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Male Call counts, Nesting Activity & Fall Density

Summer Male Call Index Relative to Nesting Chronology and Autumn Density of the Northern Bobwhite

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We studied breeding season male call counts and breeding behavior of the Northern Bobwhite (*Colinus virginianus*) to determine the relationship between male calling activity and nesting chronology. Additionally, we examined the relationship between breeding season call counts and fall population size. Standardized call count routes were conducted on 6 different sites located in southwest Georgia and north Florida during the breeding season months (1 Apr - 31 Sep) in 2001 and 2002. An information theoretic approach was used to evaluate a set of 7 candidate, linear-mixed models describing breeding season calling of bobwhite males. Of the candidate models, the model in which call counts depended on year and a quadratic effect of the number of incubating hens was the best approximating model, suggesting that the percentage of incubating hens had the greatest influence on activity of calling males. We also used multiple linear regression models to predict autumn northern bobwhite abundance from mean numbers of calling male bobwhites detected during the breeding season. Peaks in male calling activity occurring during June and July demonstrated a strong relationship (R^2 = 0.987) with autumn population size, suggesting breeding season call counts were useful indices of autumn bobwhite abundance.

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Key words: *Colinus virginianus*, mortality, northern bobwhite, southeastern USA, survival, telemetry

Introduction

The Northern Bobwhite (*Colinus virginianus*); hereafter bobwhite, uses a wide variety of vocalizations to communicate between coveys, among coveys, and individually. Stoddard (1931) defined these vocalizations based on group movement, food finding, avoidance of enemies, and reproduction. The purpose of the distinctive "bobwhite" call, from which the species receives its common name, is thought to serve both breeding and territorial functions (Stokes et al. 1994, Rosene 1969, Stoddard 1931, Brennan 1999, Guthery 2000); however, the utility of the call is less understood.

During the past 5 decades, the male call count index (the average number of males heard per stop) has been evaluated as a population monitoring technique on several occasions (Ellis and Thomas 1972, Hansen and Guthery 2001, Rosene 1969, Robel 1969, Speake and Haugen 1960, Wells and Sexon 1982). However, there is apparent disagreement as to what the male call count index measures. While some researchers have successfully used summer counts of calling males to index autumn population size (Curtis et al. 1989, Ellis and Thomas 1972, Rosene 1969, Wells and Sexon 1982), others have demonstrated the poor reliability of call counts as predictors of fall bobwhite abundance (Hansen and Guthery 2001, Norton et al. 1961). Rosene (1969) speculated that the number of whistling males was an accurate predictor of fall population size and suggested that the number of whistling males heard corresponded to the number of coveys in the fall. He further proposed that the number of whistling males forecasted the success of fall hunting (Rosene 1969). Curtis et al. (1989) reported a high correla-

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tion (r = 0.94) between male call counts and hunting success. They also found that call counts correlated well with the total number of bobwhites harvested (r = 0.89) in the fall. In contrast, Norton et al. (1961) criticized the use of whistle counts to predict fall populations and, upon meta-analysis of previous works, noted: "It must be concluded that the case for usefulness of numbers of whistling cocks in summer to estimate autumn populations is weak and that a better method is needed." Hansen and Guthery (2001) reported seasonal variation in breeding season calling between years and noted the violation of assumptions required to determine annual trends in population abundance. Speake and Haugen (1960) suggested that the bobwhite call index could be developed into a useful tool for estimating progress of the nesting season while reporting that bobwhite whistling intensity fluctuates with nesting activity and that sharp drops in the call index likely correspond to peaks in hatching. Furthermore, researchers in the southeastern U.S. have noticed seasonal peaks in whistling by males throughout the nesting season and have often assumed a correlation between male calling and nesting activity (W. E. Palmer, Tall Timbers Research Station and D. C. Sisson, Albany Quail Project, personal communication). Stauffer (1993) reported that a more controlled research effort was needed to appropriately understand exactly what call counts measure. Therefore, we studied the calling behavior of bobwhite males on multiple sites in southwest Georgia and north Florida to develop protocols that would lead to improved accuracy and repeatability of data on nesting activity and population abundance derived from call counts. The primary objective of this investigation was to determine what conclusions may be deduced from male whistling during the breeding season and whether male whistling is an accurate estimator of nesting activity and/or fall population size.

Study Area

The study was conducted on 4 private lands in south Georgia and 2 in north Florida. These included 2 study areas (4,858 ha and 8,097 ha) in Baker County, Georgia, 1 (3,644) in Laurens and Bleckley Counties, Georgia and 2 (Tall Timbers Research Station) (1,741 ha) in Leon County, Florida and 1 (1,134 ha) in Thomas and Grady counties, Florida. These sites are in the Upper Coastal Plain physiographic region and characterized by old field, pine forests with relatively low basal area that are intensively managed for bobwhites. Intensive management regimes typically included annual burning, seasonal disking, drum-chopping, mowing, supplemental feeding, and mammalian nest predator control (see (Yates et al. 1995, Sisson et al. 2000*b*,*a*)). Typical field management consisted of autumn and late winter disking to stimulate annual weed and arthropod production. As a result of these intense management regimes, these areas maintained wild bobwhite populations ranging from 1.48 birds/ha to >7.41 birds/ha.

Methods

During March and April of 2001 and 2002, we trapped wild bobwhites using standard, baited funnel traps (Stoddard 1931). We radio-tagged and monitored a minimum of 50 quail (30 females and 20 males) on all sites during 2001 and 2002. Bobwhites were outfitted with a pendant-style radio transmitter (6.4 g) equipped with an activity switch (Holohil Systems Ltd., Ontario, Canada and American Wildlife Enterprises, Monticello, Florida), leg banded, weighed, aged, and released at their capture site. Trapping, handling, and marking procedures were approved by the Auburn University Institutional Animal Care and Use Committee. Beginning April 1, radio-marked bobwhites were monitored $\geq$3 times weekly to determine onset of nesting activity and/or mortality. All bird locations were determined using the "homing" method (Stauffer 1993) and were recorded on aerial photographs. We estimated breeding season (1 Apr - 31 Sep) survival for each site using the Kaplan-Meier product limit method (Kaplan and Meier 1958, Pollock et al. 1989) on a weekly basis. To account for potential capture and radio effects, mortalities occurring within 1 week of radio attachment and release were censored.

Table 1: Descriptive statistics for response (calling males) and predictor variables used in models of breeding male Northern Bobwhite calling activity.

Parameter	n	Mean	SD	Minimum	Maximum
Calling males	260	3.330	2.940	0.000	10.420
Hatching chronology	260	1.260	1.860	0.000	14.000
Pooled survival	260	0.660	0.200	0.230	1.000
Incubating hens	260	0.170	0.160	0.000	0.710

Radios lost due to unknown reasons also were censored on the day following the last day of normal contact.

We assumed birds observed in the same location on 2 consecutive days to be nesting. We approached inactive hens and marked their location with flagging tape at a distance of 5-10 m and recorded the location on an aerial photograph. We determined the exact nest location and number of eggs when telemetry indicated that the incubating hen was away from the nest. Nests were monitored daily. A successful nest was defined as a nest that hatched ≥1 egg.

Population Indices

Breeding season call counts - We developed a protocol based on previous research of male calling behavior (Curtis et al. 1989, Ellis et al. 1969, Hansen and Guthery 2001, Rosene 1969, Wells and Sexon 1982) to ensure accurate counts and to mitigate the influence of weather (i.e. wind, fog, rain, and cloud cover) on whistling males. Counts of whistling males were conducted along standardized call count routes each week at 5-9 day intervals (1 April through 31 September) during 2001 and 2002. Male calls were counted during the first 2 hours after sunrise [the ″calling optimum″; (Hansen and Guthery 2001, Rosene 1969) on days when the wind velocity was ≤16 kmh and cloud cover was ≤75%. Call count routes were comprised of 12 listening points 0.81 km apart, evenly distributed throughout the study area. The observer stopped and listened for 5 minutes at each point and recorded the start time, the number of whistling males, and climate conditions such as wind speed and direction, cloud cover, and/or fog. The average number of males calling per route was that week's call index. The call count route was run backwards on alternating weeks to decrease bias of optimal calling time and listening point locale.

Autumn population abundance - We used covey call count indices (DeMaso et al. 1992, Seiler et al. 2002, Wellendorf et al. 2004) to evaluate fall bobwhite abundance during 2000-2002. Covey call count surveys were conducted from mid-October to late-November. We used quadrat-sampling and point-count techniques to estimate autumn bobwhite density. The quadrat technique used a 25-ha (500 m x 500 m) quadrat to survey calling coveys. A total of 4 observers were required, with 1 observer positioned along the midpoint of each quadrat side. Observers listened for the "koi-lee" covey calls (Stoddard 1931) given by bobwhites, almost always before sunrise, and recorded the unique number of calling coveys on aerial photographs. When covey calling ended, observers compared their results to determine if a particular covey detected was inside or outside of the quadrat. Coveys detected inside of quadrats were used to estimate density via quadrat-sampling estimators. Each unique covey was plotted on an aerial photograph and flushed using pointing dogs to estimate average covey size. The point-count technique required a single observer to record approximate covey locations. We estimated fall abun-

Table 2: Model selection statistics for candidate regression models used to test competing hypotheses of male northern bobwhite calling behavior.

Model	-2(Log-ℓ)	$AIC_c{}^a$	$\Delta\ QAIC_c^b$	W_i^c	K^d
Year, Inc. hens, Inc. hens^2	459.5	476.1	0.000	0.993	8
Year, Inc. hens, Inc. hens^2, Year*Inc. hens, Year*Inc. hens^2	465.0	485.9	9.800	0.007	10
Year, Hatch chronology	592.3	606.7	130.600	0.000	7
Year, Hatch chronology, Year*Hatch chronology	594.4	611	134.900	0.000	8
Year, Pooled survival	612.3	626.7	150.600	0.000	7
Year, Pooled survival, Year*Pooled survival	614.3	630.8	154.800	0.000	8
Year-only	623.2	635.5	159.400	0.000	6

[a] Akaike's Information Criteria with a small sample bias adjustment.

[b] Akaike weight of evidence that the given model in the set of candidate models is the best model.

[c] Total number of model parameters (includes parameters for estimating intercept and variance).

[d] K is the number of parameters.

dance using point counts via the fixed-radius approach (Wellendorf et al. 2004). Covey-call surveys were adjusted via calling rate estimates (Wellendorf et al. 2004). Additionally, covey-call points and quadrats were randomly distributed across the study areas. Five sites were surveyed with quadrats. The remaining site was surveyed with point counts due to limited numbers of observers.

Analyses

Call count and breeding parameters - We used linear-mixed models [PROC MIXED procedure of SAS ®software (SAS Institute, Inc. 2006)] to estimate effects of site, year, weekly periods during the breeding season, hatching chronology, pooled survival, and incubating hens on mean numbers of calling male bobwhites. Hatching chronology was defined as the number of successful nests that hatched during a given week. The "incubating hens" predictor was defined as the number of hens incubating a nest divided by the number of hens alive (i.e., the proportion of hens incubating a nest). "Pooled survival" was the survival of males and females estimated by the Kaplan-Meier product limit method (Kaplan and Meier 1958, Pollock et al. 1989). There were 6 different sites where data were collected (4 sites in both 2001 and 2002, 1 site in 2001, and 1 site in 2002). Site was treated as a random effect (Littell et al. 1996). Counts of calling males were made for 26 consecutive weeks, April through October, during the breeding seasons of 2001 and 2002. This weekly time trend variable was treated as a random effect nested within sites and years with an autoregressive error structure. An autoregressive error structure was used because we assumed that calling activity among adjacent weekly periods would be more similar than calling activity at weekly periods farther apart (Littell et al. 1996). The predictor variable year was coded as an indicator variable (year 2002 was the baseline year for comparison with 2001) and considered a fixed effect. The fixed effects predictors hatching chronology, pooled survival, incubating hens, and the response variable mean numbers of calling male bobwhites were continuous variables (Table 1). For our analysis, we were most interested in how hatching chronology, pooled survival, and incubating hens affected male bobwhite calling

Table 3: Model coefficients for effects of numbers of incubating hens on calling male.

			95% CI	
Model Parameter	Coefficient	SE	Lower	Upper
Intercept	1.270	0.350	0.580	1.960
Incubating hens	0.660	0.040	0.570	0.740
Incubating hens^2	-0.240	0.030	-0.300	-0.180
Year	-0.360	0.100	-0.570	-0.160

activity during the breeding season.

Evaluation of scatter plots suggested that calling activity had a curvilinear relationship with incubating hens. To facilitate interpretation of regression coefficients, the continuous predictors and the response variable were standardized by unit normal scaling (Montgomery and Peck 1992).

An information-theoretic approach (Anderson et al. 2000, Burnham and Anderson 2002) was used to evaluate a set of 7 candidate models describing breeding season calling of bobwhite males in our study areas. Week and site effects were included in all candidate models. The year variable was also included in all candidate models to control for variation among years. We developed 2 nested models with hatching chronology, 2 nested models with pooled survival, 2 nested models with incubating hens, and a model with year effects only (Table 2). Though some models were nested, the candidate set of models was generally non-nested. The best approximating model in the set of candidate models was determined by Akaike's Information Criteria, adjusted for small sample bias (AIC_c) (Burnham and Anderson 2002). Model likelihoods computed from the PROC MIXED procedure were used to compute AICc and used to compare each candidate model. The model with the lowest AIC_c value was considered to be the best approximating model given the data. The relative plausibility of each model in the set of candidate models was assessed by Akaike weights (W_i) (Anderson et al. 2000, Burnham and Anderson 2002), where the best approximating model in the candidate set has the greatest Akaike weight.

Goodness-of-fit for the most highly parameterized model evaluating effects of hatching chronology, pooled survival, and incubating hens on calling activity was evaluated by residual analysis. Normal probability plots were constructed to evaluate whether serious deviations from normality existed for the most highly parameterized models evaluating effects of hatching chronology, pooled survival, and incubating hens on calling activity. Model residuals were plotted against predicted values and the continuous predictor variables to assess model fit. We further evaluated model adequacy by examination of model mean squared error (MSE).

Call count and autumn abundance - We used multiple linear regression models [PROC REG procedure of SAS ®software (SAS Institute, Inc. 2006)] to predict autumn bobwhite abundance from mean numbers of calling male bobwhites detected during the breeding season. We also controlled for potential variation among sites and years by including these terms in our models. Generally, there were at least 2 relatively high peaks in breeding season calling activity at all sites (see Results), and we used these 2 peaks to separately predict autumn northern bobwhite abundance (Table 4). For the 6 sites, Tall Timbers was coded as the baseline site for comparison

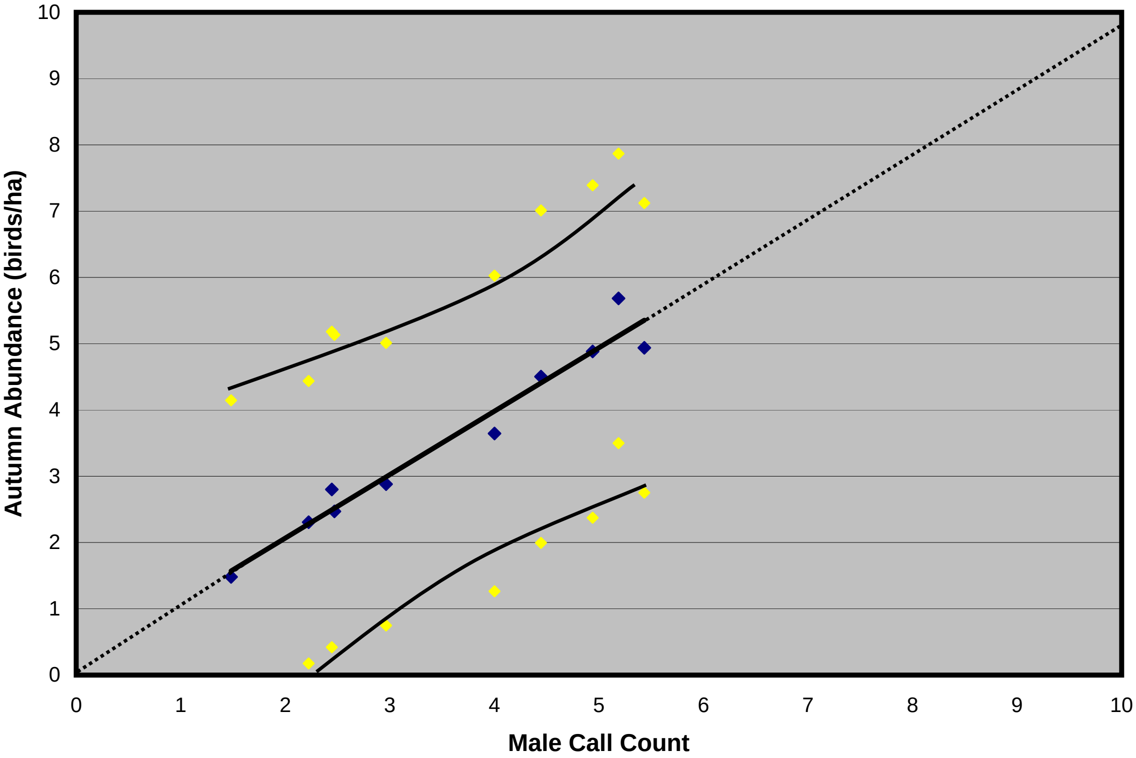

Figure 1: Regression model using the second peak in male calling with plotted prediction limits and confidence intervals for all study sites in Georgia and north Florida, 2001-2002. Dotted line denotes predicted abundance relative to predicted mean male call counts. Regression equation and coefficients: y = 0.20x + 0.22(yr) + 0.23(PBT) + 0.38(PBC) - 1.02(WTHL) + 0.20(PH) + 0.24(CP); R^2 = 0.9867.

with each of the other 5 sites. Year 2002 was coded as the baseline year for comparison with 2001.

Model fit was assessed by model coefficient of multiple determination (R^2) and mean squared error (MSE). Residual analysis was relatively uninformative because there were only 10 observations in each data set. During initial model fitting, no-intercept models of bobwhite abundance predicted from counts of breeding, calling males were found to best fit the data.

Results

Initial whistling of bobwhites occurred in early-April and continued into September. We observed as many as 3 peaks and as few as 1 peak in male calling and nesting activity dependent on year and site; however, generally 1 or 2 peaks occurred for most sites and years. The first peak was fairly consistent and occurred during the 7-9 week periods (mid- to late-May) while timing of the second peak was more variable and occurred during the 11-17 week periods (mid-June to late-July). The first peak yielded more intense calling activity than the second peak; although, the second peak in calling yielded a higher correlation to autumn abundance than the first peak.

Call Count and Breeding Parameters

The examination of residual plots suggested the fit for the most highly parameterized models evaluating effects of hatching chronology, pooled survival, and incubating hens on male calling activity was acceptable. Normal probability plots revealed some slight departure from normality for all of the models, but this departure did not appear to be severe. Estimated MSE for the most highly parameterized model with: 1) hatching chronology was 0.47;

2) pooled survival was 0.49; and 3) incubating hens was 0.26. Based on these model fit diagnostics, we assumed that the fit of the most highly parameterized models evaluating effects of hatching chronology, pooled survival, and incubating hens was acceptable, and the fit of subsequent candidate models also was adequate.

Based on model weights, the year, incubating $hens^2$ model suggested that the percentage of incubating hens had the greatest influence on activity of calling males (Table 2). There was virtually no support for any of the remaining candidate models based on model weights (Table 2). The year, incubating $hens^2$ suggested that calling activity was low when the percentage of incubating $hens^2$ was low to moderate, but calling activity was greatest when percentage of incubating hens was high (Table 3). Based on model selection criteria, pooled survival and hatching chronology were both poor predictors of breeding male calling activity compared to percentage of incubating hens.

Call Count and Autumn Abundance

Autumn bobwhite abundance demonstrated a strong, positive relationship with the mean number of calling males during both the first (MSE = 0.162; R^2 = 0.975) and second peaks (MSE = 0.105; R^2 = 0.987) in breeding season calling (Tables 5 and 6, Figure 1).

Discussion

Documentation of call count initiation and duration vary considerably depending on the study, species, and researcher (Elder 1956, Rosene 1957, Smith and Gallizioli 1965, Robel 1969, Brown et al. 1978, Hansen and Guthery 2001). Our results indicated that the initiation and duration of the call counts are critical to ensuring that peak calling is observed. Several researchers' protocols likely missed some of the valuable calling and nesting peaks we observed, due to late initiation dates and/or early cessation dates of call count surveys (Elder 1956, Rosene 1957, Smith and Gallizioli 1965, Robel 1969, Brown et al. 1978, e.g.). We found a positive relationship between male call counts and nesting activity; however, calling activity seemed to be more a function of within-season timing and nest success. Bennett (1951), Robel (1969), Kabat and Thompson (1963), Hartowicz (1964), Hansen and Guthery (2001), also reported peaks from mid-June to mid-July. Therefore, in contrast to that reported by Rosene (1957), the predictive capability of the male call index should not be based on a random 2-day sampling period; rather, the call count index should be implemented weekly for 6 to 8 weeks (1 Jun to 31 Jul) to determine the peak of calling activity. Additionally, our results suggest the peak occurring in June/July (second peak) was more descriptive of nesting activity, and purported nest success, and therefore may more accurately predict fall population levels. We note that Robel (1969) and Hansen and Guthery (2001) reported peak calling as late as August. These peaks were consistent with our findings; however, they were secondary peaks of smaller magnitude. The timing of these later, smaller peaks may be attributed to annual weather variations as reported by Hansen and Guthery (2001) or may be the result of asynchronous hatching caused by predation of nests and subsequent re-nesting attempts later in the breeding season. This latter pattern is often observed during the nesting season of the northern bobwhite resulting in the well known ”late hatch”.

Speake and Haugen (1960) concluded that bobwhite whistling activity fluctuates with nesting activity and peaks in hatching are preceded by sharp declines in calling. Robel (1969) reported hatching peaks 1 to 2 weeks following peaks of calling. We observed similar patterns in our data where, on several sites, increased hatching followed sharp declines in calling. Furthermore, when peaks in calling and nesting activity continued for several consecutive (3-4) weeks, hatching peaks were less pronounced and distributed over multiple (3-5) weeks. Robel (1969) reported similar results where in one year the whistling peak was short and sharply defined, while the next year the peak was longer and less distinct. Therefore, we surmised that sharp declines in calling and nesting activity indicate an increase in hatch-

Table 4: Descriptive statistics for response (autumn density) and predictor variables used in models of autumn northern bobwhite population density.

Parameter	n	Mean	SD	Minimum	Maximum
Autumn density	10	1.440	0.570	0.600	2.200
Calling males from first calling peak	10	7.080	3.070	1.580	10.420
Calling males from second calling peak	10	6.160	2.630	2.420	9.200

Table 5: Coefficients for regression model of autumn northern bobwhite density predicted from the first peak of breeding season counts of calling male northern bobwhites.

			95% CI	
Model Parameter	Coefficient	SE	Lower	Upper
Calling males from first calling peak	0.240	0.070	0.100	0.380
Site				
CP	-0.100	0.640	-1.350	1.150
PBT	-0.070	0.570	-1.190	1.050
PBC	0.140	0.350	-0.550	0.830
WTHL	-1.520	0.740	-2.970	-0.070
PH	0.420	0.480	-0.520	1.360
Year	-0.290	0.390	-1.050	0.470

ing activity (i.e., successful nesting) and less defined, more prolonged peaks indicate poor nest success.

Bennett (1951), Rosene (1957, 1969) suggested that the whistling male index is a reliable predictor of autumn populations. Conversely, Norton et al. (1961) indicated that such an index cannot accurately predict autumn population size because it lacks information regarding reproductive success and seasonal survival. This criticism appears unjustified because our study found that 2 peaks in breeding season calling were positively related to autumn population size. In fact, when using the second peak in breeding season calling, we observed a very strong relationship (R^2 = 0.9867) between breeding season call indices and autumn population size. These models indicate that the first and second peaks in breeding season call counts were useful predictors of autumn bobwhite abundance in 2 consecutive years at our study sites. However, it is unclear how much these relationships could change outside of year and site in this study. Therefore, the temporal and spatial context must be considered when using the call count index as a management tool for forecasting autumn population levels and subsequently establishing harvest rates.

Management Implications

This study demonstrates that the summer whistling male index of the bobwhite is a potentially useful indicator of breeding season progress

Table 6: Coefficients for regression model of autumn northern bobwhite density predicted from the second peak of breeding season counts of calling male northern bobwhites.

			95% CI	
Model Parameter	Coefficient	SE	Lower	Upper
Calling males from second calling peak	0.200	0.050	0.110	0.290
Site				
CP	0.240	0.430	-0.610	1.080
PBT	0.230	0.390	-0.540	0.990
PBC	0.380	0.260	-0.130	0.890
WTHL	-1.020	0.490	-1.980	-0.060
PH	0.200	0.380	-0.550	0.950
Year	0.220	0.240	-0.240	0.680

and autumn population levels when applied correctly. However, predictive power of the call count on fall population levels should be approached with caution as nest survival and brood survival are not accounted for in the breeding season call count index and tend to fluctuate among years depending on extrinsic factors such as weather and predator dynamics. To ensure accuracy and reliability of the call count, it is imperative to adhere to rigorous protocols to mitigate the effects of weather, site, and seasonal variation. We recommend conducting call counts weekly over a 2-month period (1 June - 31 July), rather than randomly selecting days or weeks within the breeding season, in order to ascertain the peak of calling activity (i.e., peak nesting activity). Call counts should be conducted during the optimal calling hours, within 1 hour after sunrise (Hansen and Guthery 2001), and performed under specific weather conditions as described previously in the ”Methods” section. Further study is needed to determine whether the 6- to 8-week monitoring period, as suggested in this paper, is an adequate measure of nesting activity and whether the peak observed during this period is correlated with fall population size. Our study was conducted on sites where bobwhite populations are stable to slowly increasing, and more research is warranted to determine whether these techniques are valid on low-density sites exhibiting rapid population growth or declines.

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