

Effects of food supplementation on the nesting dynamics of wild northern bobwhite

Authors: Byron R. Buckley, Alicia K. Andes, and C. Brad Dabbert

Source: Wildlife Biology, 2018(1)

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.00385>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Effects of food supplementation on the nesting dynamics of wild northern bobwhite

Byron R. Buckley, Alicia K. Andes and C. Brad Dabbert

B. R. Buckley (byron.buckley@ttu.edu), A. K. Andes and C. B. Dabbert, Dept of Natural Resources Management, Texas Tech Univ., Mail Stop 42125, Lubbock, TX 79409, USA.

Avian females with food limitation or are unable to meet nutritional requirements could result in negatively influenced egg size, nest initiation date, nesting season duration, and clutch size. Northern bobwhites *Colinus virginianus* serve as an adequate model species for supplemental feeding studies because of prolific nesting and re-nesting behavior. We monitored females on treatment and control units to determine if food supplementation influenced: 1) nest initiation, nesting duration, and nesting attempts, 2) nesting success, and 3) egg volume and clutch size. We radio-marked 196 female bobwhites during the breeding season of 2011 and 2012. Hens with access to supplemental feed produced 0.86 and 1.60 nest per hen while hens on control sites produced 0.15 and 0.81 nest per hen during the 2011 and 2012 nesting season, respectively. Average nest initiation varied slightly between treatment and control; though, average nesting season length was 16 and 31 days longer on treatment units. This benefit indicates females with access to food supplementation were in better physical condition compared to females on control units. However, nest success ($\beta = -0.03$, $SE = 0.40$), clutch size ($t = -0.37$, $p = 0.70$), and average intra-clutch egg volumes ($\beta = -0.06$, $SE = 0.20$) ($t = 0.50$, $p = 0.61$) were unaffected by food supplementation. Total net productivity estimates showed more chicks per hen were produced on treatment sites [$\bar{P} = 2.34$, $SE = 0.04$ (2011); $\bar{P} = 5.75$, $SE = 0.12$ (2012)] than control units [$\bar{P} = 0.61$, $SE = 0.001$ (2011); $\bar{P} = 3.47$, $SE = 0.13$ (2012)]. Our results suggest that bobwhites with access to supplemental feed broadcast into roadside vegetation throughout the breeding season can potentially increase nesting attempts which may result in increased production and offset population fluctuations due to drought conditions.

Avian breeding has been theorized to be timed to coincide with increases in natural food supply (Lack 1950, 1968). Food procurement prior to and during nesting season can dictate female's ability to form eggs which may negative impact chick survival (Perrins 1970). If females are unable to meet nutritional requirements egg size, nest initiation date or nesting season duration, and clutch size could be negatively influenced (Guthery et al. 1988, Christians 2002, Massaro et al. 2002). Lack (1966, 1968) concluded food acquisition was a limiting factor governing clutch size of various avian species. Increases in available food may permit individuals to end a breeding attempt in better physical condition and allow for replenishment of necessary reserves for a second or third nesting attempt (Martin 1987, Hoodless et al. 1999).

If food is limited during nesting season, chick survival could be negatively influenced by a reduced egg size (i.e.

egg volume) and therefore a reduced chick body size upon hatch. Larger egg and chick size have been positive correlated with healthier chicks and an increased breeding success (Coulson 1963, Serventy 1967, Galbraith 1988). For instance, breeding success of red grouse *Lagopus scoticus* was reduced when egg size was low (Jenkins et al. 1967). Chick weight and hatchability were positively correlate with higher egg volume (Narushin et al. 2002, Narushin and Romanov 2002). If a female can produce a larger egg it can be theorized that chicks will be in better physical condition which could increase the odds of successfully fledging.

We chose to examine the influence of food supplementation using a wild population of northern bobwhites *Colinus virginianus*; hereafter 'bobwhite'. Bobwhites serve as an adequate model for supplemental feeding studies because of their prolific nesting and re-nesting behavior (Rosene 1969, Guthery et al. 1988). Additionally, bobwhites readily select supplemental feed (e.g. milo *Sorghum bicolor*) when provided (Townsend et al. 1999, Guthery et al. 2004, Henson et al. 2012, Larson et al. 2012). Providing supplemental feed for bobwhites, by dispersing milo into road side vegetation, has also been shown to increase survival while not impacting

This work is licensed under the terms of a Creative Commons Attribution 4.0 International License (CC-BY) <<http://creativecommons.org/licenses/by/4.0/>>. The license permits use, distribution and reproduction in any medium, provided the original work is properly cited.

natural movement (Buckley et al. 2015). Natural foods consumed by bobwhites substantially decrease by mid-winter, which can cause stress and diminished body mass (Lehmann 1953, Frye 1954, Robel and Slade 1965) leading up to the breeding season. Commercial formulated feed pellets from stationary feeders or road-surface baiting have been used in previous studies to investigate the effects of supplemental feeding on quail nesting however with neutral results (Cain et al. 1982, Doerr and Silvy 2002, Tri 2010). Nestler et al. (1944) found captive bobwhite females nested earlier and longer when provided high energy food supplements. In studies of larger more numerous gallinaceous birds (e.g. wild turkey *Meleagris gallopavo*; ring-necked pheasant *Phasianus colchicus*), supplying feed resulted in increased chick production, earlier nest initiation and improved body condition (Pattee and Beasom 1979, Draycott et al. 1998).

Our objective was to determine if food supply influenced bobwhite reproduction by distributing supplemental feed into useable quail habitat along roadside edges. Our predictions were bobwhite females with access to food supplementation would: 1) begin nesting earlier, have more frequent nesting attempts, and increase breeding duration or nesting season length, 2) increase nesting success, and 3) result in an increase in clutch size and larger mean intra-clutch volume eggs than females without access to supplemental food.

Methods

Study area

The study was conducted in central King County on ~ 5665 ha pasture (33°33'38.23"N, 100°25'17.41"W) of the 6666 Ranch located ~ 8 km south of Guthrie, TX, USA, in the Rolling Plains ecoregion. The pasture was subdivided into eight interfacing, 404.6 ha tracts (Fig. 1). We selected 404.6 ha sections to minimize the overlap of radio-marked females on treatment (supplemental feed provided) and control (feed withheld) units. We randomly selected treatment and control units. Rangeland improvements applied in this pasture in late 2009 and early 2010 included redberry junipers *Juniperus pinchotti* grubbed (i.e. uprooting invasive trees) and piled in combination with strip disking to promote cover and natural food sources. Annual precipitation for the area is 59.4 cm. The average daily temperatures range from 7°C in winter to 27°C in summer. Average vegetation structure was 85.6% cover and 0.78 m height, while composition was 29.6% woody, 54.3% grass and 14.4% succulents at the study site (Andes et al. 2012). The soil is comprised of loam, fine sandy loam, and very fine sandy loam with level to steep slopes (Ressel 1997). The dominant vegetation consists of redberry juniper, sand sage *Artemisia filifolia*, side oats grama *Bouteloua curtipendula*, blue grama *Bouteloua gracilis*, little blue stem *Schizachyrium scoparium* var. *frequens*, netleaf hackberry *Celtis reticulata*, honey mesquite *Prosopis glandulosa*, lotebush *Ziziphus obtusifolia* and yucca *Yucca* spp.

Supplemental feeding

Milo was used as supplemental feed because of its energetic content (Robel and Arruda 1986) and is readily selected

by bobwhite (Michael and Beckwith 1955, Whitelaw et al. 2009). Larson et al. (2012) reported that captive bobwhites selected milo at a rate of 81% and 913% greater consumption when compared to a native seed mixture during single and multiple offering experiments. We distributed milo biweekly with a modified trip hopper range cattle feeder (T & S manufacturing, Jermyn, Texas, USA) along predetermined routes at ~ 69.1 kg km⁻¹ starting 15 September 2010 and continued year-round until 30 September 2012 (Buckley et al. 2015). Milo was broadcast to the right side of the road at a distance of ~ 0.3 m to 18 m throughout potential quail habitat.

The first year of the study, two of eight units were designated as controls units, while the remaining units received supplemental feed. We switched the two control units in year 2, with their adjacent unit and added a third control unit to minimize any potential habitat bias (Fig. 1).

Capture

We captured bobwhites using funnel traps (Stoddard 1931) baited with milo on 1 October and continued until at least 90 females (45 per treatment and control units) were fitted with radio transmitters. We determined age and sex of the birds by plumage characteristics and wings (Leopold 1939, Petrides and Nestler 1952, Rosene 1969). Each quail was weighed to the nearest gram. We placed a 7.0 g necklace style radio transmitter with a mortality sensor (American Wildlife Enterprises, FL, USA) on female bobwhites weighing > 150 g (White and Garrott 1990).

Nesting

We monitored females for nesting activity from 30 March – 30 September. Nesting period for bobwhites in north-west Texas range from 15 April – 15 September, with peak breeding in June–August (Lehmann 1984, Cox et al. 2005). We located all females 3–4 days week⁻¹ continuously though the end of September. We used homing telemetry technique (Mech 1983, White and Garrott 1990, Samuel and Fuller 1994) to monitor each hen. We homed to within ~ 50 m of a radio-marked hen using the telemetry receiver's (R-1000 digital receiver; Communications Specialist, Orange, CA, USA) gain to narrow down the precise location without flushing the hen. A female located two consecutive telemetry sessions in the same location was assumed to have initiated incubation (Burger et al. 1995) or creating a nest. If a hen was assumed to be nesting or creating a nest we monitored that individual daily. When the female was detected away from a possible nest site, we attempted to find the nest. We documented number of eggs and recorded the geographic coordinates with a Garmin eTrex Legend GPS (Garmin International, Inc., KS, USA) for the nest bowl. We used a digital caliper to measure length and width of eggs to the nearest hundredth of a millimeter for egg volume estimates (Hoyt 1979). We measured the average clutch egg volume (cm³) of each nest attempt (Moss et al. 1980). We floated all eggs to estimate a hatch date (Westerskov 1950). We calculated nest initiation date by using the difference between the onset of incu-

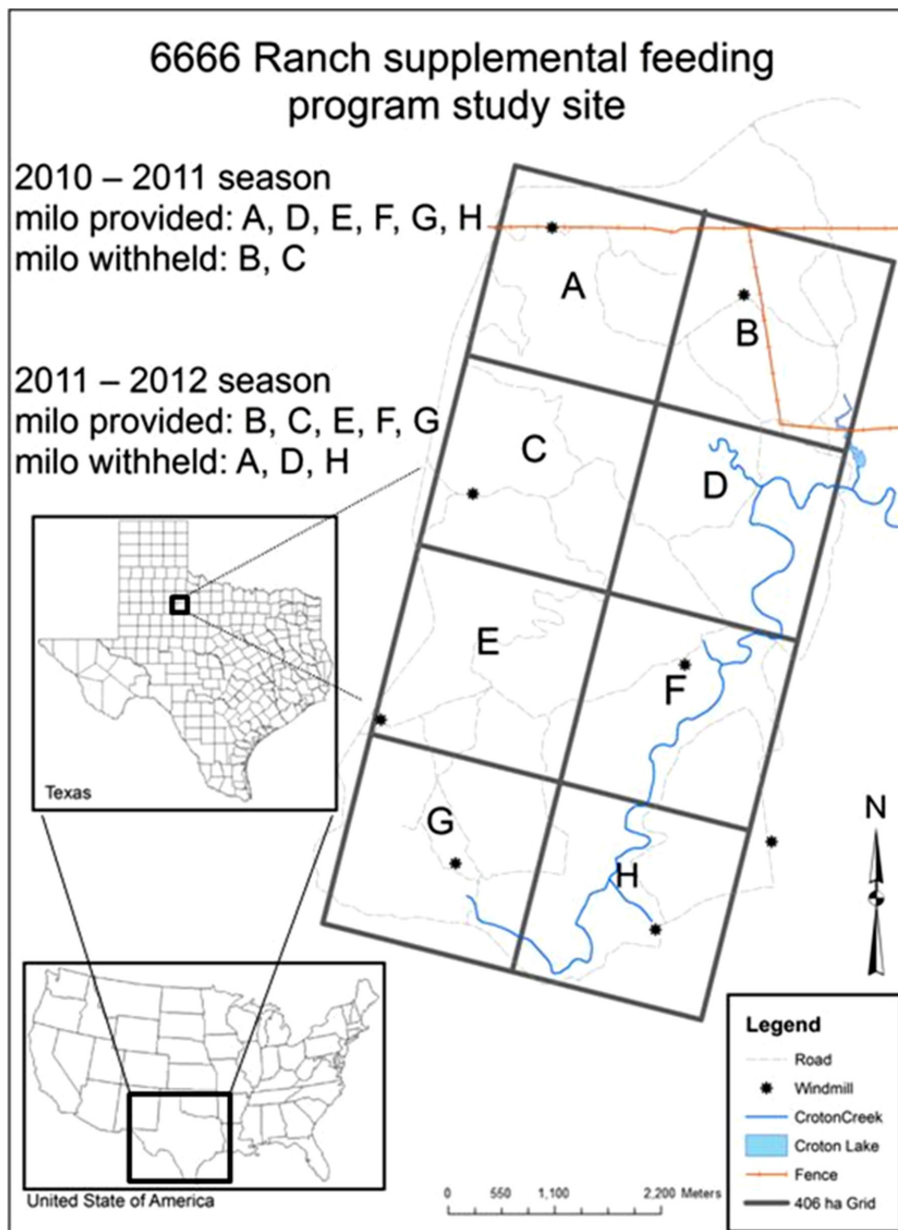


Figure 1. Study site for nesting bobwhite quail *Colinus virginianus* during a supplemental feeding study during the spring and summer of 2010 and 2011 in the Rolling Plains, King County, TX, USA.

bation date and 1.2 times the clutch size (Roseberry and Kilmstra 1975). Nesting females were monitored daily to ensure continuance of incubation. Once the female moved away from the nest site after the estimated hatch date, we investigated the nest bowl and determined the fate of the eggs (i.e. hatched, unhatched). We defined a nesting season as the time from the first known egg laid for a nest by a transmittered hen until the last known incubated nest was completed.

We classified nests as successful (> 1 egg hatch) or unsuccessful. Unsuccessful were classified as abandoned or depredated. When a female attempted to re-nest after nest failure or establishment of a new nesting event; we considered it a separate nesting event and added it to the nest survival estimates.

Statistical analysis

We used the nest survival model in Program MARK (White and Burnham 1999, Dinsmore et al. 2002) to assess nest survival between control and treatment females against seven a priori candidate models (Table 1). We chose the nest survival model because it allows for flexibility in modeling due to ‘ragged’ data for nest survival rates. We used Akaike’s information criterion for small sample sizes (AIC_c), changes in AIC_c and ΔAIC_c values, and Akaike weights (AIC_w) to evaluate model performance and select the best approximating model (Burnham and Anderson 2002). We did not incorporate a goodness of fit test (i.e. χ^2) because the models are saturated (i.e. one parameter per each encounter history) fits the data exactly (Dinsmore et al. 2002, Cooch and White

Table 1. Program MARK output for bobwhite *Colinus virginianus* nest survival model during a supplemental feed study for the breeding season of 2011 and 2012 in the Rolling Plains, King County, TX, USA.

Model	K ^a	AIC _c ^b	Δi ^c	ω _i ^d
S(.) ^e	1	242.3	0.0	0.46
S(.)+treatment	2	244.3	2.0	0.16
S(.)+year	2	244.4	2.0	0.16
S(.)+attempt1+attempt2	3	246.2	3.8	0.06
S(.)+year3treatment	3	246.3	3.9	0.06
S(.)+year+treatment	3	246.4	4.0	0.06
S(.)+treatment+year+attempt1+attempt2 ^f	5	250.2	7.8	0.00

^ano. of variables

^bAkaike's information criterion corrected for small sample size

^cchange in AICc values between current model and model with lowest AICc value

^dAkaike wt (sum of all weights=0.99)

^econstant survival over time

^fglobal model

2014, Devineau et al. 2014). We included a global model that incorporated variation in nest success between years, treatments and nesting attempts. A competing model was determined by those with ΔAICc values of < 2. Based on high degree of model uncertainty within our candidate sets (i.e. top model with AICω < 0.90), we averaged across our model candidate sets to obtain a robust estimate for model parameters (Burnham and Anderson 2002). We estimated daily survival rates for treatment and control units for the 2011 and 2012 nesting seasons however; no a priori model sets were tested using this data (Table 2). Nest survival was estimated by raising the daily nest survival (β) to the 24th power (24 is based on the average nesting length in days for bobwhite quail) (Rotella 2012).

We calculated nest per hen (total nests/available radio-marked hens on 15 April) as a measure of productivity for treatment and control units (Palmer et al. 2012). We

Table 2. Linear mixed model to assess support of covariate variables [clutch size, nest attempt (initial nest or re-nesting after success or abandonment), monthly precipitation, clutch size, and year] on bobwhite *Colinus virginianus* egg volume and treatment effects during a supplemental feed study for the breeding season of 2011 and 2012 in the Rolling Plains, King County, TX, USA.

Model	K ^b	AIC _c ^c	Δi ^d	ω _i ^e
CV~Precip+(Hen)	5	163.97	0.00	0.55
CV~(Hen)	4	166.46	2.49	0.16
CV~Year+Precip+(Hen)	6	167.08	3.11	0.12
CV~(Hen)+Clutch	5	167.97	4.01	0.07
CV~(Hen)+Year	5	169.53	5.56	0.03
CV~Treat+(Hen)	5	170.03	6.06	0.03
CV~(Hen)+(Year × Treatment)	5	170.03	6.07	0.03
CV~Treat+(Hen)+Clutch	6	171.68	7.72	0.01
CV~Treat+(Hen)+Clutch+Year	7	174.34	10.37	0.00
CV~Treat+(Hen)+Clutch+Year+Precip ^f	8	174.54	10.57	0.00

^a CV=clutch volume; Treat=treatment; (Hen)=hen for each clutch and nesting attempts (nested random intercept); Precip=monthly precipitation; Clutch=clutch size; Year=2011–2012 nesting season

^b no. of variables

^c Akaike's information criterion corrected for small sample size

^d change in AICc values between current model and model with lowest AICc value

^e Akaike wt (sum of all weights=0.99)

^f global model

also estimated total net productivity for females (\hat{P}). The estimator for \hat{P} is:

$$\hat{P} = H_1 \times CS \times HR$$

where \hat{P} is the number of chicks per female; H_1 is the number of successful nest hatched per total number of females; CS is the average clutch size per treatment or control; and HR was the nest success rate estimated by using nest survival model from program MARK (Skalski et al. 2005).

We used Welch's t test in program R (<www.r-project.org>) to compare average intra-clutch egg volume between treatments and years. Welch's two-sided paired t test was chosen for unequal variances and unequal sample sizes (De Winter 2013) as well as the robustness for small sample size. Due to the low number of adults captured during the first year and a lack of young recruitment during the second year, we could not compare differences between ages. Egg volume was calculated as follows:

$$V = Kv \times (L \times B)^2$$

where (Kv) represents the volume coefficient; (L) the length of egg (mm); (B) the maximum width (mm).

Due to the lack of information on bobwhite quail egg volume, we chose to use $Kv=0.51$. Westerskov (1950) and Hoyt (1979) applied $Kv=0.51$ for measuring egg volumes for a wide array of avian species such as pheasants *Phasianus* spp. We pooled clutch egg volume measurements across years due to the low sample size on control units during the 2011 nesting season. We used linear mixed model to assess support of covariate variable on egg volume and treatments. We chose a linear mixed model approached because our data was normally distributed (Zuur et al. 2009). Covariates chosen for analysis were clutch size, monthly precipitation, clutch size and year (2011/2012). We obtained monthly precipitation from the Texas Tech University West Texas Mesonet for Guthrie, TX; in King County (<www.mesonet.ttu.edu/site_info.html>, accessed on 13 January 2013). We used the LMER function in the lme4 package (Bates et al. 2015) in R to assess covariate effects on clutch volume and treatments. Hens and nesting attempts were considered nested random effect variable because hens re-nested several times in one season. We designated clutch size as the response variable in our models. We used AICcmodavg and MuMIn packages in program R for model selection and model averaging estimates. We then used the criteria above to evaluate model performance and select for the best approximating model.

Results

We captured 196 bobwhite females (78 treatment [52: 2010–2011; 26: 2011–2012], 118 control [69: 2010–2011; 49: 2011–2012]) from fall 2010 to spring 2012. Bobwhites produced 86 [2011: 35 (treatment: 31; control: 4); 2012: 52 (treatment: 33; control: 18) total nests over the duration of our study. The 2011 nesting season occurred during a significant drought (12.16 cm rainfall from October 2010

to September 2011 [Texas Tech Univ. West Texas Mesonet King County raw data]). Nests per hen was 0.86 (n=36 hens, SE=0.10) for treatment units and control units 0.15 (n=26 hens, SE=0.14) in 2011 (Fig. 2). During the 2012 nesting season, the study site received ~ 55.8 cm of rainfall from October 2011 to September 2012 (Texas Tech Univ. West Texas Mesonet King County raw data). All females attempted at least on nest during the 2012 breeding season. Treatment sites generated 1.60 nest per hen (n=20 hens, SE=0.21) while control sites had 0.81 nest per hen (n=22 hens, SE=0.16) (Fig. 2). Total net productivity estimates for each year showed more chicks per hen were produced on treatment sites [$\bar{P}=2.34$, SE=0.04 (2011); $\bar{P}=5.75$, SE=0.12 (2012)] when compared to control units [$\bar{P}=0.61$, SE=0.001 (2011); $\bar{P}=3.47$, SE=0.13 (2012)]. The earliest average nest initiation date was estimated to be 23 April 2011 (n=6, SE=1.13) and 14 April 2012 (n=9, SE=5.29) for hens on treatment units while hens on control started a few days later 25 April 2011 (n=2, SE=0) and 16 April 2012 (n=6, SE=0.54). The average end date for nest initiations were different for treatment [4 June 2011 (n=5, SE=3.85); 2 August 2012 (n=6, SE=11.03)] and control [19 May 2011 (n=2, SE=1.96), 1 June 2011 (n=4, SE=15.21)] units, respectively. Average re-nesting attempts for treatment sites were 13 June 2011 (n=5, SE=4.24) and 3 July 2012 (n=8, SE=11.95). No hen on control sites attempted to re-nest in 2011 while during 2012 re-nests were depredated before we could estimate incubation dates.

Even though all radio-marked females attempted nests in 2012, females on treatment units produced 19 re-nests compared to only three re-nests on control units. Some females on treatment units attempted re-nesting twice during the 2011 nesting season while no control females attempted to re-nest. During the 2012 nesting season, treatment site females attempted 19 re-nesting events which included five triple re-nests while control unit females only attempted three re-nest events. All re-nesting females in the 2011 breeding season occurred following nest failures, however we found females on treatment units re-nested 13 times after successfully hatching the previous clutch; while only a single female on control units re-nested following a successful brood fledge. Three females on supplemental feed units

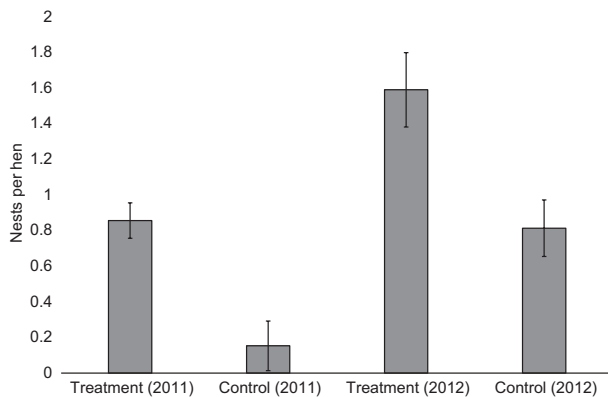


Figure 2. Nest per hen estimates for female northern bobwhites *Colinus virginianus* during a supplemental feeding study from April–September 2011–2012 in the Rolling Plains, King County, TX, USA.

attempted and successfully hatched three clutches during the 2012 breeding season. During the 2011 nesting season, all re-nesting attempts followed nest failures.

Nest success estimates were similar between treatment [(36.8%, SE=0.01, 95% CI=0.17–0.56 (2011)); 41%, SE=0.01, 95% CI=0.20–0.61 (2012)] and control [41%, SE=0.01, 95% CI=0.02–0.92 (2011); 56.8%, SE=0.02, 95% CI=0.11–0.58 (2012)] across both breeding seasons, respectively. The two generic models were the only models with $\Delta AICc < 2$ (Table 1). The data did not have a high level of support for models that incorporated nest success due to treatment effect ($\beta=-0.03$, SE=0.40, 95% CI=-0.85–0.75). Based on our model averaged estimate across all candidate models only 6.18% ($\beta=0.003$, SE=0.004, 95% CI=-0.004–0.011) of the variation in our data set can be explained by covariates in relations to nest survival of bobwhites. Average clutch size for treatment and control for 2011 and 2012 were 12.20 (SE=0.77), 12.20 (SE=0.96) and 13.7 (SE=0.93), 12.2 (SE=1.82), respectively. We pooled clutch size for both treatment and control across years due to the low sample size on control units during the 2011 breeding season. There was no difference in pooled average clutch size between treatment or control nests ($t=-0.37$, $df=27$, $p=0.70$; treatment units=12.2 [n=62, SE=0.6]; control units=12.5 [n=21, SE=1.5]). We measured the average intra-clutch egg volume (cm^3) for 50 treatment and 20 control bobwhite clutches during the 2011 and 2012 nesting season. We did not measure the egg volume of four nest due to depredation before the nest was discovered. We found each nest bowl as soon as the hen was detected away from the potential nest site. Egg fragments were found at each site to confirm a nest was present. We removed nine additional nests (n=1 treatment 2011; n=7 treatment and one control 2012) from egg volume estimates due to a malfunction with the digital calipers. We pooled intra-clutch egg volumes across years due to small sample sizes during the first breeding season. The average intra-clutch egg volumes showed no difference between control ($V=8.77 cm^3$, SE=0.30) and treatment ($V=8.83 cm^3$, SE=0.20) units ($t=0.50$, $df=37$, $p=0.61$).

Based on our model selection criteria, the top model suggested monthly precipitation influenced the intra-clutch egg volume for bobwhite hens ($\Delta AICc < 2$; $\sum AIC \omega=0.67$; Table 2). According to our model averaged estimates across all candidate models, precipitation ($\beta=0.07$, SE=0.02, 95% CI 0.03–0.10) can explain the variation observed in our data set for bobwhite intra-clutch egg volumes. Again, given our model averaged estimates for the candidate model sets, our data did not have a high level of support for models that incorporated treatment as a potential effect for intra-clutch egg volume ($\beta=-0.06$, SE=0.20, 95% CI=-0.45–0.33).

Discussion

By providing bobwhites access to widely broadcast supplemental feed, our results demonstrate a positive impact on nesting attempts and nesting duration for two consecutive breeding seasons. We documented a higher nest per hen ratio for radio-marked females with access to broadcast food supplementation when compared to hens on control units

across both years of our study. The 2011 nesting season occurred during a significant drought (i.e. 12.6 cm of precipitation) period which caused all but four hens on control units to forgo nesting when most hens on treatment units attempted to nest and even to re-nest. We hypothesize the lack of breeding on control units was due to a dearth of naturally occurring food during the drought of 2011. Previous research has shown that ring-necked pheasants delayed egg production when their diet was controlled or had a reduced energetic intake early in the breeding season (Barrett and Bailey 1972). Our research also supports the assumption of a nutritional benefit from broadcasting supplemental feed by having a longer average nesting season length (average ~ 16 days for 2011 and ~ 31 days for 2012) and a higher total net productivity estimate for treatment site. We did not examine individual body condition (i.e. body mass) of nesting hens on treatment or control units during nesting season because of the potential added stress of recapture or researcher induced nest failure/abandonment. However, a previous study noted a significantly higher body mass of bobwhites in areas where whole milo was broadcast along designated feeding routes every two-weeks in north Florida (Whitelaw et al. 2009). The potential cause for the extended nesting season could be hens on treatment units have access to higher food resources during a time when natural food availability was declining (Robb et al. 2008). Our data is further supported by ongoing research in north Florida that found hens with access to supplemental feeding being broadcast into vegetation were nesting longer than hens without access to this supplemental feed (Tall Timbers Research Station; <www.talltimbers.org/food-supplementation>).

A potential concern with the differences in nesting attempts might be due to females brooding successful nests or having higher nest failure rate on either treatment or control sites. We found nest failure rates were similar between treatments. Five females on treatment units successfully hatch their third nest following a previously successful hatch and brooding of their first attempt and a depredated second nest. No female on control units attempted a second nest after successfully fledging their first brood during the second year of the study.

Our data did not support the prediction that females with access to supplemental feed would have larger intra-clutch egg volumes or larger clutch sizes than control units during the 2011–2012 nesting seasons. Egg volumes from our study were similar to volumes documented for domesticated Japanese quail *Coturnix coturnix* (8.80 cm³; SE=0.67), a quail similar to the bobwhite, during a multi-species egg characteristic study (Paganelli et al. 1974). Even though our data showed supplemental feed had little influence on intra-clutch egg volumes our models did provide significant evidence for precipitation as driving factor on bobwhite egg volumes. Yet, it is important to note that our sample size on control sites (n = 4 nests) during the 2011 nesting season made it difficult to draw meaningful conclusions between years.

If hens with access to supplemental feed can maintain sufficient body condition to produce average size clutches throughout the breeding season they could potentially produce enough chicks to mitigate or reduce drastic environmental effects. Our data provides evidence for such an assumption based on our total net productivity estimates

where bobwhite hens on treatment sites were able to produce more chicks per hen during a drought and normal year of precipitations than hens on control units. It was documented that pheasants with access to supplemental feed provided by densely populated feeders were in better physical condition to attempt a second nest attempt following a predation event than hens on control sites in Great Britain (Hoodless et al. 1999). We found that hens with access to supplemental feed can produce more nests than control birds under extreme environmental stressors. It has been noted that wild quail in the southwestern region of North America have limited reproductive success during years of little rainfall (Cain and Lien 1985). However, our data supports the potential benefit of increased nesting attempts and nesting season length during a drought and wet year in the arid region of west Texas. This increase in nesting attempts has been documented during a long-term research project in Florida when distributing supplemental feed (i.e. milo) prior to and during nesting season (Tall Timbers Research Station; <www.talltimbers.org/food-supplementation>). Based on our positive result on nesting and the ongoing research in north Florida on providing bobwhites supplemental feed by broadcasting milo throughout usable quail habitat could potentially help mitigate population crashes after or during a drought. Following the drought of 2011, we documented 0.88 more nests per hen on treatment units when compared to control units. With these increased nesting attempts a population of bobwhite could recover faster than quail without supplemental feed following periodic droughts with the hope of increasing potential chick recruitment into the population.

Management implications

Our research provides support for positive impacts on nesting dynamics when supplemental feed was distributed into roadside vegetation prior to and during nesting season for bobwhites. It was shown bobwhites had a higher estimated total net productivity when supplemental feed was provided during and after drought conditions. Yet it is important to note broadcasting supplemental feeding into the roadside vegetation should not be the sole management technique implemented in the hopes of maintaining bobwhite populations. Providing supplemental feed for bobwhites should be used only in addition to other proper habitat and harvest management recommendations. Even though our data provides positive implications for providing supplemental feed for nesting bobwhites we do recognize that our sample sizes might reduce our statistical power to analyze certain aspects of nesting, so we advocate for additional research in this field of study to increase our knowledge base for providing sustainable management options for bobwhite populations throughout their range.

Acknowledgements – We thank the owners and managers of the 6666 Ranch for allowing us to conduct this research. We also thank the graduate and undergraduate students who devoted their time to this research project. We would like to thank the editors and reviewers who helped to increase the quality of this manuscript.

Funding – Our research was funded by the Burnett Foundation, Quail First, and the 6666 Ranch. We also would like to thank all

the Quail-Tech Alliance board members and anchor ranches for additional support and funding.

Permits – Our research was authorized by Texas Parks and Wildlife scientific collection permit number SPR-1005-1521. Additionally, all aspects of this project were in accordance with Texas Tech University Animal Care and Use committee permit number 09047-10.

References

- Andes, A. K. et al. 2012. Use of a thermal camera to aid in capturing northern bobwhite quail chicks. – *Wildl. Soc. Bull.* 36: 371–375.
- Bates, D. et al. 2015. Package ‘lme4’, ver. 1.1-10. – R Foundation for Statistical Computing, Vienna.
- Barrett, M. W. and Bailey, E. D. 1972. Influence of metabolizable energy on condition and reproduction of pheasants. – *J. Wildl. Manage.* 36: 12–23.
- Burger, L. W. et al. 1995. Survival and cause-specific mortality of northern bobwhite in Missouri. – *J. Wildl. Manage.* 59: 401–410.
- Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference, a practical information-theoretic approach, 2nd edn. – Springer.
- Buckley, B. R. et al. 2015. Effects of broadcasting supplemental feed into roadside vegetation on home range and survival of female northern bobwhite. – *Wildl. Soc. Bull.* 39: 301–309.
- Cain, J. R. and Lien, R. J. 1985. A model for drought inhibition of bobwhite quail (*Colinus virginianus*) reproductive systems. – *Comp. Biochem. Physiol.* 4: 925–930.
- Cain, J. R. et al. 1982. Effects of varying dietary phosphorus on breeding bobwhites. – *J. Wildl. Manage.* 46: 1061–1065.
- Christians, J. K. 2002. Avian egg size, variation within species and inflexibility within individuals. – *Biol. Rev.* 77: 1–26.
- Cooch, E. and White, G. (eds) 2014. A gentle introduction to Program MARK, 9th edn. – <www.phidot.org/software/mark/docs/book/>. Accessed on 23 Sep 2014.
- Coulson, J. C. 1963. Egg size and shape in the Kittiwake and their use in estimating age composition of populations. – *Proc. Zool. Soc. Lond.* 140: 211–227.
- Cox, S. A. et al. 2005. Reproduction by northern bobwhites in western Oklahoma. – *J. Wildl. Manage.* 69: 133–139.
- De Winter, J. C. F. 2013. Using the Student's *t* test with extremely small sample sizes. – *Pract. Assess. Res. Eval.* 18: 1–12.
- Devineau, O. et al. 2014. Increased flexibility for modeling telemetry and nest survival data using the multistate framework. – *J. Wildl. Manage.* 78: 224–230.
- Dinsmore, S. J. et al. 2002. Advanced techniques for modeling avian nesting. – *Ecology* 83: 3476–3488.
- Doerr, T. B. and Silvy, N. J. 2002. Effects of supplemental feeding on northern bobwhite populations in south Texas. – *Proc. Natl Quail Symp.* 5: 233–240.
- Draycott, R. A. H. et al. 1998. Effects of spring feeding on body condition of captive-reared ring-necked pheasants in Great Britain. – *J. Wildl. Manage.* 62: 557–563.
- Frye, E. O., Jr. 1954. Studies of automatic quail feeders in Florida. – *Trans. N. Am. Wildl. Conf.* 19: 298–315.
- Galbraith, H. 1988. Effects of egg size and composition on the size, quality, and survival of lapwing *Vanellus vanellus* chicks. – *J. Zool.* 214: 383–398.
- Guthery, F. S. et al. 1988. Reproduction of northern bobwhites in semiarid environments. – *J. Wildl. Manage.* 52: 144–149.
- Guthery, F. S. et al. 2004. Effects of feeders on dispersion and mortality of bobwhites. – *Wildl. Soc. Bull.* 32: 1248–1254.
- Henson, K. D. et al. 2012. Species visitation at free-choice quail feeders in west Texas. – *Wildl. Soc. Bull.* 36:735–740.
- Hoodless, A. D. et al. 1999. Effect of supplementary feeding on territoriality, breeding success and survival of pheasants. – *J. Appl. Ecol.* 36: 147–156.
- Hoyt, D. F. 1979. Methods for estimating volume and fresh weight of bird eggs. – *Auk* 96: 73–77.
- Jenkins, D. et al. 1967. Population fluctuations in the red grouse (*Lagopus scoticus*). – *J. Anim. Ecol.* 36: 97–122.
- Lack, D. 1950. The breeding season of European birds. – *Ibis* 92: 288–316.
- Lack, D. 1966. Population studies of birds. – Oxford Univ. Press.
- Lack, D. 1968. Ecological adaptations for breeding in birds. – Methuen and Co.
- Larson, J. A. et al. 2012. Preference and nutrition of quail breeder 16, common agricultural feeds, and a mix of native seeds as northern bobwhite food. – *Proc. Natl Quail Symp.* 7: 92–100.
- Lehmann, V. W. 1953. Bobwhite population fluctuations and vitamin A. – *Trans. N. Am. Wildl. Conf.* 18: 199–246.
- Lehmann, V. W. 1984. The bobwhite in the Rio Grande Plain of Texas. – Texas A & M Univ. Press.
- Leopold, A. S. 1939. Age determination in quail. – *J. Wildl. Manage.* 3: 261–265.
- Massaro, M. et al. 2002. Investigation of interacting effects of female age, laying dates and egg size in yellow-eyed penguins (*Megadyptes antipodes*). – *Auk* 119: 1137–1141.
- Martin, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. – *Annu. Rev. Ecol. Syst.* 18: 453–487.
- Mech, D. L. 1983. Handbook of animal radio-tracking. – Univ. Minnesota Press.
- Michael, V. C. and S. L. Beckwith. 1955. Quail preference for seed of farm crops. – *J. Wildl. Manage.* 19: 281–296.
- Moss, R. et al. 1980. Clutch size, egg size, hatch weight and laying date in relation to early mortality in red grouse (*Lagopus lagopus scoticus*) chicks. – *Ibis* 123: 450–462.
- Narushin, V. G. and Romanov, M. N. 2002. Egg physical characteristics and hatchability. – *World's Poultry Sci. J.* 58: 297–303.
- Narushin, V. G. et al. 2002. Relationship between pre-incubation egg parameters and chick weight after hatching in layer breeds. – *Biosyst. Eng.* 83: 373–381.
- Nestler, R. B. et al. 1944. Protein requirements of breeding bobwhite quail. – *J. Wildl. Manage.* 8: 284–289.
- Paganelli, C. V. et al. 1974. The avian egg: surface area, volume and density. – *Condor* 76: 319–325.
- Palmer, W. E. et al. 2012. Survival and reproduction of parent-reared northern bobwhites. – *Proc. Natl Quail Symp.* 7: 64–71.
- Pattee, O. H. and Beasom, S. L. 1979. Supplemental feeding to increase wild turkey productivity. – *J. Wildl. Manage.* 43: 512–516.
- Perrins, C. M. 1970. The timing of birds' breeding seasons. – *Ibis* 112: 242–255.
- Petrides, G. A. and Nestler, R. B. 1952. Further notes on age determination in juvenile bobwhite quails. – *J. Wildl. Manage.* 16: 109–110.
- Ressel, D. D. 1997. Soil survey of King County, Texas. – US Dept of Agriculture, Natural Resource Conservation Service.
- Robb, G. N. et al. 2008. Winter feeding of birds increases productivity in the subsequent breeding season. – *Biol. Lett.* 4: 220–223.
- Robel, R. J. and Slade, N. A. 1965. The availability of sunflower and ragweed seeds during fall and winter. – *J. Wildl. Manage.* 29: 202–206.
- Robel, R. J. and Arruda, S. M. 1986. Energetics and weight changes of northern bobwhites supplemental feed six different foods. – *J. Wildl. Manage.* 50: 236–238.

- Roseberry, J. L. and Kilmstra, W. D. 1975. Annual weight cycles in male and female bobwhite quail. – *Auk* 88: 116–123.
- Rosene, W. 1969. The bobwhite quail – its life and management. – Rutgers Univ. Press.
- Rotella, R. 2012. Nest survival models. – In: Cooch, E. and White, G. (eds), Chapter 17: Program MARK: a gentle introduction, 11th edn. < www.phidot.org/software/mark/docs/book/ >.
- Samuel, M. D. and M. R. Fuller. 1994. Wildlife radiotelemetry. – In: T. A. Bookout (ed.), Research and management techniques for wildlife and habitats. The Wildlife Society: Bethesda, MD, USA, pp. 370–418.
- Serventy, D. L. 1967. Aspects of the population ecology of the short-tailed shearwater (*Puffinus tenuirostris*). – Proc. 14th Int. Ornithol. Congr., pp. 165–190.
- Skalski, J. C. et al. 2005. Wildlife demography: analysis of sex, age, and count data. – Academic Press.
- Stoddard, H. L. 1931. The bobwhite quail: its habitats, preservation and increase. – Charles Scribener and Sons.
- Townsend, D. E. et al. 1999. Using supplemental food and its influence on survival of northern bobwhite (*Colinus virginianus*). – Wildl. Soc. Bull. 27: 1074–1081.
- Tri, A. N. 2010. Effects of a commercial pelleted ration on wild bobwhite nesting and harvest demographics. – MS thesis, Texas A & M Univ., Kingsville, USA.
- Westerskov, K. 1950. Methods for determining the age of game bird eggs. – J. Wildl. Manage. 14: 56–67.
- White, G. C. and Burnham, K. P. 1999. Program MARK: survival estimation from populations of marked animals. – Bird Study 46 Suppl., pp. 120–138.
- White, G. C. and Garrott, R. A. 1990. Analysis of wildlife radio-tracking data. – Academic Press.
- Whitelaw, R. E. et al. 2009. Effects of supplemental feeding on winter diet and body mass of northern bobwhites. – Proc. Natl Quail Symp. 6: 282–289.
- Zuur, A. F. et al. 2009. Mixed effects models and extensions in ecology with R. – Springer.