

Population Irruptions of Northern Bobwhite: Testing an Age-Specific Reproduction Hypothesis

FIDEL HERNÁNDEZ,¹ Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, Kingsville, TX 78363, USA

KRISAN M. KELLEY, Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, Kingsville, TX 78363, USA

JUAN A. ARREDONDO, Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, Kingsville, TX 78363, USA

FROYLÁN HERNÁNDEZ,² Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, Kingsville, TX 78363, USA

DAVID G. HEWITT, Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, Kingsville, TX 78363, USA

FRED C. BRYANT, Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, Kingsville, TX 78363, USA

RALPH L. BINGHAM, Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, Kingsville, TX 78363, USA

ABSTRACT Age-specific reproduction has been suggested for northern bobwhite (*Colinus virginianus*) and has been hypothesized as a factor contributing to population irruptions. However, little research has been conducted on the subject. We conducted a laboratory and field study to determine if age-specific reproduction occurred in northern bobwhites. Our objectives were to compare 7 reproductive measures (% F nesting, date of first incubated nest, egg-laying rate, nesting rate, clutch size, egg mass, and egg hatchability) between first- and second-year breeders and determine if differential reproduction was impacted by diet quality. The laboratory study consisted of a 2 × 2 factorial experiment with age and diet quality (low protein [12%] and high protein [24%]) as the factors. Data for the field study represented a 6-year data set of bobwhite reproduction (May–Sep 2000–2005) obtained from an ongoing radiotelemetry study in southern Texas, USA. We documented similar productivity (i.e., % F laying, egg-laying rate, and egg mass) and timing of laying (i.e., date of first egg) between juvenile ($n = 33$) and adult bobwhites ($n = 27$) in our laboratory study. However, females on the high-protein diet exhibited a greater egg-laying rate than females on the low-protein diet. Under field conditions, we also documented no difference in productivity (% F nesting, nesting rate, clutch size, egg hatchability) and timing of nesting (date of first incubated nest) between age classes ($n = 59$ juv and 32 ad). Our findings do not support early suppositions of age-specific reproduction in quail. Quail irruptions should not be influenced by population age structure as it relates to age-specific reproduction. (JOURNAL OF WILDLIFE MANAGEMENT 71(3):895–901; 2007)

DOI: 10.2193/2006.101

KEY WORDS age-specific reproduction, *Colinus virginianus*, northern bobwhite, population dynamics, reproductive ecology, Texas.

Most North American quail species exhibit irruptive population behavior; populations rapidly increase during relatively wet periods and abruptly decrease during drought. Irruptive behavior has been documented in northern bobwhite (*Colinus virginianus*; Kiel 1976), scaled quail (*Callipepla squamata*; Campbell et al. 1973), California quail (*C. californica*; Francis 1970), Gambel's quail (*C. gambelii*; Heffelfinger et al. 1999), and Montezuma quail (*Cyrtonyx montezumae*; Brown 1989). Quail populations fluctuate so drastically on semiarid rangelands that population changes have been referred to as boom and bust. Various hypotheses have been researched to explain this phenomenon including vitamin A deficiency (Nestler and Bailey 1943), phosphorus deficiency (Cain et al. 1982), phytoestrogens (Leopold et al. 1976), water deprivation (Koerth and Guthery 1991), and heat stress (Guthery et al. 2001). Despite years of research, however, the causal factor(s) of the boom-bust phenomenon remains unknown (Guthery 2002, Hernández et al. 2002).

Quail production is influenced by 4 crucial variables: proportion of females that nest, nesting rate, probability of nest success, and length of the nesting season (Guthery and Kuvlesky 1998, Hernández et al. 2005). These variables affect total nest production which is a primary determinant

of percent summer gain in bobwhite populations (Dimmick 1974, Klimstra and Roseberry 1975). As such, any factor that influences nest production can exert a profound influence on quail populations. Age-specific reproduction, the phenomenon in which experienced breeders reproduce earlier and are more productive than younger, inexperienced breeders, is a process that, if present in quail, could influence quail populations via nest production. Mere changes in population age structure through time, therefore, could affect the amplitude and frequency of quail irruptions. Moreover, quail populations also could be impacted if poor nutritional conditions further exacerbated differential productivity between age classes (Kirkpatrick 1988).

Age-specific reproduction is a common phenomenon in many avian species (Curio 1983, Forslund and Pärt 1995). Evidence for differential productivity in quail, however, is tenuous (Johnsgard 1973, Kirkpatrick 1988). Although researchers have suggested that older quail exhibit both earlier nesting (Lehmann 1953, Parmalee 1955, Rosene 1969) and increased egg production (Robinson 1963, Francis 1970, Brooks 2005), evidence for age-specific reproduction in quail is weak because low sample size limits existing data. Kirkpatrick (1988) noted that almost no data existed regarding age-specific reproduction in quail. Lacking evidence to the contrary, Johnsgard (1973) proposed that quail did not exhibit age-specific reproduction.

Age-specific reproduction is an unresolved question in

¹ E-mail: fidel.hernandez@tamuk.edu

² Present address: Elephant Mountain Wildlife Management Area, Texas Parks and Wildlife Department, Alpine, TX 79830, USA

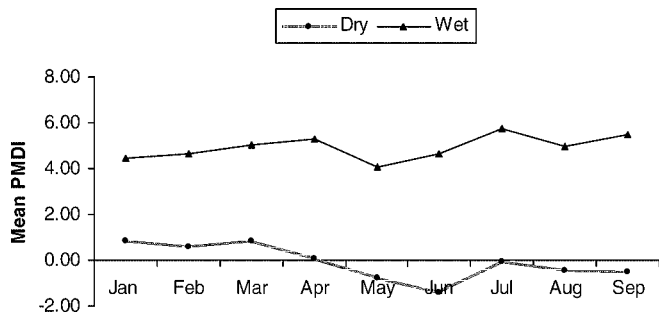


Figure 1. Mean modified Palmer Drought Severity Index (PMDI) values for southern Texas, USA, during a relatively dry period (May–Sep, 2000–2002, 2005) and wet period (May–Sep 2003–2004). Negative PMDI values represent droughty conditions whereas more positive values represent relatively more mesic conditions.

quail demography (Klimstra and Roseberry 1975, Brooks 2005). Given the impact that differential productivity may have on quail populations and the lack of rigorous testing, we conducted a laboratory and field study to determine if age-specific reproduction occurred in northern bobwhites. Our objectives were to compare 7 reproductive measures (percentage of F nesting, date of first incubated nest, egg-laying rate, nesting rate, clutch size, egg mass, and egg hatchability) between first- and second-year breeders and determine if differential reproduction was impacted by diet quality. Hereafter, we use the term juvenile and adult to signify first-year breeder and second-year or older breeder, respectively.

STUDY AREA

We conducted the field portion of this study on a private ranch in Brooks County, Texas, USA, which lies in the Rio Grande Plains ecoregion (Gould 1975). The vegetation for the ecoregion was a mixed-brush community (Scifres 1980). Predominant shrubs consisted of honey mesquite (*Prosopis glandulosa*), huisache (*Acacia farnesiana*), granjeno (*Celtis pallida*), live oak (*Quercus virginiana*), and pricklypear (*Opuntia engelmannii*). Predominant herbaceous vegetation included doveweed (*Croton* spp.), sunflower (*Helianthus* spp.), partridge pea (*Chamaecrista fasciculata*), little bluestem (*Schizachyrium scoparium*), paspalum (*Paspalum* spp.), three awn (*Aristida* spp.), gulf cordgrass (*Spartina spartinae*), and sandbur (*Cenchrus spinifex*).

The ecoregion was a semi-arid, sub-humid environment characterized by a high rate of evaporation (Williamson 1983). The months of June and September historically received the greatest amount of precipitation. Monthly precipitation ranged from 1.4 cm to 13.0 cm with a mean annual rainfall of 65.4 cm (Williamson 1983). Rainfall during the dry period (Sep 1999–Aug 2000) totaled 51 cm compared to 93 cm during the wet period (Sep 2000–Aug 2003).

METHODS

Laboratory Study

We purchased 80 bobwhite females ($n = 40$ juv [30–40 weeks] and 40 ad [>2 yr]) from a commercial breeder in Texas during March 2005. We weighed and leg-banded all

bobwhites and placed them in individual cages ($51 \times 27 \times 28$ cm) within an environmental chamber where temperature, humidity, and photoperiod were controlled. We allowed a 3-week acclimation period (16 Mar–6 Apr; 22°C , 80% humidity, 15-hr photoperiod) providing food and water ad libitum.

After the acclimation period, we randomly assigned a treatment (low protein [12%] and high protein [24%]) to bobwhite females by age. We formulated the low-protein and high-protein diet to meet the maintenance and breeding requirements of bobwhites, respectively (Nestler 1949, National Research Council 1977). We obtained initial body masses to the nearest 0.1 g using a digital, electronic scale and then began a 12-week experiment (7 Apr–23 Jun) to assess egg production. We re-weighed bobwhites every 7 days. When females began producing eggs, we collected and weighed all eggs daily throughout the experiment. We used egg mass as an index of egg quality (Giuliano et al. 1996). We conducted all data collections at the same time to minimize any diel changes in body mass (Kontogiannis 1967).

Field Study

We obtained data for 6 nesting seasons (May–Sep, 2000–2005) for this study from an ongoing radiotelemetry project on bobwhites conducted in Brooks County, Texas. Hernández et al. (2005) provided complete descriptions of study area, experimental design, and methodology. We captured bobwhites using standard funnel traps throughout the study period as needed to maintain ≥ 20 bobwhites in each of 3 spatially independent study sites (1,200–2,000 ha each). We fitted bobwhites of both sexes and age classes (i.e., juv and ad) weighing >150 g with a 5–6-g neck-loop radiotransmitter (American Wildlife Materials, Monticello, FL) and an aluminum leg band. We monitored bobwhites using radiotelemetry about 3 times per week using a hand-held, 3-element yagi antenna. We located nests via radiotelemetry and documented nest fate (i.e., successful, depredated, or abandoned), clutch size, and egg hatchability (i.e., proportion of eggs that hatch from a successful clutch) for each nest.

Hernández et al. (2005) reported that drought negatively influenced bobwhite nesting effort. Thus, we partitioned our study period into relative categories dry (May–Sep 2000–2002, 2005) and wet (May–Sep 2003–2004) based on the Modified Palmer Drought Severity Index (PMDI; Palmer 1965; Fig. 1). We identified females with complete nesting histories (alive 1 May–15 Sep) for each weather period and used this sample to document percent of females nesting and nesting rate. We only used females alive during 1 May–15 September (although radiomarked F continued to be added throughout the nesting season due to trapping) because we could account for their entire effort throughout the duration of the nesting season. For date of first incubated nest, we used females that were alive 1 May and that survived at least to first nesting.

Statistical Analyses

Laboratory study.—To test for the effect of diet and age on body mass, we used a completely randomized 2-way analysis

Table 1. Change in body mass of captive northern bobwhites fed a low-protein (12%) and high-protein (24%) diet during a 12-week productivity experiment, Kingsville, Texas, USA, March–June 2005.

Age	High-protein diet							Low-protein diet						
	Beginning mass			Ending mass		Difference		Beginning mass			Ending mass		Difference	
	<i>n</i>	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	<i>n</i>	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Ad	14	224.9	4.3	234.0	8.4	9.1	7.5	13	202.8	5.9	204.6	9.7	1.8	7.4
Juv	15	210.7	3.4	221.6	2.9	10.9	4.7	18	216.9	4.3	211.7	5.5	-5.2	5.3

of variance (ANOVA) where age and diet were the factors and the difference in body mass between the beginning and end of the experiment represented the dependent variable. We computed a Cochran–Mantel–Haenszel chi-square for the 3-way contingency table (diet [2 levels] by age [2 levels] by laying status [2 levels]) and used Breslow–Day test for homogeneity of odds ratios to determine if the percent of females laying was similar for the 2 age classes across diets (Stokes et al. 1995, Zar 1999). We evaluated the effect of age and diet on egg-laying rate and day of first egg using a completely randomized 2-way factorial ANOVA.

Field study.—We used the same analysis as above (i.e., Cochran–Mantel–Haenszel chi-square and Breslow–Day test for homogeneity of odds ratios) to determine if the percent of females nesting was similar for the 2 age classes across periods. We used ANOVA to evaluate the effect of age and period on nesting rate, clutch size, egg hatchability, and date of first incubated nest. We reported results as mean \pm standard error.

Because differential production could still exist between age classes even if individual reproductive variables did not differ (via a cumulative effect), we estimated chick production for each age class using a simple, deterministic model comprised of the various reproductive variables using age-specific field data. Estimated chick production was the product of 6 demographic variables (F population size, proportion of F nesting, nesting rate, nest success, clutch size, and egg hatchability). We estimated chick production both for a dry and wet period by using the actual values collected for these demographic variables during our study. Our hypothetical population consisted of 1,000 females whose age structure reflected that observed during a particular weather period. We did not directly incorporate any density-dependent, reproductive effect into our model because 1) population size was constant (i.e., always 1,000 F) and therefore our hypothetical density also was constant and

2) our population model inherently contained the influence of any density-dependent reproduction effect present because we used actual field data. We graphically compared estimated chick production against proportion of adults in the breeding population for each period.

RESULTS

Laboratory Study

Ten bobwhites (5 ad, 5 juv) in the high-protein group and 8 bobwhites (6 ad, 2 juv) in the low-protein group died during our study. This reduced our sample size from 39 bobwhites to 29 bobwhites in the high-protein treatment (14 ad, 15 juv) and from 39 bobwhites to 31 bobwhites in the low-protein treatment (13 ad, 18 juv). Cause of deaths was unknown.

We detected no age \times diet interaction ($P=0.48$) in body-mass change (Table 1). Pooled over age, females in the high-protein group ($n=29$) exhibited mass gain (10.0 ± 4.3 g), whereas females in the low-protein group ($n=31$) exhibited negligible mass loss (-2.3 ± 4.3 g; $P=0.07$; Table 1). Test for homogeneity of odds ratios was not significant for percent of females laying controlling for diet ($\chi^2=0.97$, $df=1$, $P=0.33$), suggesting odds ratios could be obtained from the combined data. The odds of an adult laying was 0.77 (95% CI: 0.18–3.37) times that of a juvenile ($\chi^2=0.12$, $df=1$, $P=0.73$) adjusting for diet (Table 2).

We detected no age \times diet interaction for egg mass ($P=0.94$), egg-laying rate ($P=0.48$), or date of first egg ($P=0.79$). Of females that laid eggs, mean mass of eggs was similar between adult (9.7 ± 0.2 g) and juvenile females (9.7 ± 0.1 g), as was laying rate (0.37 ± 0.05 eggs/d vs. 0.32 ± 0.04 eggs/d, respectively). We documented no difference in start of laying between adult (120.8 ± 3.0 Julian d) and juvenile females (122.0 ± 3.0 Julian d).

Regarding diet effect, we documented that mean egg mass was similar between females on a high-protein (9.9 ± 0.1 g)

Table 2. Percentage of northern bobwhite females laying eggs during a 12-week productivity experiment, Kingsville, Texas, USA, March–June 2005.

Age	High-protein diet ^a							Low-protein diet						
	<i>N</i>	Laid eggs			No eggs			<i>N</i>	Laid eggs			No eggs		
		<i>n</i>	%	SE ^b	<i>n</i>	%	SE		<i>n</i>	%	SE	<i>n</i>	%	SE
Ad	14	13	92.9	9.0	1	7.1	3.3	13	10	76.9	8.3	3	23.1	5.9
Juv	15	13	86.7	8.7	2	13.3	4.8	18	16	88.9	8.6	2	11.1	4.8
Total	29	26	89.7	8.1	3	10.3	6.0	31	26	83.9	7.9	5	16.1	7.8

^a F were fed either a low-protein (12%) or high-protein (24%) diet throughout the duration of the experiment.

^b SE(ρ) = sq root of [$\rho(1 - \rho)/n$].

Table 3. Percentage of wild, northern bobwhite females nesting during a relatively dry period (May–Sep 2000–2002, 2005) and wet period (May–Sep 2003–2004), Brooks County, Texas, USA. Classification for periods based on Modified Palmer Drought Severity Index values.

Age	Dry									Wet						Pooled					
	Nested			No nests			Nested			No nests			Nested			No nests					
	<i>N</i>	<i>n</i>	%	SE ^a	<i>n</i>	%	SE	<i>N</i>	<i>n</i>	%	SE	<i>n</i>	%	SE	<i>N</i>	<i>n</i>	%	SE	<i>n</i>	%	SE
Ad	26	23	88.5	6.7	3	11.5	18.4	6	6	100.0	0.0	0	0.0	32	29	90.6	5.4	3	9.4	16.8	
Juv	23	17	73.9	10.6	6	26.1	17.9	33	32	97.0	3.0	1	3.0	17.1	56	49	87.5	4.7	7	12.5	12.5
Pooled	49	40	81.6	6.1	9	18.4	12.9	39	38	97.4	2.6	1	2.6	15.8							

^a SE(*p*) = sq root of [*p*(1 - *p*)/*n*].

and low-protein diet (9.6 ± 0.1 g). However, females on the high-protein diet exhibited a greater egg-laying rate (0.43 ± 0.04 eggs/d) than females on the low-protein diet (0.25 ± 0.03 eggs/d). Date of first egg was similar between females on the high-protein diet (117.4 ± 2.8 Julian d) and low-protein diet (125.6 ± 3.1 Julian d).

Field Study

Univariate comparisons.—We monitored 124 radiomarked females during the nesting season of the dry period, of which 49 (26 ad, 23 juv) had complete nesting histories (i.e., alive 1 May–15 Sep). For the wet period, we monitored 99 radiomarked females during the nesting season of which 39 (6 ad, 33 juv) had complete nesting histories. Test for homogeneity of odds ratios was not significant for percent of females nesting controlling for period ($\chi^2 = 0.07$, *df* = 1, *P* = 0.79), suggesting odds ratios could be obtained from the combined data. The odds of an adult nesting was 2.8 (95% CI: 0.63–13.0) times that of a juvenile adjusting for period; however, the odds were not significant ($\chi^2 = 1.9$, *df* = 1, *P* = 0.79; Table 3).

We detected no age \times period interaction for clutch size (*P* = 0.78), egg hatchability (*P* = 0.20), date of first incubated nest (*P* = 0.98) or nesting rate (*P* = 0.90) so we pooled across period for these variables (Table 4). We documented similar clutch size between adult (11.9 ± 0.3 eggs; *n* = 86 nests) and juvenile females (11.9 ± 0.2 eggs; *n* = 163 nests) as well

as similar egg hatchability ($87.3 \pm 2.5\%$ [*n* = 45 clutches] vs. $86.2 \pm 2.2\%$ [*n* = 103 clutches], respectively). Test for homogeneity of odds ratios was not significant for nest success controlling for period ($\chi^2 = 2.2$, *df* = 1, *P* = 0.14). The odds of an adult producing a successful nest was 0.77 (95% CI: 0.47–1.26) times that of a juvenile ($\chi^2 = 1.1$, *df* = 1, *P* = 0.30) adjusting for period (Table 5).

Of females that nested, we documented similar nesting rates between adult (1.4 ± 0.2 nests/F; *n* = 32) and juvenile females (1.6 ± 0.1 nests/F; *n* = 56). Moreover, date of first incubated nest was similar between adult (153.1 ± 3.4 Julian d; *n* = 61) and juvenile females (157.7 ± 2.7 Julian d; *n* = 97; Table 4).

Production model.—Adult females comprised 44% of the 1 May population during the dry period (*n* = 141 bobwhite F) and 26% during the wet period (*n* = 98 bobwhite F). We documented that weather had a greater effect on total chick production than age structure (Table 6; Fig. 2). Although increasing the proportion of adults in the population from 0.20 to 0.50 (the approx. range in age structure observed in our study) resulted in 14.9% change in chick production during the dry period, the projected production at 0.50 was still considerably less (4,968 chicks) for the dry period than for the wet period (9,706 chicks; Fig 2). In addition, we observed an interaction between age class and cumulative effect of reproduction; increasing the proportion of adults in

Table 4. Comparison of reproductive variables for wild, radiomarked northern bobwhites during a relatively dry period (May–Sep 2000–2002, 2005) and wet period (May–Sep 2003–2004), Brooks County, Texas, USA. Classification for periods based on Modified Palmer Drought Severity Index values.

Variable	Dry			Wet			Pooled		
	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE
Clutch size									
Ad	61	11.9	0.3	25	12.2	0.6	86	11.9	0.3
Juv	71	11.8	0.4	92	11.9	0.3	163	11.9	0.2
Pooled	132	11.8	0.2	117	12.0	0.3			
Egg hatchability (%)									
Ad	32	89.5	2.2	13	82.0	6.9	45	87.3	2.5
Juv	40	84.4	4.3	63	87.3	2.4	103	86.2	2.2
Pooled	72	86.7	2.6	76	86.4	2.3			
First nest (Julian d)									
Ad	44	157.1	4.3	17	142.6	4.1	61	153.1	3.4
Juv	42	166.0	5.4	55	151.3	2.3	97	157.7	2.7
Pooled	86	161.4	3.4	72	149.3	2.0			
Nesting rate (nests/F)									
Ad	26	1.3	0.2	6	2.0	0.4	32	1.4	0.2
Juv	23	1.1	0.2	33	1.9	0.2	56	1.6	0.1
Pooled	49	1.2	0.1	39	1.9	0.1			

Table 5. Apparent nest success of wild, radiomarked northern bobwhite females during a relatively dry period (May–Sep 2000–2002, 2005) and wet period (May–Sep 2003–2004), Brooks County, Texas, USA. Classification for periods based on Modified Palmer Drought Severity Index values.

Age	Dry							Wet						Pooled							
	N	Successful			Unsuccessful			N	Successful			Unsuccessful			N	Successful			Unsuccessful		
		n	%	SE ^a	n	%	SE		n	%	SE	n	%	SE		n	%	SE	n	%	SE
Ad	67	33	49.3	8.7	34	50.7	8.6	32	13	40.6	0.0	19	59.4	11.3	99	46	46.5	7.4	53	53.5	6.9
Juv	81	39	48.1	8.0	42	51.9	7.7	107	63	58.9	6.2	44	41.1	7.4	188	102	54.3	4.9	86	45.7	5.4
Pooled	148	72	48.6	5.9	76	51.4	5.7	139	76	54.7	5.7	63	45.3	6.3							

^a SE(p) = sq root of [$p(1 - p)/n$].

the 1 May population increased production during the dry period but decreased production during the wet period (Fig. 2).

DISCUSSION

Effect of Age on Reproduction

Our laboratory and field data did not support the existence of age-specific reproduction in bobwhites. We documented similar productivity (i.e., % F laying, egg-laying rate, and egg mass) and timing of laying (i.e., date of first egg) between juvenile and adult bobwhites in the environmental chamber. Under field conditions, we also documented no difference in productivity (% F nesting, nesting rate, clutch size, egg hatchability) and timing of nesting (date of first incubated nest) between age classes. Our findings do not support early suppositions of age-specific reproduction in quail. Francis (1970) reported that captive adults of California quail ($n = 4$) exhibited greater egg production than juveniles ($n = 3$). Robinson (1963) also documented that adult bobwhite females ($n = 4$) produced more eggs than juveniles ($n = 4$). Regarding timing of nesting, Parmalee (1955) suggested that adult bobwhites nested earlier in the season than juveniles based on ovarian development of field specimens ($n = 2$ bobwhites/age class). Lehmann (1953) presented further evidence reporting that adults comprised 75% of breeding females ($n = 4$) and only 14% of nonlaying females ($n = 14$) in a sample of bobwhites collected during May. Although these data are suggestive of differential productivity in quail, small sample size limits their inference.

Brooks (2005) recently conducted a 2-year field study using a larger sample specifically to test age-specific reproduction in bobwhites across 5 variables (timing of

nesting, clutch size, nest fate, nesting rate, and no. of chicks hatched). During the first year, Brooks (2005) documented no difference in all 5 reproductive variables between juvenile ($n = 51$) and adult ($n = 51$) females. During the second year, he also documented no difference in 4 of the 5 variables; however, the fifth variable (nesting rate) was greater for adults (1.04 nests/ad vs. 0.58 nests/juv). Differences in renesting rates between adults and juveniles probably accounted for this finding because adults initiated 80% of renesting attempts ($n = 15$). However, Brooks (2005) did not report whether females with complete nesting histories (i.e., alive during the entire nesting period) were used to calculate nesting effort per female. Without this knowledge, his finding of differential nesting rates between adult and juvenile bobwhites during one of 2 years is difficult to interpret.

Brooks (2005) concluded his data were suggestive that 1) adult birds were more productive breeders than juveniles when considering the cumulative effect of reproduction, and 2) this increased production by adult females could be a mechanism allowing populations to rebound rapidly following periods of lower production. We disagree with his general conclusions. Using a production model similar to ours, Brooks (2005) actually reported juveniles produced more chicks (2,407 chicks) than adults (468 chicks) during one year of his study, a finding inconsistent with his first conclusion. Regarding his second, our production model indicated that weather had a greater impact on chick production (primarily through its negative effects on % F nesting and nesting rate) than relatively large changes (20–50%) in population age structure. An extensive literature base exists documenting the profound influence that weather has on quail populations (Guthery et al. 1988,

Table 6. Production model used to estimate production of northern bobwhite females during a relatively dry period (May–Sep 2000–2002, 2005) and wet period (May–Sep 2003–2004), Brooks County, Texas, USA. Values for each variable represent field data obtained from wild, radiomarked bobwhites monitored during each period. Classification for periods based on Modified Palmer Drought Severity Index values.

Period	Reproductive variables									
	Age	N	% nesting	Nesting rate	Nest success	Clutch size	Egg hatchability	Chicks produced ^a	Total chicks	% of total chicks
Dry										
Ad	440		0.885	1.3	0.493	11.9	0.895	2,658	4,839	54.9
Juv	560		0.739	1.1	0.481	11.8	0.844	2,181		45.1
Wet										
Ad	260		1.000	2.0	0.406	12.2	0.820	2,112	10,466	20.2
Juv	740		0.971	1.9	0.589	11.9	0.873	8,354		79.8

^a Chicks produced is the product of 6 variables (F population size, proportion F nesting, nesting rate, nest success, clutch size, and egg hatchability).

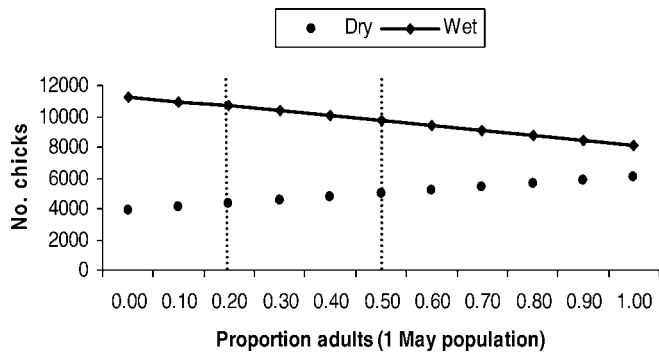


Figure 2. Estimated chick production of northern bobwhite females as a function of population age structure during a relatively dry period (May–Sep 2000–2002, 2005) and wet period (May–Sep 2003–2004), Brooks County, Texas, USA. Classification for periods based on Modified Palmer Drought Severity Index values. Vertical lines represent range in proportion of adults documented during this study.

Heffelfinger et al. 1999, Lusk et al. 2001, Hernández et al. 2005). We suggest that any potential influence that population age structure may have on bobwhite fluctuations via production is likely overridden by the strong influence of weather. We acknowledge this supposition arises from a simple, deterministic model and requires further testing using a more complex, time-based model.

Given past research, we conclude that age-specific reproduction does not occur in bobwhites in our region. Data suggestive of differential productivity in quail arise from studies limited by low sample size. Thus, data may have captured mere natural variability in reproductive measures. Data emerging from larger samples (Brooks 2005), including our study, do not indicate the existence of age-specific reproduction in bobwhites. Because the phenomenon has been reported for many avian species (Curio 1983, Forslund and Pärt 1995), our conclusion prompts the question: why do quail not exhibit age-specific reproduction? We propose that age-specific reproduction would be a maladaptive trait for short-lived species like quail based on life-history theory (Stearns 1976, Martin 2004). Life-history theory suggests that birds balance current reproductive effort against residual reproductive value (i.e., probability of future reproductive success minus current; Williams 1966). Consequently, fitness value of current reproductive effort becomes inversely related to residual reproductive value. When residual reproductive value is low (i.e., low probability of survival to future breeding), the fitness value of current reproductive effort becomes high and vice versa (Ghalambor and Martin 2001, Martin 2004). Therefore, age-specific reproduction would not be expected for species experiencing annual high mortality because probability of future breeding would be low (i.e., low residual reproductive value). For a taxon like quail that sustains high mortality (Rollins and Carroll 2001) and, therefore, possess little opportunity for future breeding, age-specific reproduction would be maladaptive for population persistence. This rationale is consistent with Curio (1983), who predicted that age-specific reproduction would be more prevalent and dramatic in long-lived species than short-lived species.

Effect of Diet on Reproduction

Quail productivity was not influenced by breeding age. However, it was affected by level of dietary protein. We documented that females on a low-protein diet exhibited a lower egg-laying rate than females on the high-protein diet. Similarly, Nestler et al. (1944) reported that bobwhite females on a low-protein diet (13%) produced fewer eggs (36 eggs/F) compared to females on a high-protein diet (23%; 69 eggs/F). Giuliano et al. (1996) reported a similar negative effect of reduced egg production resulting from lower protein intake. Our finding adds to the growing body of evidence documenting a general, negative effect of protein deficiency on avian egg production (Kirkpatrick 1988).

Nestler et al. (1944) reported a positive, albeit imprecise, trend between length of laying period and levels of dietary protein (from 13% to 23% in 2% increments). Females on a low-protein diet (13%) exhibited a shorter laying period (112 d; 13 May–2 Sep) than females on a higher level (23%; 137 d; 5 May–19 Sep). However, the relationship was not consistent because the 2% increments in dietary protein from 13% to 23% did not always result in successive increases in laying period length. We did not document a protein effect on length of laying period. Our finding could reflect the imprecise nature of the relationship observed by Nestler et al. (1944) or result from the shorter duration of our experiment (3 months [Mar–Jun] vs. 6 months [Mar–Sep], respectively). We terminated our experiment while females on both diets were still laying, thereby not providing females the opportunity for natural termination of egg laying. Giuliano et al. (1996) terminated their experiment after 4 weeks and, therefore, also did not provide data to evaluate the influence of protein intake on length of laying period.

Our finding that egg mass was not affected by protein level is consistent with prior research. Giuliano et al. (1996) reported that protein deficiencies did not affect egg mass in either bobwhites or scaled quail. Nestler et al. (1944) reported that egg mass increased in direct proportion with level of dietary protein from 9.2 g (13% diet) to 9.7 g (23% diet). However, it is questionable whether this small numerical increase in egg weights is biologically meaningful.

MANAGEMENT IMPLICATIONS

We initiated this basic research with the intent of increasing our understanding of bobwhite reproduction. We conclude that age-specific reproduction does not exist in northern bobwhites in our region and should not be influencing bobwhite population dynamics (i.e., a yr of good production should not necessarily be followed by a yr of bad production because of high no. of first-yr breeders). Our study and available data indicate that weather and nutrition appear to have a greater influence on bobwhite production than age. Thus, management practices that potentially affect population age structure (e.g., differential harvest vulnerability by age class) should not be impacting bobwhite productivity within the context of age-specific reproduction.

ACKNOWLEDGMENTS

We thank the Caesar Kleberg Wildlife Research Institute, The Richard M. Kleberg, Jr. Center for Quail Research, and Texas A&M University-Kingsville for providing financial and logistical support. The laboratory research was funded by the Harvey Weil Sportsman Conservation Trust. Field research was financially supported by the George and Mary Josephine Hamman Foundation, Amy Shelton McNutt Charitable Trust, William A. and Madeline Welder Smith Foundation, Bob and Vivian Smith Foundation, Robert J. Kleberg, Jr., and Helen C. Kleberg Foundation, Texas State Council of Quail Unlimited, the South Texas, Houston, and East Texas Chapters of Quail Unlimited, Quail Associates, and private contributions. We thank King Ranch Inc. for providing access to the study area and San Tomas Hunting Camp for in-kind support. We thank B. M. Ballard, L. A. Brennan, D. Rollins, W. C. Stasey, Associate Editor Hall, and 2 anonymous reviewers for providing helpful comments on an earlier version of this manuscript. Field data for this research were provided by the South Texas Quail Research Project. This manuscript is Caesar Kleberg Wildlife Research Institute Publication Number 06-014.

LITERATURE CITED

- Brooks, J. L. 2005. The role of covey demographics in northern bobwhite (*Colinus virginianus*) production. Thesis, Texas A&M University, College Station, USA.
- Brown, D. E. 1989. Arizona game birds. University of Arizona Press, Tucson, USA.
- Cain, J. R., S. L. Beasom, L. O. Rowland, and L. D. Rowe. 1982. The effects of varying dietary phosphorus on breeding bobwhites. *Journal of Wildlife Management* 46:1061-1065.
- Campbell, H., D. K. Martin, P. E. Ferkovich, and B. K. Harris. 1973. Effects of hunting and some other environmental factors on scaled quail in New Mexico. *Wildlife Monographs* 34.
- Curio, E. 1983. Why do young birds reproduce less well? *Ibis* 125:400-404.
- Dimmick, R. W. 1974. Populations and reproductive effort among bobwhite in western Tennessee. *Proceedings of the Southeastern Association of Game and Fish Commission* 28:594-602.
- Forslund, P., and T. Pärt. 1995. Age and reproduction in birds: hypotheses and tests. *Trends in Ecology and Evolution* 10:374-378.
- Francis, W. J. 1970. The influence of weather on population fluctuations in California quail. *Journal of Wildlife Management* 34:249-266.
- Ghalambor, C. K., and T. E. Martin. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. *Science* 292:494-497.
- Giuliano, W. M., R. S. Lutz, and R. Patiño. 1996. Reproductive responses of adult female northern bobwhite and scaled quail to nutritional stress. *Journal of Wildlife Management* 60:302-309.
- Gould, F. W. 1975. Texas plants—a checklist and ecological summary. Texas Agricultural Experiment Station Miscellaneous Publication 585, College Station, USA.
- Guthery, F. S. 2002. The technology of bobwhite management. Iowa State Press, Ames, USA.
- Guthery, F. S., N. E. Koerth, and D. S. Smith. 1988. Reproduction of northern bobwhites in semiarid environments. *Journal of Wildlife Management* 52:144-149.
- Guthery, F. S., and W. P. Kuvlesky. 1998. The effect of multiple-brooding on age ratios of quail. *Journal of Wildlife Management* 62:540-549.
- Guthery, F. S., C. L. Land, and B. W. Hall. 2001. Heat loads on reproducing bobwhites in the semiarid subtropics. *Journal of Wildlife Management* 65:111-117.
- Heffelfinger, J. R., F. S. Guthery, R. J. Olding, C. L. Cochran, Jr., and C. M. McMullen. 1999. Influence of precipitation timing and summer temperatures on reproduction of Gambel's quail. *Journal of Wildlife Management* 63:154-161.
- Hernández, F., F. S. Guthery, and W. P. Kuvlesky, Jr. 2002. The legacy of bobwhite research in south Texas. *Journal of Wildlife Management* 66:1-18.
- Hernández, F., F. Hernández, J. A. Arredondo, F. C. Bryant, L. A. Brennan, and R. L. Bingham. 2005. Influence of precipitation on demographics of northern bobwhites in southern Texas. *Wildlife Society Bulletin* 33:1071-1079.
- Johnsgard, P. A. 1973. Grouse and quails of North America. University of Nebraska Press, Lincoln, USA.
- Kiel, W. H. 1976. Bobwhite quail population characteristics and management implications in south Texas. *Transactions of the North American Wildlife Conference* 41:407-420.
- Kirkpatrick, R. L. 1988. Comparative influence of nutrition on reproduction and survival of wild birds and mammals: an overview. Caesar Kleberg Wildlife Research Institute Press, Kingsville, Texas, USA.
- Klimstra, W. D., and J. L. Roseberry. 1975. Nesting ecology of the bobwhite in southern Illinois. *Wildlife Monographs* 41.
- Koerth, N. E., and F. S. Guthery. 1991. Water restriction effects on northern bobwhite reproduction. *Journal of Wildlife Management* 55:132-137.
- Kontogiannis, J. E. 1967. Day and night changes in body weight of the white-throated sparrow, *Zonotrichia albicollis*. *Auk* 84:390-395.
- Lehmann, V. W. 1953. Bobwhite population fluctuations and vitamin A. *Transactions of the North American Wildlife Conference* 18:199-246.
- Leopold, A. S., M. Erwin, J. Oh, and B. Browning. 1976. Phytoestrogens: adverse effects on reproduction in California quail. *Science* 191:98-100.
- Lusk, J. J., F. S. Guthery, and S. J. DeMaso. 2001. Northern bobwhite (*Colinus virginianus*) abundance in relation to yearly weather and long-term climate patterns. *Ecological Modelling* 146:3-15.
- Martin, T. E. 2004. Avian life-history evolution has an eminent past: does it have a bright future? *Auk* 121:289-301.
- National Research Council. 1977. Nutrient requirements of poultry. Seventh edition. National Academy of Sciences, Washington, D.C., USA.
- Nestler, R. B. 1949. Nutrition of bobwhite quail. *Journal of Wildlife Management* 13:342-358.
- Nestler, R. B., and W. W. Bailey. 1943. Vitamin A deficiency in bobwhite quail. *Journal of Wildlife Management* 7:170-173.
- Nestler, R. B., W. W. Bailey, M. J. Rensberger, and M. Y. Benner. 1944. Protein requirements of breeding bobwhite quail. *Journal of Wildlife Management* 8:284-289.
- Palmer, W. C. 1965. Meteorological drought. Weather Bureau Research Paper Number 45, U.S. Department of Commerce, Washington, D.C., USA.
- Parmalee, P. W. 1955. Some factors affecting the nesting success of the bob-white quail in east-central Texas. *American Midland Naturalist* 53:45-55.
- Robinson, T. S. 1963. Egg production by bobwhites under a fifteen-hour photoperiod. *Journal of Wildlife Management* 27:215-220.
- Rollins, D., and J. P. Carroll. 2001. Impacts of predation on northern bobwhite and scaled quail. *Wildlife Society Bulletin* 29:39-51.
- Rosene, W. 1969. The bobwhite quail—its life and management. Rutgers University Press, New Brunswick, New Jersey, USA.
- Saether, B.-E. 1990. Age-specific variation in reproductive performance of birds. *Current Ornithology* 7:251-283.
- Scifres, C. J. 1980. Brush management: principles and practices for Texas and the Southwest. Texas A&M University Press, College Station, USA.
- Stearns, S. C. 1976. Life-history tactics: a review of the ideas. *Quarterly Review of Biology* 51:3-47.
- Stokes, M. E., C. S. Davis, and G. G. Koch. 1995. Categorical data analysis using the SAS system. SAS Institute, Cary, North Carolina, USA.
- Williams, G. C. 1966. Natural selection, the cost of reproduction, and a refinement of Lack's principle. *American Naturalist* 100:687-690.
- Williamson, D. L. 1983. Soil survey of Brooks County, Texas. U.S. Department of Agriculture, Soil Conservation Service, Washington, D.C., USA.
- Zar, J. H. 1999. Biostatistical analysis. Prentice Hall, Upper Saddle River, New Jersey, USA.

Associate Editor: Hall.