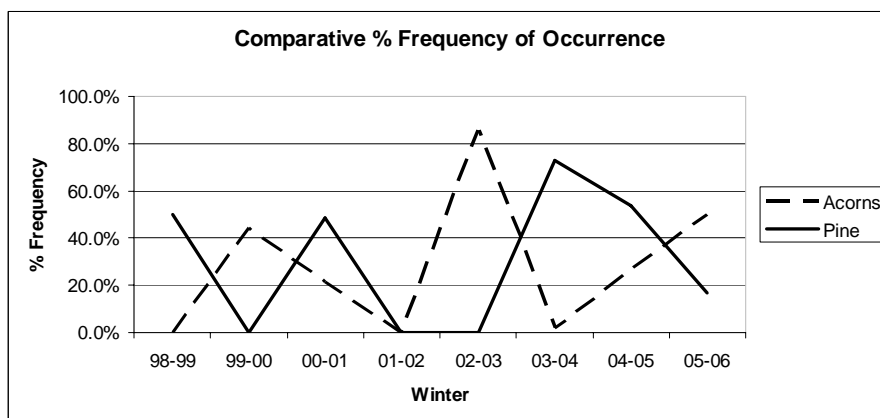


Figure 4. Pine and oak mast percent frequency of occurrence summarized by winter in crops of hunter harvested northern bobwhite from Nov 1998 – Feb 2006 on the Ouachita National Forest, Arkansas.

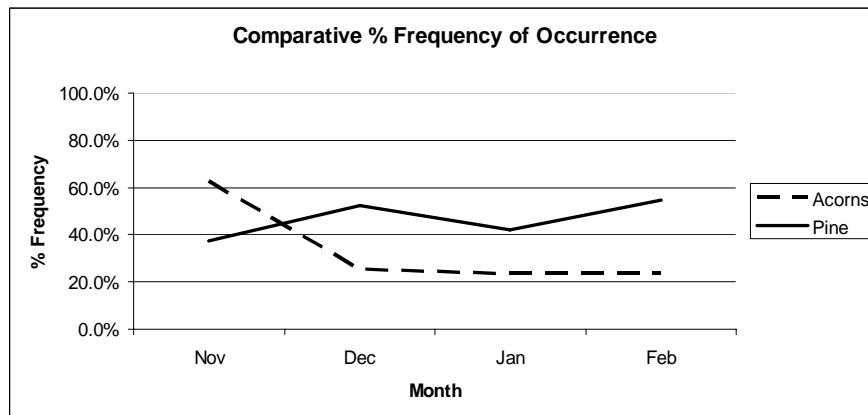


Figure 5. Pine and oak mast percent frequency of occurrence summarized by month in crops of hunter harvested northern bobwhite from Nov 1998 – Feb 2006 on the Ouachita National Forest, Arkansas.

Legume seed tended to occur in a higher percentage of crops when pine or acorn mast were less available (Figures 3, 4, 6). Collectively legume seed occurred in 59.6% of all crops. Green vegetation occurrence in diets varied ( $r=0.777$ ) with the proportion of crops that contained legumes from winter to winter (Figure 6), but it was not related to legumes when examined by monthly occurrence in diets throughout the winter (Figure 7). Legumes tended to decline in the percentage of crops found in, from November through February whereas green vegetation exhibited an increasing trend in occurrence throughout the winter. We found that relative rankings of legumes in crop contents was only roughly similar to summer abundance of legumes determined from other studies on the area (Cram 2001, Cram et al. 2007). Those studies did not sample the entire array of habitats from which these birds came from.

Invertebrate abundance seemed to be associated from year to year with winter weather conditions (Figure 6). Throughout each fall and winter invertebrate occurrence in diets declined through the colder months with the bottom point being the coldest month of January and then increased with warming temperatures (Figure 7)..

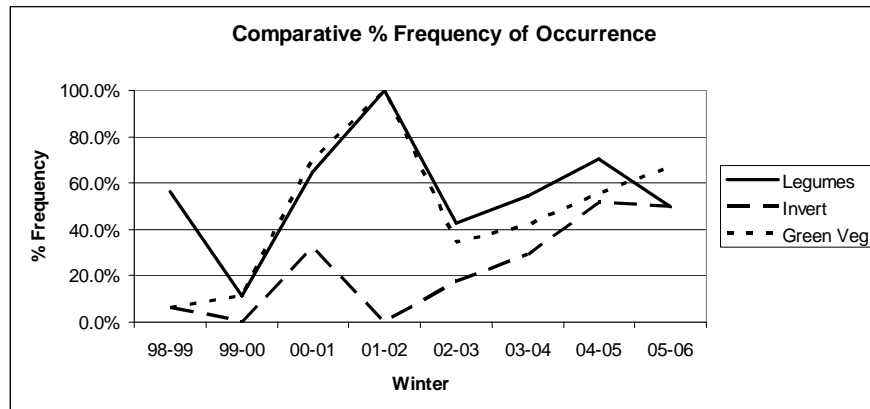


Figure 6. Legume, invertebrate and vegetation frequency of occurrence summarized by winter in crops of hunter harvested northern bobwhites, Nov 1998 – Feb 2006 on the Ouachita National Forest, Arkansas.

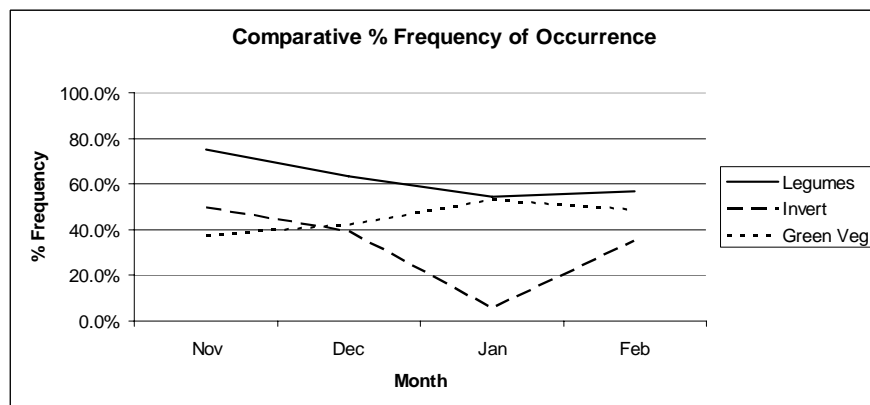


Figure 7. Legume, invertebrate and vegetation frequency of occurrence summarized by month in crops of hunter harvested northern bobwhites, Nov 1998 – Feb 2006 on the Ouachita National Forest, Arkansas.

Prostrate lespedeza seed (*Lespedeza procumbens*) ranked 3<sup>th</sup> by weight and 2<sup>nd</sup> by number of seeds and occurred in 31.15% of the crops. This abundant lespedeza species also had an importance value of 15 suggesting that it is an important staple item. The greatest number of seeds observed in a single crop was 1,297, and was also the highest count of any species. This species was also the most abundant lespedeza observed by Cram (2001). The 4<sup>th</sup> ranked food item by weight was Kobe or Japanese lespedeza (*Lespedeza striata*) and occurred in 15.4% of all

crops collected and had an importance value of 10. The greatest number of Japanese lespedeza seed observed in a single crop was 723.

Winged sumac (*Rhus copellina*) ranked 5<sup>th</sup> by weight and had an importance value of 10. In terms of frequency it ranked 11<sup>th</sup> and occurred in only 8.2% of the crops. Green vegetation was the 6<sup>th</sup> ranked food item by weight and ranked 4<sup>th</sup> by frequency. It had an importance value of 12 and occurred in 47.9% of the crops sampled. Green vegetation in order of prevalence was composed of Rue anemone (*Thalactrium thalctroides*), *Lespedeza* spp., *Dicanthelium* spp, *Panicum* spp., *Stylanthoses biflora* and the basal rosette leaves of several unidentified forbs. Black oak (*Quercus velutina*) ranked 7<sup>th</sup> by weight and 14<sup>th</sup> by frequency with an importance value of 9 as it only occurred in 2.6% of all crops. Slender lespedeza seeds (*Lespedeza virginicus*), beggarweed (*Desmodium* spp.), grasshoppers and crickets (Orthoptera) and common ragweed (*Ambrosia artemesifolia*) were respectively the next highest in rank by weight (Table 1). The greatest number of beggarweed and common ragweed seed observed in a single crop was 537 and 783 respectively. When all species of legumes were combined, legumes occurred in 159 or 59.6% of all crops.

Brennan (1999) reported that legume seeds predominate in the fall and winter diet of bobwhites and that pine and oak mast also often predominate. He also further indicated that succulent leafy green plant parts were primarily consumed in the spring but made no mention of their use in winter. As noted above green vegetation was the 4<sup>th</sup> most common food item found in our crops. Although the pine-bluestem restoration treatments apparently increased the abundance of important quail foods (Cram 2001), we do not know if the high intake of green leafy vegetation in the winter was related to nutritional needs or to availability. Lee (1948) observed green mater in over 36% of crops, but in low percentages relative to the volume of other foods, and postulated green vegetation consumption may be related to the need for specific

minerals or vitamins. A link between availability of green vegetation and breeding behavior has been postulated by Gorsuch (1934) for Gambel quail (seen in Lee 1948).

Seeds have high nutrient content per unit volume as compared to leaves (Janzen 1971), while leaves provide other essential nutrients such as vitamins and minerals (Handley 1946). Bobwhites can digest cellulose in low amounts (Inman 1973) and green vegetation may be a source of water (Handley 1946). Often intake of food items high in cellulose such as green vegetation is viewed as merely for subsistence until a more nutritious food is available (Inman 1973). Although some ingestion of green vegetation may be incidental to harvesting seed still on a plant, as in the case of some lespedezas, but items such as rue anemone were evidently selected for and sought out because they are relatively infrequent in occurrence within our study stands. Therefore we believe additional work should be done on quantifying the value of green vegetation in bobwhites diets.

Early literature suggested that the birds selected foods based entirely on availability (Errington and Hamerstrom 1936) but preferences based evidently on palatability, amount of deterioration, and experience have been shown (Ellis 1961, Preacher 1978, Robel et al. 1979a). But this is based on birds being fed *ad libitum* different specific combinations of foods in feeding trials. In a wild environment some preference might be exhibited when particular food resources are abundant and preference would become less evident when resources become scarce and birds are essentially conducting random searches for food resources. All native and domestic seeds presented in the study by Ellis (1961) were accepted to some extent by bobwhites.

A noted contrast between food habits from this study and those from across the southeast and in eastern Oklahoma, is the fact that only limited amounts of agricultural weed seed (except common ragweed and 3-seeded mercury) and no domesticated cereal grains occurred in any crops in our study (Bird and Bird 1931, Korschgen 1948, Lee 1948, Baumgartner et al. 1952,

Landers and Johnson 1976, Wiseman 1977). Baumgartner et al. (1952) and Lee (1948) listed cultivated lespedezas as the most important food item in oak-pine habitats of eastern Oklahoma and Korschgen (1948) in the Ozarks of Missouri which were oak-pine forests. Wild legume seeds were listed as highly important for birds from eastern Oklahoma (Bird and Bird 1931, Lee 1948, Wagner 1949, Baumgartner et al. 1952, Wiseman 1977) and southern Missouri (Korschgen 1948) and also were important in this study. Acorns were also listed among the most important items in eastern Oklahoma, but pine seed was not mentioned in any of the studies (Bird and Bird 1931, Lee 1948, Wagner 1949, Baumgartner et al. 1952).

The absence of pine seed in previous studies is interesting in light of its prevalence in this study and importance noted by others (Stoddard 1931, Handley 1946, Landers and Johnson 1976). Samples from some of those studies were not taken in oak-pine habitats (e.g. Wagner 1949, Wiseman 1977). However within the time frame of most of those studies Baumgartner et al. (1952) reported upland forest of oak and pine to be dense in eastern Oklahoma except where logging operations were carried out and because of tree density were unsuitable for bobwhites. This was after the time period where decades of fire suppression had allowed considerable change in forest structure in eastern Oklahoma (Masters et al. 1995, Masters et al. 2007b). Therefore we would not expect to see pine seed to any extent as those habitats did not contribute to useable space. The studies that occurred close to our study sites or within adjacent regions had a large component of agriculture in the prevailing land use and fire suppression was actively enforced at the time (Masters et al. 1995).

### **Food Value**

Gross energy values varies within plant species based on geographic region, soil type, nutrient availability, size of seed crop, stage of maturity, and factors such as year, month, day length and light intensity (Long 1934, Golley 1961, Grodinski and Sawicka-Kapusta 1970). As

such the compilation of values in Appendix 2 represents a range of values for various food items to compare against known nutritional requirements for bobwhites. Energy content of various seeds is strongly related to the amount of fat in the seed (Grodinski and Sawicka-Kapusta 1970). However, gross energy may not adequately characterize what is available to an animal in terms of metabolizable energy as each animal species varies in its ability to convert energy content of a given food item to metabolizable energy (Janzen 1971).

Diets deficient in energy have been shown to cause increased consumption of foods and to negatively affect reproductive activity, especially egg production and the bobwhites ability to maintain body mass (Giuliano et al. 1996). Diets low in protein have also been shown to negatively influence maintenance of body mass (Nestler et al. 1945, Giuliano et al. 1996), but, more importantly, specific amino acid concentrations were found to be related to body mass stability (Nestler et al. 1945). Although Giuliano et al. (1996) reported that energy appears the more important, low protein diets in that study were much higher in protein than in staple food items such as acorns in our study. They recommend management efforts should focus more on high-protein foods, such as practices that increase insects, than on high-energy foods as quail can compensate for low energy diets to some extent by increasing consumption to obtain adequate energy, but were evidently unable to compensate in a similar manner for low protein.

Dietary protein as indexed by crude protein has not been shown to influence population characteristics such as density, recruitment or survival (Roseberry and Klimstra 1984), but crude protein does not adequately characterize the content or availability of essential amino acids (Boren et al. 1995). Sulfur containing amino acids may be particularly important and are deficient in many supplemental feeds but are more than adequate in insects and other animal matter (Nestler et al. 1945, Peoples et al. 1994). These amino acids are supplemented in commercial rations for domesticated bobwhites (Dozier and Bramwell 2002). In some areas

provision of supplemental feed may decrease feeding on insects to the detriment of bobwhite nutritional status (Peoples et al. 1994).

Pine seed has been reported as an important food source (Handley 1946, Landers and Johnson 1976), but its nutritive value has not been reflected in much of the literature on quail. Pine seed is higher in fat, crude protein, and phosphorous than many commonly used supplemental feeds. It is much lower in carbohydrate content compared to supplemental feeds but is within the low moderate range of natural foods (Appendix 2). Fat however is more important in diets than is carbohydrates. Metabolizable energy trials with bobwhites have not been conducted for pine seed and gross energy has not been reported for shortleaf pine and neither has digestibility. Preacher (1978) suggested that pine seed was selected against compared to common supplemental feed items because of deterioration over time and the propensity to sprout later in the winter. However, that study was conducted in the context of placing different types of seed in a harvested crop field to measure deterioration rates which is decidedly different than the natural context of pine seed fall and ground level conditions. Whitelaw et al. 2007 observed considerable pine seed in a high percentage of quail crops even where birds were supplementally fed sorghum seed (*Sorghum vulgare*), but sorghum occurred in a higher percentage of crops. In this case the ready accessibility of feed along a feed trail may have contributed to the more prevalent occurrence of sorghum in crops versus scattered and limited occurrence of pine seed under natural conditions. They also noted the importance of pine seed and acorns in areas that were not supplemented with food and related quail occurrences to abundance of the mast crop in a given year.

Oak acorns were often listed as an important food item to bobwhites in the early food habits literature (Bird and Bird 1931, Korschgen 1948, Lee 1948, Wagner 1949, Baumgartner et al. 1952). Baumgartner et al. (1952) listed acorns as one of the top ten items in every region of

Oklahoma. Bird and Bird (1931) reported similar percentages to this study of occurrence in crops taken from southeastern Oklahoma.

Although the value of acorns to many wildlife species has been widely reported it is often overlooked with respect to bobwhites in recent literature (e.g. McShea and Healy 2002). Acorns are high in energy, very digestible, but low in fat and in protein (Kirkpatrick and Pekins 2002). Only Robel et al. (1979a,b) has made any assessment of any oak species in terms of nutritional value to bobwhites (Appendix 2). They considered that red oak (*Quercus rubra*) and pin oak (*Quercus phellos*) were of limited value. This may be because of the low relative amount of fat and low protein values of the seed. Energy content of various seeds is strongly related to the amount of fat in the seed (Grodinski and Sawicka-Kapusta 1970). However, acorns are very high in carbohydrates and they are highly digestible, particularly those in the white oak group (Kirkpatrick and Pekins 2002). Therefore they are an excellent source of energy.

It should be noted that the red oak group and white oak groups differ substantially in terms of the presence of tannins and therefore their palatability and digestibility with the later being more digestible and lower in tannins (Kirkpatrick and Pekins 2002). Robel et al. (1979a) made assessments of red oak (*Quercus rubra*) and found birds fed on diets of just sorghum or corn stabilized weights whereas those on red oak acorns alone lost approximately 24% of their body weight during their trials. Although all of these food items were low in fat they were high in carbohydrates. However, acorns are very low in protein, to the extent that negative nitrogen balance may occur if acorns are the only dietary item, possibly leading to protein catabolism (Kirkpatrick and Pekins 2002). No such feeding trials have been performed with acorns from the white oak group. Another salient point is that gross energy or even metabolic energy of a single food item may not tell the entire story on bobwhite nutrition as other nutrients are essential and no single food item supplies all requirements.

A number of studies have examined the food value of either smooth (*Rhus glabra*) or winged sumac (*Rhus copallina*) (Errington 1931, Nestler and Bailey 1944, Newlon et al. 1964, Robel et al. 1979b). In the case of both species of sumac their value as the sole emergency food was shown to be limited and that birds maintained on a sole diet of either lost considerable weight as might be the circumstances during a protracted severe winter (Errington 1931, Nestler and Bailey 1944, Newlon et al. 1964). However winged sumac is high in fat but also high in fiber possibly limiting digestibility (Appendix 2). This was also the case for sericea lespedeza (Newlon et al. 1964). However, Ellis (1961) found that smooth sumac was one of the most readily consumed seeds in a study examining consumption of native and domesticated seed. His conclusions supported the idea postulated by Korschgen (1952) that sumac was more than a starvation food and may be important to the bobwhite diet in combination with other foods. Baumgartner et al. (1952) recognized the importance of sumac across all regions of Oklahoma as an emergency food in winter and it was mentioned as important in northeast Oklahoma and also in Missouri (Korschgen 1948, Wiseman 1977).

Based on the comparison of the range of values in the literature for important bobwhite foods it is evident that no single food provides all essential nutrients, but individual items more than meet what we know about general requirements (Appendix 2) (See also Brennan 1999). Winter weights of captured bobwhites on this study area from Nov 1999 – Feb 2003 averaged  $169.6 \text{ g} \pm 10.3 \text{ SD}$  (range = 140-190) (Walsh 2004) which is within the normal average for birds from this latitude across the southeast (Brennan 1999) but some 25-30 g lower than birds associated with food plantings in Kansas to the north and the panhandle of Texas well to the west (Robel and Linderman 1966, Hiller and Guthery 2004) and some 20 g less than unsupplemented birds from the Texas panhandle (Hiller and Guthery 2004). Our weights also were almost identical to unfed birds from Tall Timbers and Pebble Hill Plantation in north

Florida and South Georgia respectively (Whitelaw et al. 2007). Hiller and Guthery (2004) and Robel (1969) reported that fall-spring bird weights peaked in December and declined through March. Birds from our study area averaged  $169.3 \text{ g} \pm 6.0 \text{ SD}$  in November and steadily increased through February averaging  $173.1 \pm 16.0 \text{ SD}$ , then declined in March to  $168.3 \text{ g} \pm 9.7 \text{ SD}$  (Walsh 2004). If nutritional needs were not being adequately met we might expect body mass to reflect the lower end of the reported range of weights (Brennan 1999) but they fall well above that.

## **Conclusions**

Food habits of quail on our study area were considerably different than the historic food habits studies conducted in the Ouachita Highlands of eastern Oklahoma or the Ozarks of southern Missouri some 50-80 years ago. The dramatic change in land use over that time was a major factor contributing to differences. The most notable difference was the absence of pine seed in quail diets of earlier studies. Another difference was the absence of domesticated cereal grains in the present study. Domesticated lespedezas were more prevalent in historic studies but still persist in today's landscape. Acorns, wild lespedezas and legumes in general were important throughout both periods of time. Acorn and shortleaf pine seed production was somewhat compensatory and both were important staples.

As expected the burned WSI stands and burned regeneration stands were where most birds were harvested. It is also likely that more effort was placed on hunting this habitat type. However, the results are fairly consistent with data from Walsh (2004) regarding habitat use in the winter in the restoration area. One exception may be the relative use of drainages as this is where most acorns would have been picked up because of the limited number of oaks retained in the restored stands (Masters et al. 1996*b*). Drainages in the uplands are dominated by oaks and are generally narrow linear strips.

It is clearly evident that burning and thinning are important practices that enhance northern bobwhite food production (Stoddard 1931, Speake 1966, Lewis and Harshbarger 1986, Cram et al. 2007). Further these practices at first application create usable space that bobwhites respond to dramatically (Masters 1991, Cram et al. 2002). As well, the creation of usable space will be associated with increased food supplies in thinned and burned forests although the later is not a requisite in defining usable space (Guthery 1997, Cram et al. 2007). Frequent fire is essential in order to maintain these stands as usable space (Walsh 2004, Guthery et al. 2005, Cram et al. 2007). Likely burns at a two year interval will maximize foods and usable space as in some years food production in 3 year intervals declines and woody vegetation becomes rank lessening usable space (Cram 2001, Walsh 2004, Guthery et al. 2005, Cram et al. 2007). Additionally, retention of oaks in drainages and at some level in uplands is of obvious importance because of the periodicity of shortleaf pine and oak masting events. It has been noted elsewhere that pines and oaks are periodic seeders and in pure stands of each food supplies may be limited on a periodic basis but that in mixed oak-pine forests one can expect some alternation in abundance (Grodinski and Sawicka-Kapusta 1970) as this study has shown.

Comparison of the top ten food items with published accounts of nutrient contents (Appendix 2) suggest that a combination of food items should provide adequate nutrition for birds within the pine-bluestem area. Observed weights and the range of weights given in Walsh (2004) would also tend to support this idea. Definitive statements about nutrient status cannot be made without further study and in particular additional data about the gross energy and metabolizable energy content of some of the staple items such as shortleaf pine and the value of green vegetation in the diet.

All of the feeding trials cited in this paper focused on comparing supplemental or domestic foods with a very incomplete subset of native foods in the context of “what was best”

as a relative comparison or as a sole emergency food. When taken in this myopic context is apparent why many managers continue to focus on practices and means of delivering supplemental foods rather on providing usable space because food is assumed to be limiting rather than habitat space (Masters et al. 2007c). We hasten to point out that it is in the face of this perspective that bobwhite populations continue to decline across their range because of the local and limited value of these type efforts (Guthery 1999). We are not arguing that supplemental feeding does not in some contexts increase body weight, survival and productivity in lean years as has been clearly illustrated in several studies where usable space already exists (Townsend et al. 1999, Whitelaw et al. 2007). Rather we hope land managers will began applying the simple tools of prescribed fire and thinning on public and private lands in an ecosystem management context to increase usable space for bobwhites and other grassland associated birds.

The theory that quail have declined as a direct result of the paucity of small patch agriculture may have limited merit in one sense as that was the common land use practice in many areas of eastern U.S. up until the 1950s. But that theory does not consider that the once common practice of burning the woods was prevalent across many areas in the southeast at that time as well. It is evident that ecosystem restoration through thinning and frequent use of prescribed fire on the scale accomplished to date, has increased usable space and food availability and abundance of the elsewhere declining northern bobwhite (Wilson et al. 1995, Cram et al. 2002, Masters et al. 2002).

Public land management agencies in the southeast and elsewhere across the bobwhite range apply little or no active forest management in an ecosystem context which includes frequent fire and management of forest density. Bobwhites are still largely a product of existing habitats that continue to undergo advanced forest succession with little recognition of the fact

that declining open woodland-grassland obligate species have declined precipitously over the last several decades. Although Stoddard (1931) recognized the importance of frequent fire for habitat maintenance for bobwhites comparatively few recent studies recognize the importance of fire for woody vegetation control in prairies, brushlands or open woodlands. Food producing plants and seed abundance and availability declines dramatically with each succeeding year post-burn (Buckner and Landers 1979, Cram et al. 2007). Walsh (2004) showed that bobwhites use of pine dominated stands began declining as little as 3 years post-burn and that stands  $\geq 5$  years post burn were not used emphasizing the importance of very frequent fire for maintaining moderate density oak-pine or pine dominated stands as suitable bobwhite habitat. Cessation of the use of prescribed fire has in our view been the number one correctable factor that has allowed range wide development of closed canopy forests and encroachment of unsuitable woody vegetation onto prairies and shrublands.

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Appendix 1. Northern bobwhite crop contents from hunter harvested birds during November 1998- February 2006, Pine-bluestem renewal area, Ouachita National Forest, Arkansas. Food items are ranks (1=highest) of average frequency (number of occurrences/crop of individual items) and in similar fashion, average weights of individual items across all crops. The importance value is based on Landers and Johnson (1976) with the highest value (16) being the most important.

Food Items	Rank (#)	Rank (wt)	Freq (# crops)	Freq (% crops)	Importance Value
Other (g)	43	40	6	2.2%	5
Debris (g)	22	39	25	9.4%	6
Rock	42	26	7	2.6%	5
Formidae	25	43	13	4.9%	2
Arachnea	33	20	22	8.2%	6
Armadillidiidae	38	51	2	0.7%	1
Coleoptera	27	25	14	5.2%	6
Diptera	62	47	2	0.7%	1
Geophilomorpha	68	61	1	0.4%	1
Hemiptera	36	33	5	1.9%	5
Homoptera	56	57	3	1.1%	1
Hymenoptera	32	31	11	4.1%	6
Lepidoptera	35	27	16	6.0%	6
Orthoptera	19	10	30	11.2%	10
Thysanura	54	48	3	1.1%	1
Mollusca-slug	37	28	14	5.2%	6
Mollusca-snail	23	19	30	11.2%	6
Uk Invert (g)	51	58	3	1.1%	1
Green veg	4	6	128	47.9%	12
Uk seed (g)	30	37	6	2.2%	5
<i>Acalyphia gracilens</i>	13	16	7	2.6%	5
<i>Ambrosia artemesiifolia</i>	6	11	9	3.4%	6
<i>Ambrosia trifida</i>	68	69	1	0.4%	1
<i>Amphicarpa bracteata</i>	24	24	17	6.4%	6
<i>Cassia fasciculata</i>	28	34	10	3.7%	6
<i>Chenopodium albumum</i>	68	60	1	0.4%	1
<i>Clitoria virginiana</i>	46	44	4	1.5%	1
<i>Croton sp.</i>	34	36	7	2.6%	5
<i>Crotonopsis elliptica</i>	68	77	1	0.4%	1
<i>Desmodium spp.</i>	10	9	29	10.9%	10
<i>Diodea teres</i>	46	75	2	0.7%	1
<i>Euphorbia</i>	46	32	5	1.9%	5
<i>Galactica</i>	20	21	19	7.1%	6
<i>Geranium carolinianum</i>	68	71	1	0.4%	1
<i>Helianthus spp.</i>	56	45	2	0.7%	1
<i>L. bicolor</i>	12	13	6	2.2%	5
<i>L. cuneata</i>	51	59	1	0.4%	1
<i>L. hirta</i>	15	18	10	3.7%	6

<b>Food Items</b>	<b>Rank (#)</b>	<b>Rank (wt)</b>	<b>Freq (# crops)</b>	<b>Freq (% crops)</b>	<b>Importance Value</b>
<i>L. intermedia</i>	43	70	3	1.1%	1
<i>L. repens</i>	9	14	29	10.9%	6
<i>L. procumbens</i>	2	3	83	31.1%	15
<i>L. striata</i>	3	4	42	15.7%	10
<i>L. stipululaceae</i>	8	17	17	6.4%	6
<i>L. spp</i>	40	50	2	0.7%	1
<i>L. virginicus</i>	7	8	41	15.4%	10
<i>Oxalis stricta</i>	62	63	2	0.7%	1
<i>Phytolacca americana</i>	68	53	1	0.4%	1
<i>Polygonium pennsylvanicum</i>	41	73	4	1.5%	1
<i>Prunella vulgaris</i>	56	56	1	0.4%	1
<i>Psoralea sp.</i>	68	62	1	0.4%	1
<i>Rhynchosia sp</i>	45	42	3	1.1%	5
<i>Strophostyles sp.</i>	39	30	9	3.4%	6
<i>Stylothanses biflora</i>	68	72	1	0.4%	1
<i>Tephrosia virginiana</i>	68	77	1	0.4%	1
<i>Aristida purpurea</i>	68	55	1	0.4%	1
<i>Carex sp.</i>	68	81	1	0.4%	1
<i>Cyperus sp.</i>	68	65	1	0.4%	1
<i>Panicum spp.</i>	29	35	12	4.5%	6
<i>Panicum anceps</i>	46	54	5	1.9%	1
<i>Paspalum</i>	62	68	1	0.4%	1
<i>Secale cereale</i>	16	23	1	0.4%	5
<i>Scleria spp.</i>	17	12	43	16.1%	6
<i>Setaria sp.</i>	30	46	4	1.5%	1
<i>Uniola sessiliflora</i>	62	80	1	0.4%	1
<i>Acer rubrum</i>	68	66	1	0.4%	1
<i>Bumelia lanuginosa</i>	68	52	1	0.4%	1
<i>Crataegus sp.</i>	54	41	1	0.4%	5
<i>Hypericum hypericoides</i>	56	67	1	0.4%	1
<i>Fraxinus americana</i>	26	38	4	1.5%	5
<i>Nyssa sylvatica</i>	51	49	3	1.1%	1
<i>Ostrya virginiana</i>	56	76	1	0.4%	1
<i>Parthenocissus quinquefolia</i>	62	77	1	0.4%	1
<i>Pinus echinata</i>	1	1	125	46.8%	16
<i>Q. marilandica</i>	46	29	4	1.5%	5
<i>Q. stellata</i>	5	2	69	25.8%	15
<i>Q. velutina</i>	14	7	7	2.6%	9
<i>Rosa caroliniana</i>	67	74	2	0.7%	1
<i>Rhus copallina</i>	11	5	22	8.2%	10
<i>Rhus glabra</i>	18	15	5	1.9%	5
<i>Smilax spp.</i>	61	64	3	1.1%	1
<i>Toxicodendron radicans</i>	21	22	9	3.4%	6

Appendix 2. Published energy and nutrient content values of foods important to northern bobwhite on the pine-bluestem renewal area<sup>1</sup> Ouachita national Forest, Arkansas and other similar or important foods such as domesticated cereal grains used for supplemental feeding for comparative purposes.

Species	Gross Energy (kcal/g)	Metabolizable Energy (kcal/g)	CWC or digestibility index (%)	Nitrogen-free extract (%) (carbohydrates)	Fat	Fiber	Crude Protein	P	Ca	Reference(s)
<i>Ambrosia artemesiifolia</i> <sup>1</sup>	5.286 5.300	4.028								Kendeigh and West (1965) Robel et al. (1974)
<i>Ambrosia trifida</i> <sup>1</sup>	5.283 5.283 5.802 5.482-5.771 5.700	4.332			23.6					Johnson and Robel (1968) Korschgen (1964) Kendeigh and West (1965) Robel (1972) Robel et al. (1974)
<i>Carex</i> spp. <sup>1</sup>	4.788									Kendeigh and West (1965)
<i>Cassia chamaecrista</i>				42.8-45.4	3.4-6.6	7.9-8.8	36.1-40.0	0.46-0.54	0.59-0.63	King and McClure (1944)
<i>Cassia fasciculata</i> <sup>1</sup>	4.476 4.638	2.000 2.416					36.3	0.50	0.17	Madison and Robel (2001) Smart et al. (1972) Robel et al. (1979b)
<i>Cassia nictitans</i>	4.550	2.371								Robel et al. (1979b)
<i>Centrosema virginianum</i>				58.5	2.7	10.4	26.4	.38	.24	King and McClure (1944)
<i>Chenopodium</i> spp. <sup>1</sup>	4.913									Kendeigh and West (1965)
<i>Crataegus crusgalli</i>					3.3	32.8	2.8	0.04	0.42	Halls (1977)
<i>Crataegus marshallii</i>					-	47.3	7.8	0.14	1.56	Halls (1977)

Species	Gross Energy (kcal/g)	Metabolizable Energy (kcal/g)	CWC or digestibility index (%)	Nitrogen-free extract (%) (carbohydrates)	Fat	Fiber	Crude Protein	P	Ca	Reference(s)
<i>Desmodium</i> spp. <sup>1</sup>	4.905 5.540	3.487 3.51-3.71		16.3	14.2	24.5	32.8			Madison and Robel (2001) Spurlock and Savage (1993)
Legumes <sup>1</sup>					6.7	15.6	31.2	0.54	0.24	Short and Epps (1976)
<i>Lespedeza bicolor</i> <sup>1</sup>	5.025									Robel et al. (1979a)
<i>Lespedeza cuneata</i> <sup>1</sup>		2.200					34.7	0.40	0.15	Smart et al. (1972)
<i>Lespedeza sericea</i>				40.1-42.7 35.22	4.0-4.9 4.93	13.3-16.7 14.81	32.3-38.3 28.44	0.50-0.59 0.37	0.14-0.58 0.11	King and McClure (1944) Newlon et al. (1964)
<i>Lespedeza</i> spp.				35.4-42.0	4.5-12.3	11.1-16.7	33.1-42.7	0.49-0.59	0.14-0.61	King and McClure (1944)
<i>Lespedeza stipulaceae</i> <sup>1</sup>	5.14  4.965	3.73-3.89		27.72 26.0	6.73 6.7  8.2-8.7	9.59 13.1  9.8-11.7	40.75 41.3  40.7-43.7	0.55  0.82-0.87	0.43  0.40-0.38	Newlon et al. (1964) Spurlock and Savage (1993) King and McClure (1944) Kendeigh and West (1965)
<i>Lespedeza striata</i> <sup>1</sup>	  5.025	2.200  2.693		33.2	6.9	12.0	40.6 43.9	0.40 0.83	0.15 0.29	Smart et al. (1972) King and McClure (1944) Robel et al. (1979b)
<i>Lolium</i> sp.					2.0	10.5	8.9	0.35	0.23	King and McClure (1944)
<i>Nyssa sylvatica</i> <sup>1</sup>					10.4	-	3.5	0.18	.06	Halls (1977)
<i>Panicum agrostoides</i>					0.88-4.3	23.2-29.5	11.7-17.3	0.21-0.33	0.12-0.30	King and McClure (1944)
<i>Panicum capillare</i>	4.700									Kendeigh and West (1965)

Species	Gross Energy (kcal/g)	Metabolizable Energy (kcal/g)	CWC or digestibility index (%)	Nitrogen-free extract (%) (carbohydrates)	Fat	Fiber	Crude Protein	P	Ca	Reference(s)
<i>Panicum dicotomiflorum</i>	4.647									Kendeigh and West (1965)
<i>Paspalum floridanum</i>					1.0-1.8	28.4-43.2	6.1-9.1	0.13-0.14	0.08-0.09	King and McClure (1944)
<i>Phytolacca americana</i> <sup>1</sup>	5.230									Kendeigh and West (1965)
<i>Pinus echinata</i> <sup>1</sup>				9.9-22.2	17.6-22.1 22.1	32.7-32.9 32.9	26.7-28.6 28.6	0.65-0.76 0.76	0.05-0.08 0.08	Halls (1977) King and McClure (1944)
<i>Pinus palustris</i>				13.5-28.9	28.8 19.3-28.4	23.9 23.9-37.1	33.8 26.7-33.9	0.43 0.68-0.73	0.08 0.04-0.08	King and McClure (1944) Halls (1977)
<i>Pinus taeda</i>	5.086-5.341			17.0-19.7	6.7 6.7-13.5	56.4 48.8-56.4	15.8 15.9-17.4	0.35 0.35-0.47	0.04 0.04-0.05	Asaro et al. (2003) King and McClure (1944) Halls (1977)
<i>Polygonium pennsylvanicum</i> <sup>1</sup>	4.315 4.514				2.3	21.8	9.0			Frederickson and Reid 1988 Kendeigh and West (1965)
<i>Polygonium scandens</i>	4.500	2.295								Robel et al. (1979)
<i>Polygonium sp.</i>	4.423				2.8	22.0	9.7			Frederickson and Reid (1988)
<i>Prunus serotina</i> <sup>1</sup>					4.9	-	7.8	0.16	0.22	Halls (1977)
<i>Quercus marilandica</i>	5.401			57.4 60.1	16.2 10.7	19.0 20.9	7.0 6.3	0.11 0.09	.26 .37	Burns and Viers (1973) King and McClure (1944) Short and Epps (1976)

Species	Gross Energy (kcal/g)	Metabolizable Energy (kcal/g)	CWC or digestibility index (%)	Nitrogen-free extract (%) (carbohydrates)	Fat	Fiber	Crude Protein	P	Ca	Reference(s)
<i>Quercus Phellos</i>	5.296 5.062			58.6 31.2	18.9 19.6	14.7 -	6.4 5.9	.08	.18	Burns and Viers (1973) Fredrickson and Reid (1988) Halls (1977)
<i>Quercus rubra</i>	5.149	2.980								Robel et al. (1979a)
<i>Quercus stellata</i> <sup>1</sup>	4.382		47.7	65.3 37.9-66.7	6.7 5.1-5.7 5.7-7.6	18.1 15.8-19.5 19.4-19.6	6.8 5.2-8.3 4.8-5.1	0.09 0.10-0.11 0.10-0.11	0.22 0.15-0.40 0.38-0.40	Burns and Viers (1973) Short (1976) Halls (1977) King and McClure (1944)
<i>Quercus velutina</i> <sup>1</sup>	4.698		34.8 30.9	- 57.9	17.8 17.5	18.4 16.6	5.9 5.7	0.10 0.10	0.24 0.19	Short & Epps (1976) Short (1976) Burns and Viers (1973)
<i>Rhus copallina</i> <sup>1</sup>				39.1	26.1	26.8	7.4	0.32	0.13	Halls (1977)
<i>Rhus glabra</i> <sup>1</sup>	4.748-4.831 5.199-5.452 5.148 5.205 5.205 5.200	1.581		40.0-47.3 45.8-50.0 41.12	16.3 11.2-22.4 10.0-17.2 7.81	30.4-34.9 21.9-35.1 33.26	6.1-6.4 3.0-5.2 5.19	0.16-0.35 0.10-0.25 0.40	0.16-0.27 0.41-0.94 0.14	Robel (1972) 65-66 Robel (1972) 66-67 Burns and Viers (1973) Johnson and Robel (1968) Korschgen (1964) Halls (1977) Robel et al. (1979b) King and McClure (1944) Newlon et al. (1964)
<i>Setaria spp.</i> <sup>1</sup>	4.402				5.2					Korschgen (1964)
<i>Setaria lutescens</i>	4.402									Johnson and Robel (1968)
<i>Smilax bona-nox</i> <sup>1</sup>				62.1	7.8	18.6	11.1	0.15	0.19	Halls (1977)
<i>Strophostyles helvola</i>				49.1-52.5	0.58-0.81	10.9-13.1	31.7-33.1	0.54-0.60	0.10-0.14	King and McClure (1944)

Species	Gross Energy (kcal/g)	Metabolizable Energy (kcal/g)	CWC or digestibility index (%)	Nitrogen-free extract (%) (carbohydrates)	Fat	Fiber	Crude Protein	P	Ca	Reference(s)
<i>Toxicodendron radicans</i> <sup>1</sup>				64.4	4.9	21.5	5.8	0.19	0.33	Halls (1977)
<b>Invertebrates</b>										
Aracnae <sup>1</sup>				2.4	1.6	15.2	49.3	0.258	1.3	Beck and Beck (1955)
Coleoptera <sup>1</sup>				0.0	2.9	21.9	40.6	0.168	1.2	Beck and Beck (1955)
Lepidoptera <sup>1</sup>				15.67	2.8	12.0	26.6	0.143	1.0	Beck and Beck (1955)
Orthoptera <sup>1</sup> <i>Acheta domesticus</i>	5.903	4.882		7.22	2.7	11.0	45.3	0.204	1.2	Beck and Beck (1955) Robel et al. (1979b)
Snails <sup>1</sup>	1.000			1.4	0.4	1.4	12.2-16.9 9.8	0.480	17.2	Frederickson & Reid (1988) Beck and Beck (1955)
<b>In Comparison:</b>										
<i>Panicum miliaceum</i> (Dove proso millet)	4.417	3.525								Madison and Robel (2001)
<i>Sorghum vulgare</i> (grain sorghum, milo)	4.160-4.322 - 4.228  - 4.304 4.304 4.335 4.300	   3.500 3.706 3.664 3.702		69.62 72.2	2.8 3.1	3.75 6.0	6.06 10.2  11.1	0.25  0.31	0.03  0.04	Robel (1972) Newlon et al. (1964) Frederickson & Reid (1988) Smart et al. (1972) Robel et al. (1979a) Robel et al. (1979b) Madison and Robel (2001) Robel et al. (1974)

Species	Gross Energy (kcal/g)	Metabolizable Energy (kcal/g)	CWC or digestibility index (%)	Nitrogen-free extract (%) (carbohydrates)	Fat	Fiber	Crude Protein	P	Ca	Reference(s)
<i>Zea mays</i> (corn)	4.137 4.830 4.300 4.511 4.435	3.400 4.370-4.600 3.700 3.861		74.9  79.8 68.16	4.2  3.8 4.19	1.4  2.3 1.9	8.7 8.4 10.8 7.5	0.31   0.28	0.04   0.02	Kendeigh and West (1965) Smart et al. (1972) Spurlock and Savage (1993) Robel et al. (1979a) Robel et al. (1979b) Frederickson & Reid (1988) Newlon et al. (1964)
Control (commercial ration)				68.05	2.92	2.30	11.44	0.38	0.53	Newlon et al. (1964)
Recommended Commercial Diet-finisher		1.349					22.0*	0.50	1.00	Dozier and Bramwell (2002)

\*Supplemented with essential amino acids.