AGE-SPECIFIC NESTING PERFORMANCE BY NORTHERN BOBWHITES

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ABSTRACT

Greater reproductive productivity of adult versus juvenile northern bobwhites (*Colinus virginianus*) has been hypothesized as a factor for rapid population growth. Research on bobwhites in the western portions of the species' range has not supported this hypothesis; however, no effort has been made to investigate age-specific reproduction on population dynamics in the southeast. We measured age-specific reproductive parameters between adult and juvenile bobwhites during 2000–2010. We radio-marked 1,069 females of which 308 were adults and 761 were juveniles. Nests per hens for adults (0.78 nests/hen) was slightly greater than that for juveniles (0.65 nests/hen) ($P = 0.09$). Adult productivity was 1.7 times greater than for juveniles in 4 of 10 years which corresponded to years of population growth. No differences were found in initial clutch sizes or nesting success. Adult hens began incubation earlier than juveniles in all but 1 year suggesting increased nesting may be due to early recrudescence in adults. The magnitude of age-specific reproductive differences in short-lived species like bobwhites is not as great as long-lived species, but has implications for understanding bobwhite population dynamics and harvest.

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Key words: age-specific reproduction, *Colinus virginianus*, Florida, northern bobwhite, population dynamics, reproductive ecology

INTRODUCTION

Northern bobwhite populations exhibit large fluctuations over time as a result of high annual mortality and variable reproductive productivity (Stoddard 1931, Rosene 1969, Guthery et al. 1988). Factors that influence reproductive productivity of bobwhites may help to explain population fluctuations. One potential factor is age and its affect on reproductive effort and success. Yearling birds have been found to recrudesce later in spring, begin incubation later in the breeding season, and produce smaller clutches and fewer nests than adults (Curio 1983, Sæther 1990, Martin 1995). Additionally, adults may have better chick-rearing skills than juveniles (Hepp and Kennamer 1993, Caizergues and Ellison 2000). Alternatively, older females in long-lived species may have reduced fertility rates due to senescence (Sæther 1990). Age-specific reproduction among galliforms has been shown to occur in some species of grouse (Caizergues and Ellison 2000) and eastern wild turkeys (*Meleagris gallopavo silvestris*) (Roberts et al. 1995, Norman et al. 2001). Improvement in parenting skills with age has been demonstrated in ring-necked pheasants (*Phasianus colchicus*) (Brittas et al. 1992). Other studies of galliforms, such as lesser prairie-chickens (*Tympanuchus pallidicinctus*), have not found age-specific differences in reproductive performance (e.g., Pitman et al. 2006).

Hernández et al. (2007) conducted the most comprehensive study on age-specific reproduction in bobwhites and found no differences in major reproductive variables used to explain productivity. However, they cited a study with a larger sample size of wild radio-marked bobwhites that had a greater nesting rate among adults than subadults during a stressful (e.g., drought) weather year (Brooks 2005) and suggested field studies with large sample sizes should consider the effects of age on reproduction. Other researchers have suggested earlier nesting and increased nest production among older bobwhites (Lehmann 1953, Rosene 1969). No field studies have been conducted to date to examine the effect of age on reproduction for bobwhites in the southeastern United States. Annual population fluctuations in this region are more stable than in arid portions of the bobwhites' range, although populations may fluctuate 50% or more annually (Palmer et al. 2002). Thus, the role that age-specific reproduction has on population fluctuation is important for southeastern populations as well. Age-specific information could be useful for modeling bobwhite populations and for examining harvest rates.

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The objective of our study was to examine differences in nesting productivity between adult and juvenile bobwhite hens in north Florida. We specifically were interested in differences in age-specific clutch size, nest initiation dates, nesting rate, and nesting success to learn if age-specific productivity of bobwhites may be influenced by these factors.

STUDY AREA

Tall Timbers Research Station (~1,570 ha in size) is in north Leon County, Florida. The property primarily consists of rolling hills with the majority (66%) being upland forests of loblolly pine (*Pinus taeda*), shortleaf pine (*P. echinata*), and a lesser amount of longleaf pine (*P. palustris*). Pine uplands are intermixed with hardwood drainages (21%) and annually-disked fallow fields (13%), 0.4 to 1.2 ha in size. The property is maintained as a frequently-burned pine savanna with approximately half of the upland area burned each year to maintain suitable groundstory for bobwhites. Other management practices include mowing and roller chopping to reduce hardwood and pine encroachment. Supplemental feeding occurred on a portion of the property during this study. Radio-marked bobwhites were equally distributed on areas with and without supplemental feed.

METHODS

Data Collection

We monitored reproduction of radio-marked bobwhites from 2000 to 2010. Too few adults ($n = 4$) were monitored in 2001 to include in this analyses. We captured bobwhites in walk-in funnel traps (Stoddard 1931) during January each year. We recorded gender, age, and mass of each bobwhite and banded them with uniquely-numbered aluminum leg bands (National Band and Tag Co., Newport, KY, USA); a sample of birds was equipped with a 6.5-g necklace-style radio transmitter (American Wildlife Enterprises, Monticello, FL, USA). We classified bobwhite age as juvenile or adult based on their primary coverts (Rosene 1969). Trapping, handling, and marking procedures were consistent with the guidelines of the Tall Timbers Research Inc. Institutional Animal Care and Use Committee Permit (#GB2001-01).

Radio-marked bobwhites were tracked during the breeding season (15 Apr–1 Oct) ≥ 5 times a week using a 3-element, directional, yagi antenna and hand-held receivers using homing techniques (White and Garrott 1990). We plotted bobwhite locations on detailed land cover maps created using ArcGIS 9.3 (ESRI 2007). Bobwhites were assumed nesting if we observed them at the same location over 2 consecutive days. We monitored the incubating hen each morning and afternoon to ascertain clutch size when the incubating bird was off the nest. We checked incubating bobwhites daily until the nest hatched or failed. We counted hatched egg shells to ascertain the number of fledged chicks.

Data Analysis

We considered a hen to be part of the breeding population if they were alive on 15 April each year. We calculated age-specific nests per hen by dividing the total number of nests produced by each age cohort during the entire nesting season by the respective number of hens in each age cohort. We used the ratio of nests per hen for adults and juveniles on a yearly basis, rather than summing over all years, because we were interested if the ratio was stable or varied from year to year in relation to population growth. We tested the prediction that adult hens produce more nests during a nesting season than juvenile hens by comparing the ratio of nests per hen for adults to juveniles to unity using a one sample t-test. We would reject the hypothesis that age had no effect on nest productivity of bobwhite hens if the ratio was greater than unity.

We tested the hypothesis that adults may have higher nesting success as a result of previous nesting experience by comparing the ratio of nesting success for adults to juveniles to unity using a one-sample t-test. Greater nesting success for adults than juveniles would suggest survival of nests during egg-laying may be greater for adults as well. Thus, any increase in incubated nests observed for adults could be a function of higher survival of nests during egg-laying than increased nesting rate of hens. We considered a nest successful if at least 1 chick fledged. Abandoned nests were censored from nest success calculations.

We considered that age-specific survival could influence our ratio of nests produced per hen for adults and juveniles. Increased nesting could be from longer opportunity to nest rather than from increased nesting tendency if adult hens survived at a greater rate during the nesting season than juvenile hens. We did not conduct inferential statistics on this data set due to small sample sizes (< 10) of radio-marked adult hens surviving the nesting season in most years which made the annual ratios unstable. We were interested, however, if the direction of the relationships was similar when survival rate was removed as a potential influence on nests per hen. We also compared the ratio of nests per hen for adults and juveniles for hens surviving the nesting season for all years combined. We computed age-specific clutch sizes and the date of first incubation and the proportion of hens that nested at least 1 time for each age class.

RESULTS

Overall, 1,069 females (308 adults, 761 juveniles) produced 689 nests of which 218 were incubated by adults and 471 by juveniles (Table 1). Adult hens on average produced 0.78 nests/hen whereas juvenile hens produced 0.65 nests/hen. The ratio (mean $\pm$ SE) of nests per hen for adults to juveniles averaged 1.25 ± 0.133 and was marginally greater than 1 ($t_9 = 1.9$; $P = 0.09$). Nests per hen for adults was greater than juveniles in 5 of 10 years; however, the magnitude was substantially greater in 2000, 2004, 2006, and 2008.

Table 1. Nesting rate and nest success of radio-marked adult and juvenile northern bobwhite hens alive at the beginning of the nesting season (15 Apr) and those that survived the entire nesting season, Tall Timbers Research Station, Leon County, Florida, USA, 2000–2010.

Year	Age	*n*	Nests	Nests/hen	Nest success	Number surviving season	Nests/hen per season
2000	Adult	22	25	1.14	0.44	10	1.8
	Juvenile	63	54	0.86	0.56	22	1.45
2002	Adult	48	31	0.65	0.63	18	1.17
	Juvenile	99	77	0.78	0.70	47	1.15
2003	Adult	32	13	0.41	0.54	6	1.17
	Juvenile	95	44	0.46	0.54	19	1.16
2004	Adult	25	22	0.88	0.71	5	1.20
	Juvenile	76	36	0.47	0.67	15	1.00
2005	Adult	29	14	0.48	0.86	7	1.14
	Juvenile	64	33	0.52	0.69	20	1.05
2006	Adult	29	35	1.21	0.59	16	1.63
	Juvenile	85	56	0.66	0.64	24	1.17
2007	Adult	33	17	0.52	0.47	10	0.50
	Juvenile	63	25	0.40	0.56	18	0.78
2008	Adult	49	23	0.84	0.70	14	1.21
	Juvenile	55	19	0.49	0.67	15	0.33
2009	Adult	17	13	0.76	0.62	4	1.00
	Juvenile	93	76	0.83	0.64	34	1.41
2010	Adult	24	25	0.91	0.48	11	0.91
	Juvenile	68	51	1.00	0.65	29	1.03
All	Adult	308	218	0.78	0.60	101	1.17
years	Juvenile	761	471	0.65	0.63	243	1.03

Overall 344 hens survived from 15 April to 1 October including 101 adults and 243 juveniles. The annual ratio (mean ± SE) of nests per hen for adults to juveniles was 1.28 ± 0.27, although sample sizes of adults were low in several years. Summing over all years, adult hens produced 122 nests (1.21 nests/hen) versus 269 nests for juveniles (1.11 nests/hen) ($P = 0.025$). The greatest differences in nests per hen for adults and juveniles occurred in 2000, 2006, 2007, and 2008.

Nesting success (± SE) was 0.60 ± 0.041 for adults, similar to nesting success of juveniles (0.63 ± 0.018) (Table 1). The ratio of adult to juvenile nesting success was 0.92 but was not statistically different from 1 ($t_9 = -1.53$; $P = 0.16$).

Adult hens that survived the entire nesting season began incubating nests earlier than juveniles in 6 of 7 years (Table 2). Differences in incubation dates for adults to juveniles ranged from 1 day later to 24 days earlier with adults on average beginning nesting 11 days earlier than juveniles over all years. The proportion of hens that survived the nesting season that incubated at least 1 nest was not different for adults (0.87) or juveniles (0.82) ($P = 0.37$). Clutch size averaged (± SE) 12.48 ± 0.79 eggs for adult hens and 12.93 ± 0.08 eggs for juvenile hens.

Table 2. Nesting rate, clutch size, and date of first incubation of nests for radio-marked adult and juvenile northern bobwhite hens that survived the nesting season (15 Apr to 1 Oct), Tall Timbers Research Station, Leon County, Florida, USA, 2000–2006.

Year	Age	*n*	Nesters	Proportion that nested	Clutch size Mean ± SE	Date of first incubation
2000	Adult	10	9	0.90	13.9 ± 0.79	8 Jun
	Juvenile	22	21	0.95	12.9 ± 0.55	18 Jun
2002	Adult	18	17	0.94	12.8 ± 0.72	4 Jun
	Juvenile	47	42	0.89	12.7 ± 0.86	17 Jun
2003	Adult	6	5	0.83	13.5 ± 0.68	3 Jul
	Juvenile	19	16	0.84	12.3 ± 0.94	2 Jul
2004	Adult	5	3	0.60	8.6 ± 1.09	23 Jun
	Juvenile	15	10	0.67	12.6 ± 1.29	4 Jul
2005	Adult	7	5	0.71	13.2 ± 0.66	17 Jun
	Juvenile	20	15	0.75	12.5 ± 0.72	11 Jul
2006	Adult	16	15	0.94	12.9 ± 1.11	8 Jun
	Juvenile	24	20	0.83	12.5 ± 1.04	17 Jun
All	Adult	62	54	0.87	12.5 ± 0.79	
	Juvenile	164	134	0.82	12.9 ± 0.08	

DISCUSSION

Adult bobwhite hens incubated more nests over the course of a nesting season but the magnitude of the difference varied significantly among years. Adults produced on average for all years ~ 25% more nests than juveniles in the breeding population. However, most of the difference in productivity occurred in 4 of 10 years, 2000, 2004, 2006, and 2008 during which the average nest per hen for adults (1.02) was 1.7 times greater than that of juveniles (0.62). Each of these years was followed by 1 to 3 years in which juvenile and adult nest production was approximately equal. The bobwhite population in each of these years increased significantly over the previous year, based on mark-recapture estimates, fall covey counts, and hunter success per unit of effort (W. E. Palmer, unpublished data), especially in 2000, 2006, and 2008; bobwhite populations peaked during 2002 and 2010.

Comparisons of nesting productivity for bobwhites that survived the nesting season also had the same directional relationship as that for our entire data set. However, ratios on an annual basis were unstable due to low sample sizes ($n < 10$) of adults in most years. Nesting productivity of adult hens, averaged across all years, was greater than juveniles. These results suggest adult bobwhites in some years nest more prolifically than juveniles and this may be part of how bobwhite populations increase substantially when conditions permit. There was no difference in the proportion of adult and juvenile hens that incubated 1 or more nests, suggesting greater renesting by adults was the cause of higher nest productivity. Total nest production has been found to be a major factor in percent summer gain in bobwhites (Dimmick 1974, Klimstra and Roseberry 1975). However, further research is needed regarding the causal mechanisms of age-specific nesting in bobwhites and its demographic impact on population dynamics. Adults typically compose ~10–30% of bobwhite populations (Rosene 1969). Demographically, an increase in productivity by a small proportion of the population would not likely impact population growth. However, we have observed juvenile to adult ratios closer to unity following periods of population decline suggesting higher productivity of adults during those years resulted in steeper increases in population size due to adult reproductive performance.

Greater survival of adults could explain increased nest productivity of adults; however, we do not believe this was the cause during our study. Annual survival of adult and juvenile bobwhites on Tall Timbers did not differ in 2 long-term studies (Pollock et al. 1989, Palmer and Wellendorf 2007). Terhune et al. (2007) found no difference in survival of adults and juveniles during a long-term study in Georgia. Thus, we do not believe differences in survival were causal to increased nesting of adults.

There was no difference in nesting success which suggests increased nesting was not likely a function of higher pre-incubation survival of nests of adults versus nests of juveniles. Other studies have found previous experience increases nesting success of birds (Hepp and Kennamer 1989, Martin 1995). There was no difference in success of nests, but adult hens began nesting earlier than juveniles, adding up to 3 weeks to the nesting season. Earlier recrudescence may provide increased nesting season length providing for more time for renesting and increased nest production over the nesting season. That adult bobwhites nested earlier than juveniles is a common finding among birds (Martin 1995).

Hernández et al. (2007) found minor differences in nesting parameters among adults and juveniles. Our study suggests large sample sizes of radio-marked bobwhites over many years is necessary to identify increased nesting productivity because it did not occur each year of study. Sample sizes for adults, even with > 1,000 radio-marked hens, were marginal in many years, especially for hens that survived the entire nesting season. Our results agree with those of Brooks (2005) who suggested, at least in some years, adult bobwhites have higher nesting rates.

MANAGEMENT IMPLICATIONS

This study suggests adult bobwhites have higher productivity in some years and we cautiously suggest this result may influence population growth in some years. This indicates the importance of maintaining high quality nesting and brood-rearing habitat to take advantage of high productivity of adults. Further, it suggests the increase in productivity of adults, if associated with population increases following declining years, may be an important density-dependent process and harvest of adult bobwhites following periods of poor productivity (i.e., few juveniles in the population) could have increased additive effects on population growth. This suggests conservative harvests are more important when juvenile to adult age ratios are skewed towards adults (Williams et al. 2004). Additional research and modeling are needed to verify these implications.

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