National Quail Symposium Proceedings

Volume 8 Article 55

2017

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ABSTRACT

Distribution of food resources may influence northern bobwhite (*Colinus virginianus*) foraging decisions and demographic rates. We tested whether covey movements were sensitive to food availability by spreading sorghum (*Sorghum bicolor*) every 15 days at 3 rates; high rate (174 L/ha/yr), low rate (44 L/ha/yr), and no feed on 3 sections (~240 ha each) of Tall Timbers Research Station, 2009–2010. We measured sorghum availability spread along a 17 km feeding trail every 5 days. We determined seasonal (1 Nov - 15 Mar) home ranges of radio-tagged coveys ($n = 89$) and daily movement rates and home ranges of a subset of coveys located every 30 mins, sunrise to sunset (1 Feb - 15 Mar). Diet was determined from harvested bobwhites. Mean sorghum availability (seeds/0.5m^2) on the feed trail declined from 50 seeds at day 1 to 12 seeds at day 15, and 11 seeds at day 1 to 0 seeds at day 10, for high and low rates, respectively. Seasonal home ranges did not differ among treatments; however, daily home ranges were smaller for coveys on the high rate areas, as was dispersion of locations within home ranges. Distances to the feed trail from covey and random locations were similar. There was no difference in distance traveled (25.20 m; SE = 0.65) between consecutive covey locations among treatments. Proportion of sorghum in the diet declined precipitously when <15 seeds/0.5m^2. We estimated an empirical giving up density of 10–14 seeds/0.5m^2, ~1.6 kcals/0.5m^2. Food availability, even at high levels, marginally affected covey space use and movement rates during late winter. Other factors affecting bobwhites, such as predator avoidance, or thermal regulation, may have a more significant effect on bobwhite covey daily movements and space use.

Citation: Miller, R. S., W. E. Palmer, S. D. Wellendorf, and L. W. Burger, Jr. 2017. Foraging behavior of northern bobwhites in relation to resource availability. National Quail Symposium Proceedings 8:207–214.

Key words: behavior, foraging movements, northern bobwhite, range, supplemental feed, telemetry

INTRODUCTION

Providing supplemental food resources, through habitat manipulation, establishment of food plots, or direct distribution of wildlife feed has been a common practice in wildlife management (The Wildlife Society, 2006) and bobwhite management specifically (Stoddard 1931, Rosene 1969, Robel et al. 1974, Landers and Mueller, 1986, Guthery et al. 2004). More recently, bobwhite managers spread cereal grains, typically corn (*Zea mays*) or sorghum, along dedicated feed trails through bobwhite habitat (Michener et al. 2000, Sisson et al. 2000, Haines et al. 2004, Whitelaw et al. 2009, Wellendorf et al. this volume). Supplemental feed trails are relatively long, averaging 2.4 km of feed trail per 40.5 ha of bobwhite habitat based on a survey of 12 managed properties in the Red Hills (Wellendorf et al. this volume). Typically, supplemental feed is distributed into bobwhite habitat from a tractor mounted spreader across a 10–20 m band on the feed trail every two weeks such that approximately 62–125 kg of grain are spread per hectare (e.g., 1–2 bushels/acre) of habitat on an annual basis. Herein, we define supplemental feeding as spreading cereal grains along a dedicated feed trail through bobwhite habitat as detailed in Wellendorf et al. (this volume) and the "feed patch" as the area over which grain is spread.

Bobwhites readily use cereal grains even when habitat provides abundant and diverse natural food resources. Whitelaw et al. (2009) reported that sorghum accounted for over 67% of bobwhite diets on 2 intensively-managed areas that spread supplemental feed. Bobwhite managers spread cereal grains in part to

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improve hunting and believe spreading supplemental feed localizes coveys increasing their accessibility to the area around the feed patch searched by pointing bird dogs. If true that coveys reduce their daily home range and localize movements near the feed patch, hunting within or near the feed patch should improve hunting success and increase harvest. However, if false, hunters focusing effort in or near the feed patch may experience reduced hunting success except when bobwhite are using the feed patch.

In general, increased susceptibility to harvest from providing supplemental feed to game species is a concern of professional biologists (The Wildlife Society, 2006). DeMaso et al. (1999) found that using feeders to provide grain to bobwhites increased the proportion of bobwhite mortality attributed to harvest, but did not increase overall mortality rates of bobwhites. Townsend et al. (1999) and Sisson et al. (2000) found supplemental feeding did not increase harvest rate of bobwhites or predispose bobwhites to predation. Limited research on bobwhite movements in relation to supplemental feeding found smaller home ranges on fed sites, suggesting bobwhites may shift space use to the areas with supplemental feed (Sisson et al. 2000, Buckley et al. 2015). Sisson et al. suggested that bobwhites in the supplemental fed area had lower susceptibility to harvest because they spent less time feeding and more time displaying escape behaviors than bobwhites without access to supplemental feed.

Optimal Foraging Theory (OFT) predicts that foragers ignore low "profitability" food items when more profitable food items are abundant and available (Stephens et al. 2007). Sorghum spread along the feed trail provides an abundant and recurring source of high energy (i.e., profitable) food for bobwhites. As highlighted previously, bobwhites include supplemental feed as a major diet item (Whitelaw et al. 2009), therefore they obviously use the feed patch. However, it is unknown how much time bobwhites associate with the feed patch, how it affects their overall space use, or how many seeds of grain per unit area is required to elicit changes to their behaviors. Therefore, we determined bobwhite use of the feed patch and how bobwhites moved in relation to the feed patch to better understand the likelihood that supplemental feeding localizes bobwhites movements and potentially increases their susceptibility to hunters.

The currency by which bobwhite choose to remain or leave a patch is energy gained per unit of time spent foraging (Stephens et al. 2007). The marginal value theorem (Charnov 1974) of OFT predicts bobwhites within the supplemental feed patch experience diminishing foraging returns as grain seeds decline in abundance over time requiring increasing effort per seed. At some unknown availability of seeds remaining in the feed patch, a foraging threshold is reached and the currency of the feed patch will decline to or below the currency available in natural feed patches. At this foraging threshold bobwhites should reduce use of the feed patch, or abandon the patch, and choose to forage in patches with more profitable natural sources of food. In this context, we assessed how bobwhites used the supplemental feed patch by determining their diet and use of the patch in relation to availability of sorghum seeds per unit area. We measured when bobwhites shifted their use from the feed patch and foraged more on other food items as an empirical "giving up density" of grain, or the energy per unit area at which foraging within the feed patch was no longer profitable (Brown et al. 1988).

The mechanisms through which food availability influences demographic parameters are poorly understood. While several studies demonstrated equivocal effects on survival of bobwhites from point feeders and food plots (Frye 1954, Robel et al. 1974, DeMaso et al. 1999, Guthery et al. 2004), supplemental feeding as defined in this study has been found to increase bobwhite survival rates (Sisson et al. 2000, Buckley et al. 2015). A 10-year study at Tall Timbers also measured greater annual survival in 9 of 10 years (Palmer and Wellendorf, unpublished data). Therefore, while not the primary focus of this study, a secondary interest was to determine whether supplemental feed would result in lower space use and movements as a mechanism for reduced predation and increased survival. Less time spent foraging by bobwhites could equate to lower movements and lower vulnerability to predation and harvest by increasing vigilance behaviors. Consistent with this idea, Sisson et al. (2000) observed smaller home ranges and more localized movements on fed sites. However, no studies have determined how supplemental feeding affects foraging behavior and daily movements which may indirectly influence survival rates.

To understand potential costs and benefits of supplemental feeding requires knowledge of how food resources influence individual behavior. Therefore, we examine effects of supplemental feeding on bobwhite behavior by determining temporal variation seed availability and its relationship to bobwhite diet, seasonal home ranges, space use, and daily movement of bobwhites. We hypothesized that as supplemental feed availability increased, bobwhite movements and daily and seasonal space use should decrease and that daily movements should be concentrated nearer to the feed patch, especially when supplemental food resources were abundant. Further we predicted that bobwhites would abandon supplemental food resources before they were entirely gone, indicating an empirical giving up density energy value for habitat on our study area.

STUDY AREA

Tall Timbers Research Station (TTRS 30.66° N, 84.22° W) is located in north Leon County, Florida in an area that is commonly referred to as "the Red Hills". Tall Timbers Research Station is ~1,570 ha in size. Most of the property (66%) was upland pine forests which consist of longleaf pine (*Pinus palustris*), loblolly pine (*Pinus taeda*) and shortleaf pine (*Pinus echinata*) with a groundstory of warm season grasses, forbs, legumes and hardwood shrubs and resprouting tree species. Pine uplands are intermixed with hardwood drains (21%) and annually disked fallow fields (13%). Prescribed burning, mowing, and roller chopping are techniques frequently used at TTRS to reduce hardwood encroachment while maintaining diverse grass-forb-shrub ground cover vegetation suitable for bobwhite. Over 20 years of telemetry data demonstrate that 100% of the upland habitats on TTRS was used as habitat by bobwhites.

Climate is considered relatively moderate with mean annual temperatures ranging from 1-34 °C. Average humidity is 77.5%. Average rainfall is 145 cm with most rain falling between June and September. Average elevation at TTRS is 61 m.

METHODS

TTRS was divided into 3 study areas (244 ha, 242 ha, and 232 ha). Each year a feeding rate was assigned to an individual treatment area. Sorghum was used as the supplemental feed. Feed rate treatments consisted of a high rate of 174 L/ha/year (2.0 bushels/acre/year), a low rate of 44 L/ha/year (0.5 bushels/acre/year), and a zero feed rate in the control. These feeding treatments were applied to the study areas for one year. The high feed rate is similar to that used on managed quail lands in the region. We randomly assigned treatment and control during year one then treatment and control were rotated counter-clockwise in year two to minimize confounding study area with treatment.

Bobwhite were captured using baited walk-in funnel traps (Stoddard 1931). Traps were baited with sorghum and covered with recently cut pine boughs in an attempt to minimize stress of captured birds and to keep traps hidden from predators. Gender, age class, and weight for each captured bobwhite were recorded (Rosene 1969). Additionally, a uniquely numbered aluminum leg band was attached (National Band and Tag Co., Newport, KY). Bobwhite were then fitted with 6.4–6.9 g necklace radio transmitters (American Wildlife Enterprises, Monticello, FL). Trapping, handling, and marking procedures were consistent with the guidelines of the Tall Timbers Research, Inc. Institutional Animal Care and Use Committee Permit (IACUC no. GB2001-01).

Spreading Sorghum and Seed Loss Rates

Supplemental feed was distributed on a biweekly feeding schedule throughout the year. Supplemental feed was applied using John Deere 6400 tractor equipped with a 40 bushel 3-point spreader (Vicon Spreaders, Peach Bottom, PA, 17536) to half of the feeding trail on both feed treatments on the first day and then the remainder of the feed trail on both treatments on the second day.

Prior to conducting the feeding trials, we calibrated the spreader to distribute the low and high feeding rates and determine the distance distribution of seed thrown from the spreader. We did this by counting sorghum seeds collected in buckets placed at 0.91 m intervals perpendicular to the direction of the tractor and spreader until the correct gate settings on the spreader were determined. Once we determined the correct gate settings, we conducted 10 trials for each setting of the seed release gate to determine the number of seeds spread at different distances from the tractor. We determined that the spreader distributed seeds 7 m to either side of the centerline of the feed trail and defined this 14 m-wide swath as the ‘feed patch’ which covered about 11% of the total habitat within the low and high feed treatments based on the distance in each study area.

We determined sorghum availability through time by sampling sorghum in both treatments during February and March at 60 random points placed within the feed patch using Hawth’s tools (Hawth’s Analysis Tools for ArcGIS. Version 3.27 http://www.spatialecology.com/htools). Each point was flagged by placing pin flags at each of the four corners of a 0.5 m^2 plot. Preexisting sorghum seed was removed, along with debris, to the soil humus layer using a 5.5 hp wet-dry vacuum (Shop-Vac, Williamsport, PA) powered by a portable generator. Then a known number of seeds, specific to each feeding treatment as predetermined from spreader calibration, were hand deposited within each plot. We replaced debris collected by the vacuum back over the plot mimicking the surrounding environment. We counted residual seed availability within 20 of the 60 plots during 3 sampling periods on days 5, 10, 15, using the same vacuum system.

We estimated the relationship of seed abundance versus time data using Curve Expert 1.3 (CurveExpert software, http://www.curveexpert.net). We considered a set of models that included linear, exponential, power law, yield-density, and sigmoidal and selected best fit model based on largest coefficient of determination (r^2).

Diet

We determined diet of bobwhites harvested on the study area in February, 2009–2010. Hunting effort was not constant among study areas. Crops of harvested bobwhites were collected and time of harvest, date, feed treatment, and gender were recorded. Crop contents were removed and food items were dried to a constant mass in an industrial sized dryer set at 27 °C for 72 hours (Masters et al. 2007). Seed items were identified to lowest taxon possible using Tall Timbers Research Station reference seed collection, along with reference manuals by Martin and Barkley (1961). Whitelaw et al. (2009) provided comprehensive bobwhite diet data for TTRS on supplemental fed and control areas, therefore we presented percent (by dry weight) of sorghum and other seed types that made up a large proportion of the diet.

Daily Telemetry

During 1 February through 15 March 2009 and 2010, locations and daily movements of radio-marked bobwhites were monitored on average 4 times a week in a manner that coincided with the seed availability schedule. This resulted in an even distribution of samples throughout the two-week feeding cycle. A covey was chosen at random using a random number generator within each of the two feed treatments and these coveys were then located every 30 minutes diurnally. Coveys to be monitored were located on the roost the night prior to monitoring to minimize disturbance when first locating a covey pre-dawn the next monitoring (Kenward 2001). Observers maintained a distance of at least 40 m from the monitored coveys and were as quiet as possible in order to limit any potential influence on covey movements. Observers were trained to estimate distance through a combination of triangulation, homing, and signal strength. Using an orienteering compass, observers took bearings and estimated distances to covey locations, producing an average of 21 (17–24) locations/covey/day. Observers used GPS units that did not have the feed patch in the background to eliminate any potential bias for locations on or near the feed patch.

Observer locations were then georeferenced (+/- 1 m) using a differentially corrected Trimble Geoexplorer GPS unit and Pathfinder Software (Trimble Navigation Limited, Sunnyvale, CA). Covey locations were triangulated using a minimum of 3 positions within LOAS 4.0 software (Ecological Software Solutions LLC, Hegymagas, Hungary) using a maximum likelihood estimator. We censored locations with an error eclipse greater than 0.01 ha.

Seasonal Telemetry

Individual bobwhites in the low, high, and control treatments were located >3 times per week from 1 November to 15 March during both 2008–09 and 2009–10 winter seasons using homing techniques (Fuller et al. 2005). Locations were plotted on detailed aerial photos at a scale of 1:1000 in the field which were created in Arc Map and included land cover types as well as terrain features and transferred into a Geographical Information System ArcGIS 9.3 (ArcGIS, Version 9.3. Environmental Systems Research Institute, Redlands, California, USA) to determine spatial coordinates.

Telemetry locations were used to estimate daily and seasonal 95% utilization distributions of radio-marked bobwhite in relation to supplemental feed availability. We used daily telemetry locations for all radio-collared birds in the three treatments to estimate seasonal utilization distributions. We used intensive telemetry locations from bobwhite coveys to estimate daily utilization distributions. Utilization distributions as well as the smoothing parameter (h) were created using ADEHABITAT package in R (Calenge 2006). A smoothing parameter was created for ranges in each year of the study as the mean, least-squares cross-validation-derived h over all individuals where the algorithm converged (bivariate normal kernel; Kenward 2001, Terhune et al. 2010).

Area within 95% utility distributions were then calculated using X tools Pro extension in ArcGIS 9.3. An analysis of variance (ANOVA) within a general linear model (GLM) in SAS® software, Version 9.2 (SAS Institute, Cary, North Carolina, USA) was used to compare daily and seasonal ranges by treatment, year and year by treatment effects. Estimates were reported as least squared means and associated standard errors.

Proximity to Feed Patch

To determine if bobwhite selected locations closer to supplemental feed patch, we compared mean distance to feed patches between covey locations and an equal number of randomly generated locations. We generated an equal number of random locations using Hawth's tools within the treatment area used by each covey. We generated distances to the feed patch using the NEAR function in ArcGIS 9.3. Unless noted otherwise, all statistical analyses were conducted using SAS® software, Version 9.2 (SAS Institute, Cary, North Carolina, USA). An overall mean was determined for each radio-marked covey and paired random locations using PROC MEANS. Individual coveys were used as sampling unit (random effect) for an analysis of variance (ANOVA) within a mixed model.

We classified locations of coveys from intensive daily monitoring as in or out of feed patch in a binary fashion. We treated covey-days as independent sampling units and estimated the proportion of 30-minute relocations in feed patch for each covey-day. To determine if proportional use of feed patches was influenced by supplemental feed, we modeled probability of being in a patch using an events/trials (locations in feed patch/total number of locations in covey day) response in a logistic regression within PROC LOGISTIC.

We used multi-response permutation procedures (MRPP) to test for distributional differences between locations of bobwhite in low and high feeding treatments as it is possible for locational distributions to differ without influencing either mean daily movements, distance to feed lines, or range size. MRPP can be used to simultaneously test for distributional differences in central tendency and dispersion for univariate and multivariate analyses in a completely randomized one-way design (Cade and Richards, 2005). We used MRPP to test for differences between feed treatments in dispersion of daily locations within BLOSSOM version W2008.04.02 (Blossom Statistical Software. United States Geological Survey. Fort Collins Science Center. Fort Collins, Colorado, USA). We centered the daily locational data relative to the mean x and y coordinate for each individual covey, scaling all locations to a common origin. Having removed differences in central tendency through centering, subsequent MRPP test on the centered data then became a test of bivariate dispersion.

RESULTS

We sampled sorghum seed availability in 326 0.5 m^2 plots (164 high rate and 162 in the low rate) between 1 February 2009 and 15 March 2009 and 255 0.5 m^2 plots (125 high rate and 130 low rate) between 1 February 2010 and 15 March 2010. Seed depletion for the high feed treatment declined at 5-day intervals from 50 seeds to an average of 37, 24, and 12 and fit a linear model ($r^2 = 0.998$). Seed depletion for the low feed treatment declined at 5-day intervals from 11 seeds to an average of 5, 1 and 0 and followed a modified power function ($r^2 = 0.998$).

We harvested 285 bobwhites, with 122 in the high feed rate treatment, 102 in low feed rate treatment, and 61 in control. Mean crop weight did not differ significantly between years ($F_{1,279} = 2.34$, $P = 0.13$) or among feed treatments ($F_{2,279} = 1.90$, $P = 0.15$). Mean weight of crop

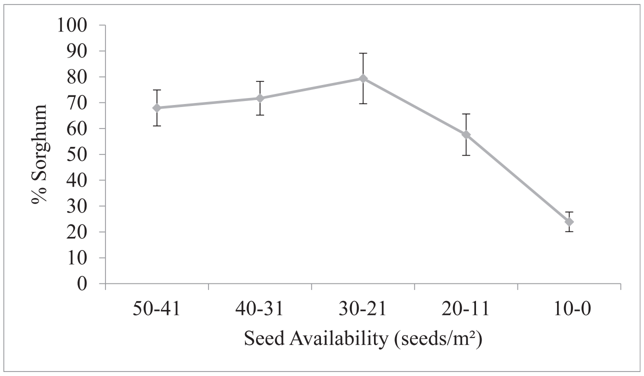

Fig. 1. Mean percentage of sorghum in northern bobwhite crops collected in February 2009 and 2010, at Tall Timbers Research Station, Leon Co, Florida, USA. Error bars indicate ± 1 standard error.

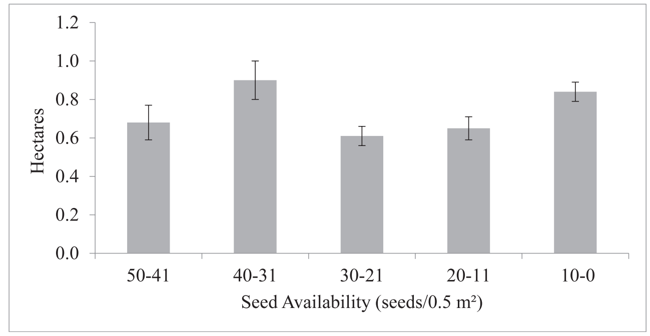

Fig. 2. Daily range sizes (ha) for radio-marked northern bobwhite coveys, in relation to daily sorghum seed availability, February and March, 2009 and 2010, at Tall Timbers Research Station, Leon Co., Florida, USA. Error bars indicate 1 standard error.

contents were 2.2 g and 2.4 g for high feed treatment in 2009 and 2010, 2.6 g and 2.8 g for low feed treatment in 2009 and 2010, and 2.3 g and 2.9 g for the control in 2009 and 2010. Crop contents of bobwhites harvested in the high feed treatment consisted of 74 % sorghum in 2009 and 95% sorghum in 2010. Crop contents of bobwhites harvested from the low feed treatment comprised of partridge pea (*Chamaecrista* spp.) (30%), sorghum (27%), acorn (*Quercus* spp.) mast (19%) in 2009, and partridge pea (40%), sorghum (29%), and acorn mast (0.2%) in 2010. Crop contents of birds harvested in the control treatment in 2009 were primarily comprised of partridge pea (49%) and acorn mast (25%). In 2010, crop contents from control feed treatment were predominantly partridge pea (65%) with less acorn (9%). At sorghum counts greater than 20 seeds / 0.5 m^2, sorghum comprised 68.0 % (SE = 6.96) to 79.4 % (SE = 8.01) of crop contents, declining to 57.6 % (SE = 8.01), when sorghum availability was between 11 and 20 seeds / 0.5 m^2 and 23.9 % (SE = 3.8) at 10 seeds / 0.5 m^2 or less (Figure 1).

Winter seasonal range sizes of coveys did not differ significantly among feeding levels ($F_{2,83} = 0.60$ $P = 0.55$) or between years ($F_{1,83} = 1.29$ $P = 0.25$). During 2009, mean winter range sizes of 37 coveys were 18.03 ha (SE = 1.24) in high feed treatment, 18.6 ha (SE = 1.77) in low feed treatment and 18.7 ha (SE = 1.75) for control treatment. In 2010, mean winter range sizes of 52 coveys were 18.3 ha (SE = 1.18), 20.4 ha (SE = 1.19) and 21.2 ha (SE = 2.53) for high, low, and control treatments, respectively.

Daily range size ($n = 107$ coveys) were slightly lower for coveys in high feed rate treatments ($F_{1,103} = 3.47$ $P = 0.06$) with no difference among years ($F_{1,103} = 0.07$ $P = 0.79$). In 2009, mean daily ranges were 0.72 ha (SE = 0.06) in high feed treatment and 0.85 ha (SE = 0.06) for low feed treatment and in 2010 mean daily ranges were 0.71 ha (SE = 0.06) and 0.83 ha (SE = 0.08) for the high and low feed rate treatments, respectively. Mean daily range sizes, grouped by seed availability classes, had overlapping confidence intervals and as such did not differ substantively (Figure 2).

Bobwhite traveled a mean 25.2 m (SE = 0.65) between consecutive locations during daily intensive focal periods. Mean step length between consecutive locations did not differ between feeding treatments ($F_{1,2178} = 0.99$, $P = 0.32$) or years ($F_{1,2178} = 0.81$, $P = 0.36$). During 2009, mean step lengths were 24.5 m (SE = 1.19) and 27.2 m (SE = 1.53) for high and low feed treatments, respectively. In 2010, the mean step lengths were 24.8 m (SE = 1.29) and 24.6 m (SE = 1.2) for high and low feed treatments, respectively.

Similarly, total distance that bobwhite coveys traveled throughout the day did not differ between treatments ($F_{1,103} = 0.17$, $P = 0.68$) or years ($F_{1,103} < 0.01$, $P = 0.95$). In 2009 total distance traveled over the entire day was 495.8 m (SE = 33.04) for the high feed treatment and 528.3 m (SE = 33.01) for the low feed treatment. In 2010, bobwhites total travel distance of 514.9 m (SE = 39.2) for the high feed treatment and 513.5 m (SE = 40.99) for the low feed treatment.

Centered bivariate locational distributions were different among feed rates ($P < 0.001$). Mean Euclidian distance between all pairwise combinations of centered locations in high feed treatment (D = 1.43 m) was 23% lower than in the low feed treatment (D = 1.75 m) indicating greater dispersion in the low feed treatment.

We used telemetry locations from 38 intensively monitored bobwhite, 16 in 2009 and 22 in 2010, to examine proximity of daily locations to the feed patch. The mean distance to feed patch was 42.0 m (SE = 1.0) and 41.3 m (SE = 3.15) for random and actual covey locations, respectively ($F_{1,71} = 0.04$, $P = 0.83$). Mean distance to feed patch did not differ significantly between treatments ($F_{1,71} = 0.43$, $P = 0.52$), or years ($F_{1,71} = 0.27$, $P = 0.60$). While mean distances over the 15-day feeding period did not differ from random, coveys tended to choose locations closer to feed line as seed availability decreased from 40 to 11 seeds / 0.5 m^2, reaching a minimum distance of 26.6 m (SE = 6.07) at about 11 seeds. This decreasing trend was followed by an increase in the mean distance to feed line to 40.4 m (SE = 3.17) when seed availability decreased below 10 seeds (Figure 3) which corresponded to a reduction in sorghum in bobwhite diets.

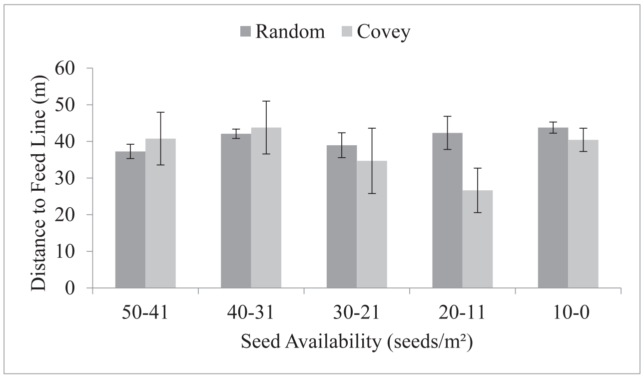

Fig. 3. Mean distance to feed line for radio-marked northern bobwhite coveys and randomly-generated locations, February 2009 and 2010, at Tall Timbers Research Station, Leon Co., Florida, USA. Error bars indicate 1 standard error.

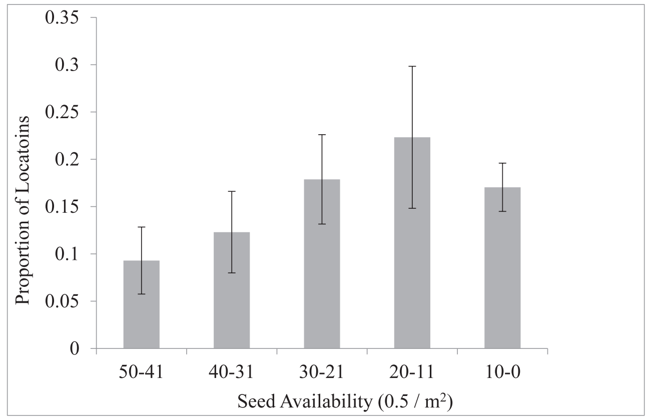

Fig. 4. Mean proportion of covey locations within feed patch, February 2009 and 2010, at Tall Timbers Research Station, Leon Co., Florida, USA. Error bars indicate 1 standard error.

We used locations from 102 covey/days to estimate proportion of time within feed patch. Mean number of locations per covey/day was 20.8 (SD = 2.2). Proportion of daily locations within feed patch (9–22%) varied in relation to seed availability (Figure 4). The model that best explained proportional use of feed patches included seed availability and seed availability squared. At 40 to 50 seeds / 0.5 m^2, approximately 9% of locations were within the feed patch, increasing to 22% at 10 to 20 seeds / 0.5 m^2 then declining to slightly to 17% at 1 to 10 seeds / 0.5 m^2 .

DISCUSSION

We designed our feeding rates so that bobwhites experienced a range from abundant sorghum availability commonly spread on wild bobwhite properties to none through each 15-day feeding period. Sorghum spread at the high rate declined monotonically to a starting level of the low rate and provided us an opportunity to observe bobwhite behavior along a continuum of food availability. Sorghum spread at the low rate declined to zero and was no longer available to bobwhites after about 10 days. We could not find previous studies on depletion of supplemental feed spread in an upland pine ecosystem; however, research in Tennessee characterized loss of agricultural seeds in fields after harvest using an exponential decay function yielded similar results to this study (Foster et al. 2010).

As predicted by OFT, when supplemental feed was abundantly available, bobwhite selected for sorghum over less profitable native seeds and greens. Use of the feed patch by bobwhites varied slightly in relation to seed availability however patterns in their movements and diet in relation to seed availability suggested a giving up density at which bobwhites choose native seeds over sorghum. At higher feed densities (30–50 seeds / 0.5 m^2) bobwhites apparently fed quickly and left the feed patch. This is supported by observed high amounts of sorghum in the diet and low use of the feed patch (e.g., shorter foraging effort); thus resulting in similar distances to random points from the feed patch as bobwhites travelled through other parts of their home range. Use of sorghum in their diet remained high ($>$ 85%) until seeds declined to 10–21 seeds / m^2. At this density of seeds, bobwhite locations were 33% closer to the feed patch, than at higher densities and the proportion of their daily range in the feed patch was highest. This suggests that bobwhites were increasing foraging time for sorghum as seed availability declined. At $<$10 seeds / m^2 bobwhites diet shifted to primarily native foods and distance to, and locations within, the feed patch was similar to higher seed densities, however, for different reasons. At this point, bobwhite reduced foraging time in the feed patch which suggests at approximately $<$15 seeds / 0.5 m^2 energy gained within that feed patch is equal to or falls below that of the surrounding habitat. This diet switching follows predictions of the marginal value theorem (Charnov 1976) and suggested a foraging threshold at this time of year was $\sim$15 sorghum seeds and $\sim$1.6 kcals / 0.5 m^2 (Robel et al. 1974). Miller (2011) found similar levels of metabolizable energy in the crops of bobwhites harvested in this study (8.39 kcals) among high, low, and control treatments. He also reported little difference among treatments in whole body lipid levels, although lipid levels were significantly greater in the high feed rate treatment in 2010 when acorn mast was less available. Given adequate energy is available in native seeds bobwhites could choose to forage exclusively on native seed sources. That they chose a higher energy seed relative to native foods, suggests bobwhites selected the sorghum over native seeds to minimize foraging time (Schoener 1971, Charnov 1976). By minimizing foraging time, bobwhites may be able to increase time spent in habitats with better thermoregulatory or predator avoidance qualities (Lima 1985), thus improving their fitness

Seasonal range sizes were similar among feeding rates. Similarly, total daily movements and distance moved between locations was not affected by the presence of the feed patch. This suggests that despite a well dispersed feed patch system, bobwhite coveys moved to meet other behavioral needs, such as predator avoidance and thermoregulation. Buckley et al. (2015) also found no difference in winter home range size of bobwhites with access to supplemental feed. Sisson et al.

(2000) observed smaller winter ranges on fed versus unfed sites. Their study occurred on a property with lower soil fertility and less native food than our study site; thus their bobwhite may have had to move greater distances to find feed patches that minimized foraging time.

Some studies have documented increased survival rates for bobwhites provided with a well-dispersed feeding line system such as the program used in this study (Sisson et al. 2000, Buckley et al. 2015). While bobwhites used the feed patch, they did not significantly alter their daily and seasonal use patterns. We hypothesized that bobwhites with access to super abundant, high energy foods, would move significantly less and reduced movements may be a mechanism for predator avoidance and reduced predation. Because bobwhites moved similarly among treatments suggests that other factors, such as increased buffer prey as a result of supplemental feeding (Doonan and Slade 1995), may be a more important mechanism to reduce predation. In more northerly climates, access to high energy foods during periods of severe weather is a nutritional mechanism for increasing bobwhite survival (Buckley et al. 2015, Janke et al. 2015). Severe winter weather is not an issue for survival of bobwhites in sub-tropical regions (Stoddard 1931, Terhune et al. 2007). This suggests that increased survival rates from supplemental feeding observed in southern latitudes may largely be a result of indirect mechanisms.

Unlike point feeders that may concentrate bobwhites, sorghum was well dispersed across our study site, covering 11% of the habitat area throughout the pine uplands. Applying supplemental feed by this method does not concentrate coveys because they were not disproportionally selecting locations close to the feed line, or spending more time in or near the feed patch than spatially-available. Well-dispersed feed lines allow individuals to forage without increasing the likelihood of directly contacting other individuals. It also permits individuals to choose suitable portions of the feed patch that are associated with suitable habitat to match changing conditions. In these manners, chances of disease transmission or predation as compared to stationary wildlife feeders (The Wildlife Society 2006) is mitigated.

Over the feeding cycle and in both the high and low feeding treatments, bobwhites were not closer to feed patches than random. This is likely because the continuous feed patch winding through the habitat permits bobwhites to forage more or less naturally. This is different from systems such as point feeders or feeding along roads which are not designed to reach the home ranges of each covey on an area in many different locations (Lehman 1984, Boyer 1989, Haines et al. 2004). Sisson et al. (2000) used a similar supplemental feeding system in their study and found no evidence of increased harvest for bobwhites on the fed area versus the unfed area. While bobwhites used the feed patch, their limited association with it suggests that broadcasting supplemental feed would not serve as "baiting" coveys such as found with point feeding systems (DeMaso et al. 1999). However, the lack of bobwhites association with a feeding patch may depend on how the distribution of feed patches on the landscape. Research that compares bobwhite space use and harvest at a range of feed patch densities may better address at what point supplemental feed would concentrate bobwhites around a feed patch and increase susceptibility to harvest.

MANAGEMENT RECOMMENDATIONS

If supplemental feeding programs are used, we suggest feeding at the rate of 2.0 bushels per acre of habitat per year to allow bobwhites access to high energy foods at all times during the feeding cycle. We suggest that by distributing feed across the landscape, rather than at point feeders, limits the potential for baiting bobwhites to a specific location potentially increasing harvest rate. This study underscores the importance of managing for diverse native food sources, including mast producing overstory, especially when supplemental feeding is depleted or not used. Hunting along a supplemental feeding patch is likely to be unproductive as bobwhites spend only a small proportion of their day associated with it.

ACKNOWLEDGEMENTS

This project was funded by the Pamela H. Firman Quail Management Research Fund and the Gerry Quail Endowment at Tall Timbers Research Station and Land Conservancy. We appreciate the field assistance by many of the dedicated graduate students, technicians, and interns that collected field data for this project. T. M. Terhune provided assistance with analyses. Additionally, Tall Timbers Research Station and Land Conservancy staff provided much appreciated logistical support.

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