REPRODUCTION BY NORTHERN BOBWHITES IN WESTERN OKLAHOMA

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Abstract: We studied northern bobwhites (*Colinus virginianus*) in western Oklahoma, USA, during the nesting seasons of 1992–2001. We obtained latitude-specific information on nesting biology and tested hypotheses on the cause of declines in clutch size with progression of the nesting season and on the phenological relation of first, second, and third nesting attempts. For pooled data on bobwhites alive during 15 April–15 September, 64 ± 6.5% of juvenile females ($n = 56$), 90 ± 10.0% of adult females ($n = 9$), 13 ± 4.1% of juveniles males ($n = 68$), and 41 ± 10.7% of adult males ($n = 22$) incubated ≥1 nest. Bobwhites that entered the reproduction period starting on 15 April ($n = 229$) accumulated 203 nesting attempts (male and female incubations), which translated to 1.7 attempts/hen for all hens that entered ($n = 117$) and 3.1 attempts/hen for hens that survived to 15 September ($n = 65$). Overall success for incubated nests (48 ± 2.8%, $n = 331$) was independent of sex-age class and nesting attempt (1, 2, 3), but it declined at a rate of 2.37%/year (95% CL = 1.10–3.64%/year) during the study. Clutch size declined by 1 egg for every 14–20 elapsed days in the nesting season and the rate of decline was independent of incubation attempt (1 or 2); this result suggests that lower clutch sizes later in the nest season were not necessarily a function of re-nesting. Ending of nest-incubation attempts (1, 2, 3) occurred within an 8-day period from 26 August–2 September. Our results implied that early-season nesting cover is a management concern and that high nest success is possible in the absence of nest predator suppression where abundant nest sites occur across the landscape.

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The first documentation of multiple-brooding in northern bobwhites (Sermons and Speake 1987) and the subsequent observance of polyandry in bobwhite populations (Curtis et al. 1993, Burger et al. 1995) have generated a series of studies on the breeding behavior of these birds. The ensuing empirical (Taylor 1991, DeVos and Mueller 1993, Suchy and Munkel 1993) and theoretical (Guthery and Kuvlesky 1998) results have changed biological understanding of reproduction behavior in this species. That is, the hypotheses that bobwhites are monogamous and raise at most 1 brood (Stoddard 1931:492, Leopold 1933:49, Davison 1949:37–38) have been discredited.

Concurrently, research has led to a better understanding of expectations in demographic traits of bobwhite populations as function of geographic location, particularly latitude (Guthery 1997). Bobwhites in northern latitudes tend to be poor survivors and good producers; whereas, bobwhites in southern latitudes tend to be poor producers and good survivors (Guthery et al. 2000). Density dependence seems to act more strongly on reproduction in northern latitudes; whereas, it acts more strongly on fall–spring survival in southern latitudes.

We conducted a 10-year study of bobwhites in western Oklahoma to obtain descriptive data on reproduction for a mid-latitude population and to test 2 hypotheses. First, we assessed reproduction performance (participation by males and females in incubation, per-capita nest attempts relative to populations that started and that started and survived the nesting season, and nest success rates). Second, we assessed seasonal trends in clutch size. This assessment provided data to test the hypothesis that clutch size declines as the nesting season progresses because later nesting attempts represent second or third attempts, presumably associated with smaller clutches than first nest attempts. An alternative hypothesis is that clutch size declines independent of nesting attempt. Finally, we assessed phenology of nest initiation. This assessment provided a test of the hypothesis (modeling assumption) that initiations for first, second, and third attempts end on a common date (Guthery and Kuvlesky 1998).

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STUDY AREA AND METHODS

We conducted our study on the Oklahoma Department of Wildlife Conservation's Packsaddle Wildlife Management Area (6,475 ha) in southern Ellis County, Oklahoma, USA, during October 1991–October 2001. DeMaso et al. (1997) and Townsend et al. (2001) provided information on climate, soils, and vegetation of the study area.

The Packsaddle Area had a diverse predator fauna, none subject to control measures on site. Common raptors included Cooper's hawks (*Accipiter cooperii*), sharp-shinned hawks (*A. striatus*), red-tailed hawks (*Buteo jamaicensis*), and northern harriers (*Circus cyaneus*; DeMaso et al. 1998). Mammalian predators included bobcats (*Lynx rufus*), coyotes (*Canis latrans*), gray foxes (*Urocyon cinereoargenteus*), raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), and swift foxes (*Vulpes velox*).

We captured bobwhites with baited funnel traps (Stoddard 1931:442) and with night-lighting (Labisky 1968) throughout the study. Individuals were classified by sex and age (Rosene 1969:44–54), leg-banded, and fitted with mortality-sensing radio transmitters (Holohil Systems Ltd., Carp, Ontario, Canada; Wildlife Materials Inc., Carbondale, Illinois, USA) weighing <7 g if the bird weighed >150 g. Collar attachment was necklace-style (Shields et al. 1982). We used radio-tagged bobwhites to locate nests as judged from consecutive locations of a bird at the same point. When a nest was found, we counted the numbers of eggs and estimated the date of initiation and hatch. Initiation date was estimated by subtracting $1.2c$ from the nest-location date, where c was the number of eggs upon location (Burger et al. 1995). As date of hatch neared, a subject was monitored ≥2 times/day.

Reproduction Performance

We defined the nesting season as 15 April–15 September. To assess reproduction performance within this period, we created 3 datasets: (1) all bobwhites that entered and survived the nesting season, whether or not they incubated; (2) bobwhites that entered and survived the nesting season and incubated; and (3) bobwhites that entered the nesting season, incubated, and either survived or died. The first dataset was necessary to estimate true reproduction performance in the population by analyzing birds that did and did not incubate. The second dataset provided complete nesting histories for birds that entered and survived the nesting season; we did not analyze data from birds captured during the nesting season because there was no way to identify the incubation attempt (1, 2, or 3). The third dataset provided a means of assessing the reproduction effort relative to surviving birds. Bobwhites that reproduced and died before the end of the nesting season influenced the demographic nature of the standing population at the end of the period.

The sample started with 2,012 bobwhites (1.1 males/female) that were radiomarked and that survived a 14-day conditioning period after capture (Cox et al. 2004). The restrictions that bobwhites were alive at the beginning of the nesting period and that birds captured during the nesting season were excluded from analysis of reproduction performance (though not from estimation of clutch size and nest success), severely truncated that resulting sample size for analyses of reproduction performance. In some years, certain sex-age classes were not represented in the sample. Accordingly, we pooled over the study period and present simple, descriptive statistics on these data. In some cases, we could not estimate uncertainty associated with point estimates of demographic variables (e.g., attempts/hen) because of pooling.

Data for estimating nest success (≥1 chick fledged) came from all bobwhites that entered the laying season and had ≥1 nesting attempt with a known fate. We did not attempt to ascribe nest loss to sources because of ambiguity in identifying cause of loss based on evidence at a nest site (Hernandez et al. 1997, Larivière 1999). Because we knew approximate nest initiation dates, we report the binomial probability of success for incubated nests rather than invoking time considerations (Mayfield 1961).

Clutch Size Trends

For descriptive analysis of clutch size (means and percent hatch of eggs within clutch), we limited data to clutches that hatched, regardless of whether the individual responsible for the hatch survived the nesting season. In estimating trends in clutch size as a function of Julian day, we truncated the data to clutches that hatched for hens that survived the nesting season. These truncations ensured that we knew the number of an incubation attempt and that we had data on complete clutches. We then regressed clutch size on Julian day for first and second incubation attempts (the sample size was too small for third attempts).

Nesting Phenology

Phenological analyses were based on data pooled over all nesting seasons (1992–2001) and were limited to female bobwhites with complete nest histories (alive during 15 Apr–15 Sep inclusive). Bobwhites captured at any time in April were included in the sample. The data were segregated into first, second, and third incubation attempts. Then the cumulative frequency of nest initiations as a function of Julian day was modeled with polynomials for each attempt. The polynomials were differentiated and scaled to probability density functions (pdf) to portray frequency distributions of nest starts in time (Guthery and Kuvlesky 1998). The resulting pdfs were scaled by multiplying each function by the proportion of first, second, and third incubations in the total sample (e.g., the proportion of first starts in the sample × the pdf for first starts). These transformations provided an estimate of the relative importance of incubation attempts to the total nest-incubation effort.

RESULTS

Reproduction Performance

Sixty-four bobwhites entered the nesting season, survived, and incubated, and 155 bobwhites entered the nesting season, survived, and either did or did not incubate (91 bobwhites did not incubate). For the pooled data, 64 ± 6.5% of juvenile females ($n = 56$), 90 ± 10.0% of adult females ($n = 9$), 13 ± 4.1% of juveniles males ($n = 68$), and 41 ± 10.7% of adult males ($n = 22$) incubated ≥1 nest.

Bobwhites that entered and survived the nesting season and incubated ($n = 65$) accumulated 92 nesting attempts. Most of these attempts were by juvenile females (67 ± 4.9% ; $n = 62$), followed by adult females (13 ± 3.5%; $n = 12$) and males (10 ± 3.1%; $n = 9$ each for juvenile and adult males). On a per-hen basis with male incubations allocated to hens, there were 2.0 attempts/hen conditional on incubation (1.6 attempts/hen including females that did not incubate).

The 229 bobwhites that entered the reproduction period, including those that did not survive it, accumulated 203 nesting attempts. This total translates to 1.7 attempts/hen ($n = 117$) that entered the season and 3.1 attempts/hen ($n = 65$, including hens that did not incubate) that survived the season.

For hens that started and survived the nesting season ($n = 65$), we observed 21 (32 ± 5.8%) that incubated 2 clutches and 4 (6 ± 3.0%) that incubated 3 clutches. Five double-clutching hens and 2 triple-clutching hens hatched 2 broods. We did not observe a hen hatch >2 broods.

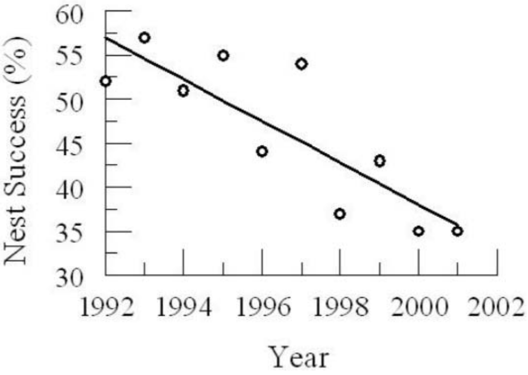

Fig. 1. Annual trends in nest success for northern bobwhites, Packsaddle Wildlife Management Area, Ellis County, Oklahoma, USA, 1992–2001.

The overall probability of success for incubated nests was 48 ± 2.8% ($n = 331$). We observed similar success rates for nests incubated by juvenile females (49 ± 3.6%; $n = 191$), adult females (48 ± 6.2%; $n = 65$), juvenile males (43 ± 7.3%; $n = 47$), and adult males (57 ± 9.5%; $n = 28$). Likewise, nest success appeared independent of incubation attempt for nests where the attempt number was known (individuals that started and survived the nesting season). Estimates were 56 ± 6.3% for first attempts ($n = 64$), 54 ± 10.4% for second attempts ($n = 24$), and 50 ± 28.9% for third attempts ($n = 4$). Nest success (y) declined (Fig. 1) during the 10 years (x) of study according to

$$y = 4{,}777 - 2.37x \; (r^2 = 0.70).$$

Confidence intervals (95%) on the rate of decline were 1.10–3.64%/year.

Clutch Size Trends

We observed 161 completed (hatched) clutches. The average clutch contained 13.6 ± 0.22 eggs, of which 12.2 ± 0.29 hatched. The percent hatch rate for eggs within clutches was 90.2 ± 1.4%.

Clutch size (y_i, i = attempt 1 or 2) for females that started and survived the nesting season declined with Julian day (x) for first and second nesting attempts (Fig. 2). The relations were

$$y_1 = 21.8 - 0.05x \; (n = 59,\ r^2 = 0.30) \text{ and}$$
$$y_2 = 26.0 - 0.07x \; (n = 21,\ r^2 = 0.30).$$

The rates of decline for first and second attempts were similar based on overlap of 95% confidence intervals. The rates suggested an average loss of 1 egg/clutch for every 14–20 days that

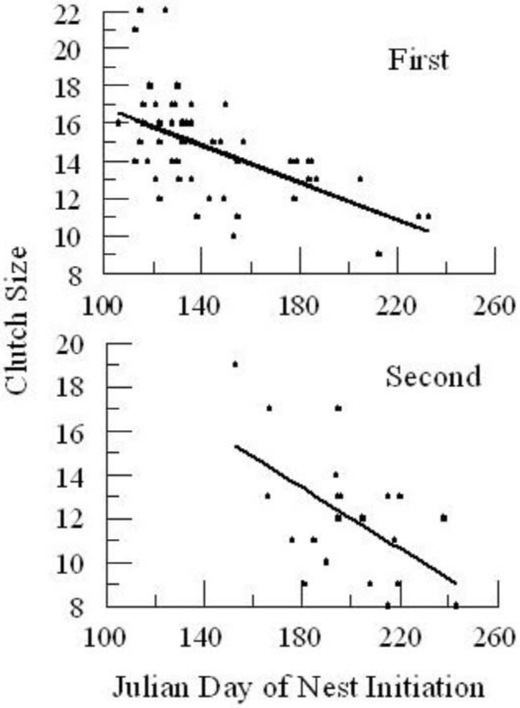

Fig. 2. Relation between clutch size and Julian day of the nesting season for first and second nesting attempts by female northern bobwhites with known nesting histories, Packsaddle Wildlife Management Area, Ellis County, Oklahoma, USA, 1992–2001.

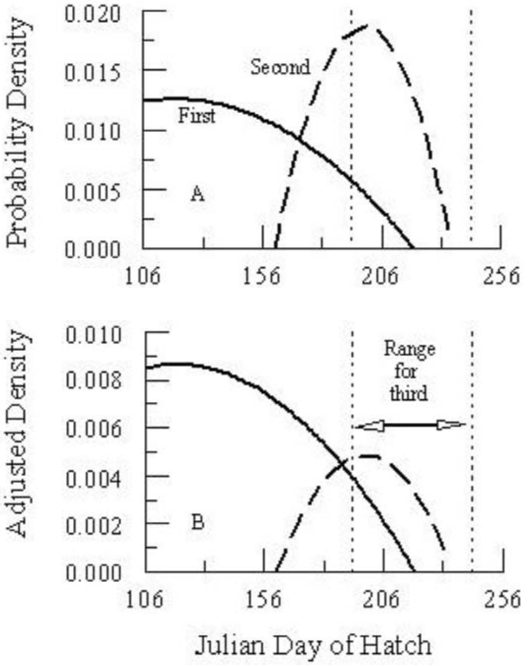

Fig. 3. Phenology of nest initiation for female northern bobwhites with known nesting histories, Packsaddle Wildlife Management Area, Ellis County, Oklahoma, USA, 1992–2001. A: Raw probability distributions. B: Probability distributions adjusted to account for the proportion of initiations in the sample. The dashed vertical lines show first and last initiation dates for hens with 3 nesting attempts ($n = 4$).

elapsed in the laying season, and this rate was independent of first or second nesting attempt.

Nesting Phenology

We obtained 81 complete nesting histories for female bobwhites, including 56 first attempts, 21 second attempts, and 4 third attempts. Within this dataset, which was truncated to birds alive during April–15 September, initiation of incubation for first nests was observed over a 133-day period (23 Apr–2 Sep), initiation for second nests over an 86-day period (2 Jun–26 Aug), and for third nests over a 51-day period (12 Jul–31 Aug). Observed initiation dates, pooled over all nesting attempts ($n = 331$), encompassed 140 days (23 Apr–2 Sep); hatching occurred over 129 days (26 May–2 Oct).

Cubic polynomials provided satisfactory models of the cumulative frequency of female incubation initiations (y_i, $i = 1, 2$ attempts) as a function of Julian day (x) within the observed range of x values:

$$y_1 = -39.66 - 0.3089x + 0.00875x^2 - 0.00002x^3 \quad (n = 56,\ r^2 = 0.99),$$

$$y_2 = 727.24 - 11.67x + 0.0610x^2 - 0.0001{-}x^3 \quad (n = 21,\ r^2 = 0.97).$$

The data were too few ($n = 4$) to model third nest initiations. The quadratic pdfs derived from the cubic polynomials (Fig. 3) suggested peak rate of nest initiation occurred on about 30 April for first attempts. Initiation of first nests was a threshold-like phenomenon (i.e., the rate of nest incubation initiation went from zero to its highest value in ≤3 weeks). The peak rate of initiation for second attempts occurred around 17 July.

Collapsing the pdfs (Fig. 3A) to account for proportion of initiations (Fig. 3B) revealed the importance of first initiations relative to second or third initiations. First incubation initiations accounted for 69 ± 5.2% of total initiations compared with 26 ± 4.9% for second initiations and 5 ± 2.4% for third initiations. The area under the 2 curves in Fig. 3A is 2.0; whereas, the area under the 2 curves in Fig. 3B is 0.95 (the curve for third initiations is not given). Thus, Fig. 3B provides an image of relative importance of incubation attempt in the total nest-incubation effort.

DISCUSSION

Reproduction Performance

Our results on reproduction effort were similar to previously published results. For all incubations, the 20% rate of male incubation we observed fell within reported ranges of 14–28% (Curtis et al. 1993, DeVos and Mueller 1993, Suchy and Munkel 1993, Burger et al. 1995). Burger et al. (1995) observed that 40.2% of females and 13.5% of males alive 15 April hatched ≥1 nest; respective estimates from this study were 28 ± 4.5% and 6 ± 2.1%. Burger et al. (1995) also observed 74% of females and 26% of males that survived the nesting season hatched ≥1 nest. We observed 43 ± 6.2% of females and 9 ± 3.0% of males.

Rollins and Carroll (2001) reviewed 11 studies of bobwhite nest-success rates and found a weighted mean of 28%. The highest reported rate (Peoples et al. 1996; 50%) was based on early results from the present study. The lowest rate reported was 12% based on a small sample from north Texas (Jackson 1947, *n* = 34). Thus, the overall success rate of incubated nests observed in this study (48%) was high relative to the average expectation. However, the rate declined as the study progressed (Fig. 1) and we did not obtain data on loss of nests during pre-incubation.

The Packsaddle Area had ample amounts of nesting cover in the form of perennial grasses and low shrubs distributed throughout the area. The area was grazed seasonally at a light–moderate rate with stockers (Townsend et al. 2001), which facilitated the quantity of nesting cover. This high availability of nest cover could contribute to nesting success (Taylor et al. 1999).

The reason for the decade-long decline in nest success (Fig. 1) is more difficult to explain. Townsend et al. (2001) observed that visibility of nest contents influenced nest success in 1996 and 1997 on the Packsaddle Area (lower visibility implied higher success). During these years, visibility at successful nests was about half that at unsuccessful nests. In contrast, 1998 was a hot, droughty summer and visibility at successful and unsuccessful nests was similar and at about the same level as unsuccessful nests in the previous 2 years. Townsend et al.'s (2001) data imply that a long-term decline in the structural density, and, therefore, the visual obstruction properties of nesting cover, could plausibly be associated with the decline in nest success we observed, despite the widespread availability of nest cover per se. Weather data from Arnett, Oklahoma (27 km from the Packsaddle area), revealed no trend in May–August precipitation during the study. However, mean maximum daily temperature during May–August increased at a rate of 0.3 °C/year (95% CL = 0.0–0.7 °C/year, $P = 0.0538$) during 1992–2001. Nest obstruction might have declined given non-trending precipitation and upward trending temperature. Of course, other factors such as trends in predator abundance could be responsible for the trend we observed.

Clutch Size Trends

Decline in clutch size as the laying season progresses is well documented in bobwhites throughout their range (Stoddard 1931:28, Rosene 1969:68, Lehmann 1984:86, Roseberry and Klimstra 1984:74, Burger et al. 1995). Stoddard (1931:28) hypothesized that the decline was due to a high prevalence of dump nesting early in the laying season and a low prevalence later in the season. Roseberry and Klimstra (1984:74), on the contrary, implicitly took declining clutch size to be a reflection of first nests (early season) and renests (later season), with renests containing smaller clutches. Our results suggested that clutch size declined independently of nesting attempt and that the rate of decline was similar for first and second clutches. Based on the regression equations presented in results, predicted size of a first clutch initiated on Julian day 180 (29 Jun) was 13.0 vs. 13.5 for a second clutch on the same Julian day. Thus, under the models, second clutches were not necessarily expected to be smaller than first clutches (we did not obtain data on pre-incubation laying). Therefore, our results were inconsistent with the hypothesis that later clutches are smaller because they represented renesting attempts, which presumably would be associated with reduced energy reserves in females, given an earlier nesting attempt.

Our results were consistent with the hypothesis that some overriding factor might influence clutch size as the laying season progresses. Two such factors are plausible. First, Farnsworth and Simons (2001) argued that a decline in clutch size as the breeding season progresses maximizes annual fecundity for multiple-brooding birds. This result accrues from the interplay of predation rates and time remaining in the breeding season for laying and incubating.

A second plausible factor is temperature, which generally increases from start to end of a laying season. Higher temperatures reduce the length of the laying season (Klimstra and Roseberry 1975) and the intensity of the breeding effort (Guthery et al. 1988) in bobwhites. However, these observations do not explain why a hen would lay smaller clutches later than earlier. Smaller clutches later in the nesting season could be an adaptive response to reduced storage (pre-incubation) time, perhaps associated with a lower daily rate of egg-laying because of higher temperatures (Thomason et al. 1972, Tanor et al. 1984, Muiruri and Harrison 1991) and vulnerability of embryos to hyperthermia. Blastoderm development in bobwhite eggs begins at 24.4–25.6 °C (Miller and Wilson 1975). The temperature of bobwhite eggs (not incubated) in natural nests can exceed 40 °C in mid-latitudes in late July; during hot weather, incubating bobwhites serve an important cooling, as well as a warming, function for eggs (Smith 2003). In general, high temperatures are more deleterious to avian embryos than low temperatures (Webb 1987). Thus, there are possible adaptive reasons (e.g., reduced storage time and protection of embryos from hyperthermia) for reducing clutch size as the laying season progresses and ambient temperature increases. We recognize these arguments are hypothetical, and we encourage the generation and testing of additional hypotheses that explain decline in clutch size.

Nesting Phenology

We observed a threshold-like increase in nest initiation over about a 3-week period starting in early April. That is, nesting bobwhites went from no initiations to a relatively high sustained rate (incubation initiations/bird/day) in this period. Stanford's (1972) hatch distributions (a translated version of the nest-initiation distribution) suggested approximately a 5-week period from start of initiations to peak rates in Missouri. Likewise, Klimstra and Roseberry (1975) observed a 5–6-week time frame in Illinois. In Missouri, the nest initiation rate of females went from zero to a peak value in about 3 weeks (Burger et al. 1995).

Our results on nest-initiation phenology were somewhat ambiguous relative to the modeling assumption of Guthery and Kuvlesky (1998). They assumed hatching distributions (and by translation, nest-initiation distributions) ended on a common date. Our empirical observations suggested initiation for first, second, and third incubations ended in an 8-day period (26 Aug–2 Sep). However, a mixture of modeling and empirical results indicated a more protracted ending for first, second, and third initiations (Fig. 3). Thus, the empirical results implied the assumption of Guthery and Kuvlesky (1998) was reasonable though inaccurate; whereas, the mixed modeling and empirical results implied possible bias in the modeling results of Guthery and Kuvlesky (1998).

MANAGEMENT IMPLICATIONS

Our results primarily represented descriptive biology on reproduction in a mid-latitude bobwhite population and perhaps have no practical management implications, except insofar as they lead to better understanding of bobwhite demographics. However, managers might take note of the importance of first nest initiations relative to second and third initiations (Burger et al. 1995, Fig. 3B). This importance might imply that management of nesting cover should focus on its availability in the early nesting season. Finally, our results provide an empirical example of high nest success rates, especially during the early years of the study, in the absence of any form of nest predator suppression. Leopold (1933:240) observed provision of food and escape cover was "one of the most effective forms of 'predator control'" for wintering bobwhites. In that the Packsaddle Area had large quantities of nesting cover, Leopold's conjecture might hold for nesting as well as wintering bobwhites. However, this observation is correlational, and it does not preclude the possibility that high nest success accrued because of low populations of nest predators or some other factor.

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