Reproductive Effort and Success of Northern Bobwhite in Mississippi

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Abstract: An understanding of the mechanisms by which northern bobwhite (*Colinus virginianus*) populations respond to old-field habitat management is important to evaluate efficacy of these practices. We examined reproductive strategies and success of 114 radio-marked bobwhite on a managed wildlife area in east-central Mississippi during 1994–1996. Fifteen female and 5 male bobwhite incubated 23 nests. Male-incubated nests, female-incubated first nests, and female-incubated renests contributed 21.7%, 65.2%, and 13.0% to total nesting effort, respectively. Female-incubated first nests and male-incubated nests each accounted for 44% of successful nests. Of birds alive on 15 April (40 female and 74 male), 37.5% of females and 6.8% of males attempted ≥1 nest, whereas 12.5% of females and 5.4% of males were successful. Female nest initiation peaked in mid-May prior to the onset of male nesting. Clutch size ranged from 8 to 18, and mean clutch size was 12.3, 9.5, and 10.8 for female-incubated first nests, female-incubated renests, and male-incubated nests, respectively. Mayfield nest survival was 0.40 during the incubation period, and 0.21 from the start of laying through the incubation period. Nest predation (79%) was the primary cause for nest failure and mammals were the most common predators. Despite intensive habitat management, low reproductive success and declining breeding-season survival during the study period halted population growth on this area and contributed to declining breeding populations.

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Northern bobwhite populations have declined throughout most of their range since the 1960s (Droege and Sauer 1990, Brennan 1991, Church et al. 1993). These declines have been attributed to habitat changes associated with agricultural and silvicultural practices (Vance 1976, Roseberry et al. 1979, Exum et al. 1982, Roseberry 1993). Although bobwhite populations exist in a range of seral stages (Spears et al. 1993), efforts to reverse population declines typically focus on proactive habitat management regimes (Brennan 1991) characterized by maintenance of plant communities to which the species is adapted. In agricultural and forested landscapes of the Midwest and Southeast, this management typically involves maintenance of early successional plant communities.

Soil disturbance and fire are 2 management tools that can inhibit natural succession, reduce perennial grasses and woody invasion, and increase annual forbs, legumes, and bare ground (Stoddard 1931, Rosene 1969, Burger et al. 1990). These practices may improve habitat quality of grasslands and old fields for bobwhite (Stoddard 1931, Rosene 1969, Buckner and Landers 1979, Lewis and Harshbarger 1986, Burger et al. 1990, 1994). Although the efficacy of these practices in increasing food availability (Buckner and Landers 1979, Lewis and Harshbarger 1986) and invertebrate abundance (Hurst 1972, Manley et al. 1994) and improving vegetation structure (Stoddard 1931, Rosene 1969, Manley 1994) has been well demonstrated, bobwhite population response to management has not been as thoroughly investigated. Moreover, the mechanisms of population response (changes in survival, reproductive effort, nest success, brood survival) often have not been identified or demonstrated (Webb and Guthery 1982). Lack of efforts to evaluate the efficacy of management practices illustrate an inadequate knowledge of processes affecting bobwhite populations (Brennan 1991, 1993; Church et al. 1993; Robel 1993; Stauffer 1993).

Bobwhite experience high annual mortality, ranging from 70% to 95% (Roseberry and Klimstra 1984, Curtis et al. 1988, Pollock et al. 1989, Burger et al. 1995*a*), with mean annual mortality varying with latitude (Guthery 1997). Yet bobwhite populations exhibit a remarkable ability to recover from high overwinter mortality, rebound from catastrophic weather events, and exploit newly available resources. Intuitively, high recruitment of juveniles into the fall population must be the primary factor that allows populations to persist under such high mortality and recover from low densities.

Two studies correlated indices of total nest production and fall population size (Dimmick 1974, Roseberry and Klimstra 1984). However, several components of reproduction (nesting effort, nest success, renesting rate, double-clutching rate, male-incubation, and brood survival) may contribute to high recruitment (Guthery 1997). Bobwhite may renest multiple times during a given breeding season (Rosene 1969, Curtis et al. 1993, Suchy and Munkel 1993, Burger et al. 1995*b*). Female bobwhite may lay a clutch that is incubated by a male while they incubate a subsequent clutch (Curtis et al. 1993, Suchy and Munkel 1993, Burger et al. 1995*b*). Additionally, females may incubate a second clutch after successfully hatching an initial nest (Stanford 1972, Sermon and Speake 1987, Curtis et al. 1993, Suchy and Munkel 1993, Burger et al. 1995*b*). The relative contribution of these individual components to total reproduction has been quantified in Missouri and Iowa. However, their role in population to habitat management has rarely been addressed.

We studied the reproductive ecology of radio-marked bobwhite in intensively managed, old-field habitats in east-central Mississippi to better understand the mechanisms of northern bobwhite (*Colinus virginianus*) population response to old-field habitat management practices. Our objectives were to estimate the individual components of reproductive effort and success for male and female bobwhite and to document temporal patterns in productivity relative to an ongoing habitat management program.

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Methods

Study Area

We studied bobwhite on the Trim Cane Wildlife Research and Demonstration Area (TCWA) in Oktibbeha county in east-central Mississippi. The TCWA consisted of approximately 320 ha of old-field, ditch-bank and fencerow habitat located on Mississippi Highway 389, 10 km north of Starkville, Mississippi. The area came into possession of the MDWFP through a default Farmers' Home Administration loan, lies within the Trim Cane Creek floodplain, and was under row crop production until 1986. Natural plant succession began following the last row crop harvest in 1986, and the developing vegetation community consisted primarily of broomsedge (*Andropogon virginicus*), Johnsongrass (*Sorghum halepense*), and annual and perennial forbs. Pioneer hardwood species such as box elder (*Acer negundo*) and green ash (*Fraxinus pennsylvanica*) also invaded moist areas in fields adjacent to Trim Cane Creek and areas of poor drainage throughout the study area.

TCWA has nearly flat topography with 0 to 5% slope. Urbo silt clay loam is the predominant soil type; however, Leeper silt clay loam and Adaton, Longview, Prentiss, Longview, and Providence silt loams also occur on the area (Brent 1973). Soil pH is strongly acidic to very strongly acidic, and soil permeability is slow (Brent 1973). Soils generally have slow runoff and ponding frequently occurs during periods of heavy rainfall. The area is dissected by a network of drainage canals left after the channelization of Trim Cane Creek. Most of TCWA is subject to frequent inundation in the winter and spring.

Bobwhite habitat management practices were initiated by TCWA in 1991 (Manley 1994) to evaluate bobwhite habitat use of fallow fields under 4 management practices (prescribed burning, strip-disking, burning-disking, and natural succession). Prior to 1991, mean field size was 28 ha. Since 1991, the area has been managed as a mosaic of 50 small fields averaging 6.5 ha. From 1993 to 1996, average composition of the area was 10.3% control (unmanipulated old-field vegetation with substantial woody component), 20.7% burned, 14.0% disked, 14.8% burned-disked, 23.0% wooded, 7.4% pasture, and 9.8% row crops.

Trapping and Telemetry

We trapped bobwhite in late winter, 1994–1996, while coveys were intact, to detect pair formations from the onset of the breeding season. We continued trapping through mid-May to replace birds lost to mortality and maintain an adequate radio-marked sample. We captured bobwhite with collapsible walk-in funnel traps baited with commercial, 3-grain chicken scratch or cracked corn (Stoddard 1931). Birds were aged, sexed, weighed to the nearest g, banded with a #7 aluminum legband, radio-instrumented with a 5-6-g, pendant-style transmitter, and released at the capture site. Radio-transmitters operated on the 148–150 MHz band and included a mortality sensor switch and a 25-cm antenna. We assumed that capture, handling, and radio-marking did not affect reproductive effort or reproductive success. We also assumed captured birds were drawn randomly from the population.

We located radio-marked bobwhite 5 days/week using programmable scanning receivers and handheld Yagi and H-series antennas. We approached birds to within 25 m from ≥2 directions, and plotted the estimated location on reproduced copies of aerial photos or used a differentially corrected global positioning system to determine location (Burger et al. 1995*a*). Radio-marked birds observed in the same location for 2 consecutive days were assumed to be incubating. We placed flagging >10 m from the estimated nest location, and determined the exact location and number of eggs when the bird was away from the nest. We minimized direct observation of the nest, and assumed observer activities had no effect on nest success. We monitored nesting radio-tagged birds daily from >25 m and determined nest fate to within 1 day. Successful nests were those that produced ≥1 chick; abandoned nests were those for which the incubating bird left the nest intact, survived, and did not return; and destroyed nests included those in which ≥1 egg was destroyed and any remaining eggs were not incubated for the remainder of the 23-day period.

In 1992, we established 11 permanent call count stations distributed throughout the study area. From 1992 to 1996, we conducted 5-minute, calling male counts on each of 3 mornings during the second week of June. Counts were completed during the first 3 hours after sunrise. The mean number of calling males/station was used as an index to breeding density.

Analyses

We estimated nesting rate, nest success, and renesting rate for each sex based on a spring population of radio-marked birds, surviving past 15 April. We were not able to detect nesting activity until the 1st day of incubation; therefore, our estimates of nest success and renesting rate may over- and underestimate their true respective population parameters, respectively. In the analysis, we included birds that were captured up to the final trapping day (24 May). We defined nesting rate as the percentage of radio-marked birds that attempted to incubate ≥1 nest, and nest success as the percentage of birds that successfully hatched ≥1 nest (Burger et al. 1995*b*). Renesting rate was the proportion of birds incubating a second nest after unsuccessfully incubating an initial nest. We estimated nest success for each nest type using the Mayfield method (Mayfield 1961). We tested the null hypotheses of no differences in nest success among years and nest types using likelihood radio tests.

We tested the null hypothesis of no difference in mean number of calling males among years (as an index to population density) using 2-way analysis of variance

(ANOVA) with station and time as main effects. We used the mean number of males/station over the 3 observation days each year as the response variable and tested the year main effect using the year*station interaction as an error term. We used Tukey's HSD multiple comparison to test for differences among years following a significant ($P < 0.05$) ANOVA F-test.

We incorporated reproductive parameter estimates (sex ratio, nesting rate, nest success, clutch size, renesting rate, male nesting rate) and survival estimates in a deterministic population model (L. W. Burger, unpubl. data) to examine predicted percent summer change, spring to spring population change, and number of chicks/female. This model was fully specified, including all potential components of reproduction and survival (initial sex ratio; male and female incubation rate; male- and female-incubated nest success; clutch size for female first nests, female-incubated renests, and male-incubated nests; nest success of female first nests, female-incubated renests, and male-incubated nests; nest success of female first nests, female-incubated renests, and male-incubated nests; renesting rate; double-clutching rate; brood survival; adult breeding season survival; and adult overwinter survival; L. W. Burger, unpubl. data). We did not have valid estimates of brood survival and overwinter survival, so we substituted estimates from the literature. We assumed that in an unhunted population, fall-spring survival would equal or exceed spring to fall survival (Roseberry and Klimstra 1984, Curtis et al. 1988), thus we used estimates of breeding season survival on this area (Taylor et al., in press) as an approximation to fall-spring survival. Estimates of brood survival are scarce in the published literature and typically based on small samples. In our population model, we used estimates of brood survival from 59 radio-marked broods in Oklahoma (DeMaso et al. 1997).

Results

We used 74 male and 40 female radio-marked bobwhite to estimate reproductive success and contribution to production. Of these, 5 males and 15 females incubated 23 nests. We also report the chance encounter of an aggregate nest (Stoddard 1931:27–28) containing 22 eggs that was incubated for 1 day by a male, abandoned, and destroyed 6 days later.

Nesting Rate and Success

Male nesting rate was similar between years ($\chi^2 = 0.07$, 2 *df*, $P = 0.95$). However, we detected a greater proportion of females nesting in 1995 and 1996 than in 1994 ($\chi^2 = 6.06$, 2 *df*, $P = 0.05$; Table 1). Of adults in the spring population, 5.4% of males and 12.5% of females successfully hatched a nest (Table 1). Of birds that survived until 1 September (9 F, 12 M), 78% of females and 25% of males incubated ≥1 nest, 22% of females and 25% of males hatched ≥1 nest, and 27% of females that failed on an initial nesting attempt renested. No males renested and we observed no instances of double-clutching or shared incubation by bobwhite. Male-incubated nests accounted for 21.7% of total nesting effort whereas female first nests and renests contributed 65.2% and 13.0%, respectively (Table 2). Female-incubated first nests

Table 1. Reproductive effort and success of radio-marked male and female northern bobwhite at Trim Cane Wildlife Research and Demonstration Area, Mississippi, 1 April–27 September, 1994–1996.

Year	Sex	*N*	Nesting rate	Success rate	Renest rate[a]
1994	M	33	0.06	0.06	0.00
	F	18	0.17	0.00	0.00
1995	M	29	0.07	0.03	0.00
	F	11	0.55	0.18	0.25
1996	M	12	0.09	0.09	0.00
	F	11	0.55	0.27	0.50
Pooled	M	74	0.07	0.05	0.00
	F	40	0.38	0.13	0.27

a. Birds that failed on their initial nesting attempt and subsequently renested.

and male-incubated nests each contributed 44.4% to total production over the 3 years at TCWA (Table 2).

Nest Initiation Dates and Clutch Size

Female nest initiation peaked in mid-May before the onset of male nesting (Fig. 1). Initiation of male-incubated nests and female-incubated nests commenced by the 2nd week in June, and additional attempts were recorded throughout August

Table 2. Number of incubated nests ($N = 23$) and successful nests ($N = 9$) of radio-marked northern bobwhite resulting from female first attempts, female renesting after initial nest failure and male incubation at Trim Cane Wildlife Research and Demonstration Area, Mississippi, 1 April–27 September, 1994–1996

	Nest type		
	F-incubated first nest	F-incubated renest	M-incubated nest
Incubated nests			
1994	3	0	2
1995	6	1	2
1996	6	2	1
Pooled	15	3	5
Successful nests			
1994	0	0	2
1995	2	0	1
1996	2	1	1
Pooled	4	1	4

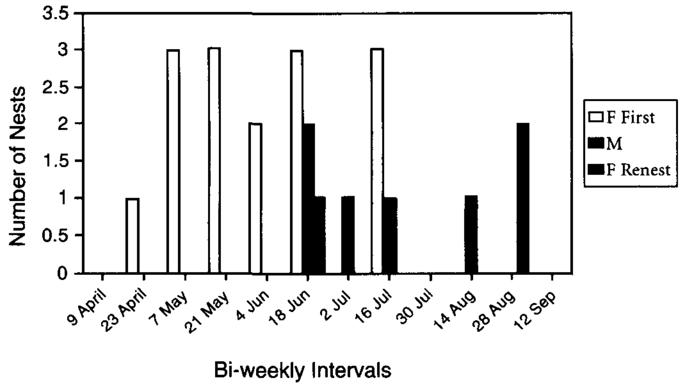

Figure 1. Distribution of nest initiation for female-incubated first nests, male-incubated nests, and female-incubated renests of radio-marked northern bobwhite at Trim Cane Wildlife Research and Demonstration Area, Mississippi, 1994–1996.

(Fig. 1). Incubation of female-incubated first nests was highest during the 1st week in June and fluctuated through the 1st week in August (Fig. 2). Initiation of male incubation peaked early in July, while incubation of female renests peaked in early August; however, we observed males initiating incubation as late as 21 August (Fig. 2).

Mean clutch size was 11.7 ($N = 21$; $SD = 2.9$). Mean clutch size (and associated standard deviation) for female first nests, female renests, and male-incubated nests were 12.3 (3.2), 9.5 (0.7), and 10.8 (2.0), respectively.

Nest Survival

Daily nest survival rates did not differ among years (1994, 0.9625; 1995, 0.9552; 1996, 0.9647; $\chi^2 = 0.2$, 2 *df*, $P = 0.95$). Daily survival did not differ among female-incubated first nests (0.9455), female-incubated renests (0.9574), and male-incubated nests (0.9906; $\chi^2 = 4.7$, 2 *df*, $P = 0.09$), although we observed a non-significant pattern of seasonally increasing daily survival. Overall nest survival for the 23-day incubation period was 0.40 (Table 3). Overall nest survival extrapolated to the length of the mean laying period (14 days) and the 23-day incubation period (36 days) was 0.21. This is a conservative estimate of nest success because it assumes constant daily survival during the laying and incubating periods. Daily nest survival is likely lower during the laying period, resulting in an overestimate of nest survival. Nest depredation (79%) was the primary cause for nest failure and mammals were the most common nest predators (57% of depredated nests). Two attending adults were killed at the nest site.

Relative Abundance

The mean number of calling males/station differed among years ($F = 11.52$; 5,50 *df*; $P < 0.01$) on TCWA. Call counts increased from 1.9 to 3.0 males/station

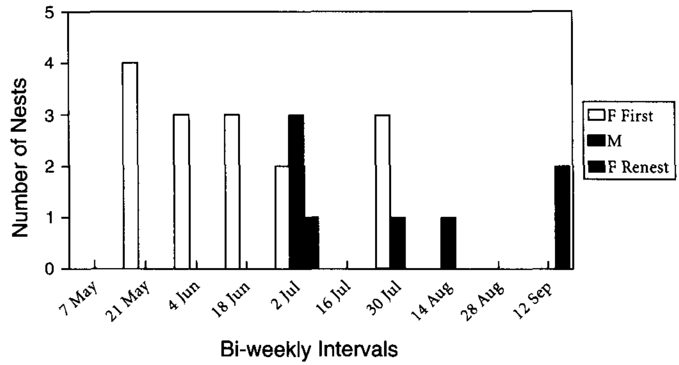

Figure 2. Distribution of nest incubation for female-incubated first nests, male-incubated nests, and female-incubated renests of radio-marked northern bobwhite at Trim Cane Wildlife Research and Demonstration Area, Mississippi, 1994–1996.

following initiation of disking and burning management practices (1992 to 1993); however, the difference was not significant ($P > 0.05$). Relative abundance was similar in 1993 (3.0), 1994 (3.4), and 1995 (3.3), but higher than 1996 (1.2) and 1997 (1.0).

Population Simulation

Given the strongly skewed sex ratio in our trapped sample (63% male), and observed mean rates of reproductive effort, reproductive success, and breeding season survival, our population simulation resulted in a percent summer change of -23% and recruitment of 2.09 chicks/hen in the female population. A simulation with parameter values set to our observed means resulted in a 70% decline in spring to spring population levels. To evaluate a "best case scenario," we substituted our highest observed values for each parameter in the model. Under this scenario, percent summer gain was only 42% with 2.95 chicks/hen produced, and spring to spring populations declined by 24%. Populations clearly are not sustainable under the recruitment and survival rates that we observed.

Table 3. Mayfield nest survival rate (S) of female-incubated first nests, female-incubated renests, and male-incubated nests of radio-marked northern bobwhite at Trim Cane Wildlife Research and Demonstration Area, Mississippi, 1 April-27 September, 1994–1996.

	Nest Type											
	F first nests			F renests			M nests			All nests		
Year	*N*	*S*	SE	*N*	*S*	SE	*N*	*S*	SE	*N*	*S*	SE
1994	3	0.12	0.15	0			2	1.0	0.00	5	0.42	0.2
1995	6	0.33	0.21	1	0.14	0.27	2	0.54	0.23	9	0.35	0.15
1996	6	0.33	0.18	2	0.51	0.11	1	1.0	0.00	9	0.40	0.16
Pooled	15	0.28	0.11	3	0.37	0.26	5	0.81	0.17	23	0.39	0.03

Discussion

Nest survival during incubation in our study (0.40) was similar to that reported in Florida (0.45, DeVos and Mueller 1993) and Missouri (0.44, Burger et al. 1995*b*). As in these other studies, our estimates of nesting rate and success rate are based on incubated nests and thus may overestimate true nesting rate and success. Our estimate for the proportion of females surviving the nesting period that ultimately produce a successful nest (0.22) was much lower than previous studies (0.71, DeVos and Mueller 1993; 0.76, Suchy and Munkel 1993; 0.74, Burger et al. 1995*b*); and our report of nesting rate for all males (0.07) and females (0.38) in the spring population was much less than that reported in Iowa and Missouri (Suchy and Munkel 1993, Burger et al. 1995*b*). Stoddard (1931:24–25) suggested that most pairs surviving the breeding season ultimately produced a successful clutch. Roseberry and Klimstra (1984:78) suggested that ca. 75% of females that survive to fall successfully incubated ≥1 clutch. Given the high rate of nest predation experienced by bobwhite throughout their range, Roseberry and Klimstra (1984:83) estimated that each female that survived the season would have to attempt 2–3 nests to be successful. Although our nest survival rate (based on incubated nests) was similar to that reported in other locales, the nesting rate, mean number of nests per female (1.3), and success rate we observed were insufficient to offset nest destruction. Mean clutch size for female-incubated first nests and male-incubated nests also was lower than that reported by Burger et al. (1995*b*) in Missouri and Roseberry and Klimstra (1984:72) in Illinois.

The lowest percent summer gain observed by Roseberry and Klimstra (1984) was 17% with gains <100% observed in only 5 years of a 26-year study in Illinois. Our model predicted 2.09 chicks per hen in the spring population under mean parameter estimates and 2.95 under highest parameter estimates. Roseberry and Klimstra (1984:83) reported that their observed mean rate of percentage summer change (205%) would require a production of 5.2 chicks/female. Mean parameter estimates from Burger et al. (1995*b*) resulted in production of 5.4 chicks/female in Missouri.

Low apparent reproductive effort and success could result from a combination of poor physiological condition going into the breeding season, high nest destruction rate during the laying period (thus giving the appearance of low reproductive effort), and high mortality of adults during the breeding season prior to initiation of incubation. Roseberry and Klimstra (1984:104–119) suggested that winter and spring weather and habitat conditions, through their effects on body condition and timing of reproduction, might affect reproductive performance. Winter habitat was limited on TCWA and most birds were annually forced off the area during winter by flooding from Trim Cane Creek. Birds radio-marked on TCWA during the breeding season typically wintered on adjacent rowcrop and pasture lands (J. D. Taylor, unpubl. data). We did not quantify the quality of winter resources or physiological condition of birds, consequently we cannot make inferences regarding relationships among breeding condition and reproductive effort or success. However, from 1994 to 1996, we observed apparently increasing reproductive effort and success as our index to breeding density declined, suggesting density-dependent reproduction (Roseberry and Klimstra 1984), but the duration of our study was too short to adequately test this relationship.

Taylor et al. (in press) reported a decline in breeding-season survival rates for radio-marked bobwhite on TCWA following initiation of habitat manipulations in 1991. Survival rates were 0.51, 0.36, 0.34, and 0.17 in 1993, 1994, 1995, and 1996, respectively. High mortality of breeders during the period 1994–1996, coupled with high nest predation, could have contributed to the low apparent nesting rate and success as measured by proportion of the spring population initiating and successfully incubating a nest. Mean breeding season survival rate of 0.37 for radio-marked bobwhite on TCWA was similar to that reported in Missouri (0.33; Burger et al. 1995*a*), where reproductive success was higher. However, Guthery (1997) reported that recruitment per female declined with latitude. Consequently, at lower latitudes, a higher breeding-season survival would be required to achieve a given level of reproductive success. High mortality of adults during the breeding season would not, however, account for the low reproductive effort and success observed for birds that survived to 1 September. Poor physiological condition and/or high nest destruction during the laying period might account for the apparently low success of birds surviving the breeding season.

Call counts indicated an initial response by quail to habitat manipulations on TCWA. However, in the third year of management, populations peaked and began to decline. This phenomenon is frequently reported by land managers, but rarely discussed in the scientific literature. Taylor and Burger (in press) quantified habitat use on TCWA from 1994 to 1996 and reported that bobwhite consistently used manipulated old fields for nesting, brood-rearing, loafing, and roosting. Thus, given the mosaic of habitat patches at TCWA, breeding bobwhite were apparently able to meet seasonal habitat requirements. However, habitat quality may not be purely a function of plant communities and food resources.

The density and diversity of predators may influence habitat quality as measured by fitness of the individual. The response of bobwhite predators to habitat management is unknown. Habitat management for bobwhite may increase habitat suitability for other prey species and contribute to a functional and numerical response of predators. Because of the apparently low proportion of hens reaching incubation from 1994 to 1996 (i.e., low number of nests located at onset of incubation), we suggest that mammalian and reptilian nest predators substantially reduced nest success by depredating nests during the laying and incubation intervals at TCWA. Low production coupled with high mortality of breeders resulted in low recruitment into the fall population. Although northern bobwhite populations likely benefit from habitat manipulations such as prescribed burning and strip-disking, the predator community may respond equally. Studies that quantify only the response of a prey species without quantifying predator abundance, habitat use, and population performance will create an incomplete picture of the ecological relationships among habitat quality and population responses of target species (Leopold and Hurst 1994).

Reproductive effort and success of bobwhite during our study were insufficient to offset high mortality and sustain populations, despite intensive vegetation management. This pattern may be attributable to low physiological condition, high nest predation, high mortality of breeders, or a combination thereof. Future bobwhite research will likely provide a similarly incomplete picture of population processes unless resource availability, physiological condition, predator communities and bobwhite population processes are monitored concomitantly in an integrated research approach. Such studies also should quantify the scale at which habitat manipulations are imposed with respect to the bobwhite-habitat interface suggested by Guthery (1997).

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