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SEASONAL SURVIVAL AND CAUSE-SPECIFIC MORTALITY OF NORTHERN BOBWHITES IN MISSISSIPPI

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ABSTRACT

Knowledge of northern bobwhite (*Colinus virginianus*) survival and rates at which specific mortality agents remove individuals from the population is important for implementation of science-based harvest and habitat management regimes. To better understand population response to habitat management, we monitored 194 radio-marked northern bobwhites in managed old-field habitats in east-central Mississippi, 1993 to 1996. Bobwhite populations increased during the first 3 years following initiation of disking and burning practices. During the 2nd year of bobwhite habitat management breeding season survival (0.509) was high relative to other southeastern populations. However, breeding season survival declined from the 2nd through the 5th year of management (1993, 0.509; 1994, 0.362; 1995, 0.338; 1996, 0.167; $P < 0.001$). Declining seasonal survival was attributable to increasing mammalian mortality from 1993 to 1996 ($P < 0.01$). Avian mortality rates were stochastic and differed among years ($P = 0.04$), while unknown mortality rates were similar ($P = 0.13$). Avian mortality evidently operated in a density-dependent fashion, whereas mammalian mortality continued to increase despite declining bobwhite population. Northern bobwhite cause-specific mortality rates among years differed by sex ($P < 0.01$) and age ($P < 0.01$). Indices of breeding season relative abundance declined with declining survival. We hypothesize that manipulations (burn, disk, burn/disk) which created habitat that met the seasonal requirements of breeding bobwhites and other early successional prey species, may have resulted in a functional and numerical response of mammalian predators.

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INTRODUCTION

Northern bobwhite populations have declined over most of the species range during the last 3 decades (Droege and Sauer 1990, Brennan 1991, Church et al. 1993). In the southeastern United States, North American Breeding Bird Surveys indicate an average annual decline of 3.5% from 1966 to 1996 (Sauer et al. 1997). These declines have been attributed to loss of early successional habitats associated with changing agricultural and forestry practices (Vance 1976, Exum et al. 1982, Roseberry et al. 1979, Klimstra 1982, Roseberry and Klimstra 1984, Brennan 1991). Habitat management is the prescription most frequently offered by wildlife biologists to halt population declines or enhance local bobwhite populations (Brennan 1991).

Numerous studies have described habitats used by bobwhites; several studies have reported population

trends in relation to changing land use practices (Kabat and Thompson 1963, Vance 1976, Exum et al. 1982, Roseberry et al. 1979, Roseberry and Klimstra 1984). However, few studies have monitored bobwhite population response to habitat management. Webb and Guthery (1982) reported that habitat management (disking, brush piles, grazing exclosures, and half-cutting mesquite trees) on mesquite and sand shinnery oak rangelands in Texas apparently increased bobwhite use by 1.5- to 2.2-fold. From 1957–1965, bobwhite populations on Remington Farms, Maryland increased from 5 to 38 coveys/1214 ha following habitat improvements (Burger and Linduska 1967). Ellis et al. (1969) reported that on public wildlife management areas in Illinois, habitat management based on a food-patch system did not maintain quail populations; however, management regimes based on sharecropping and prescribed fire produced densities near 0.4 birds/ha. Burger et al. (1998) reported high seasonal and annual survival of bobwhites on an intensively managed plantation in Georgia. Taylor and Burger (1997) reported reproductive success of bobwhite in relation to successional vegetation management in Mississippi. How-

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ever, no study has monitored temporal changes in bobwhite survival following initiation of a habitat management regime.

Survival, reproduction, and movements into and out of the population are important determinants of population size (Johnson 1994). Precise and unbiased estimates of these parameters are necessary for science-based harvest and habitat management (Curtis et al. 1988, Pollock et al. 1989a, Murphy and Noon 1991, Burger et al. 1994, 1995). To quantify bobwhite population response to management, we examined temporal variation in survival and cause-specific mortality during the 2nd through 5th years following implementation of a vegetation management regime designed to create and maintain early successional plant communities in old-field habitats of northern Mississippi.

STUDY AREA

We captured, radio-marked and monitored bobwhites on the Trim Cane Wildlife Research and Demonstration Area (TCWA), 10 km north of Starkville, Oktibbeha County, Mississippi. The 320 ha-area was under rowcrop production until 1986; natural plant succession began following harvest in 1986. The developing vegetation community consisted primarily of broomsedge (*Andropogon virginicus*), Johnson grass (*Sorghum halepense*), and annual and perennial forbs (Manley 1994). A network of drainage canals left by the channelization of Trim Cane Creek dissected the area, most of which was subject to frequent inundation during winter and spring. Pioneer hardwood species such as box elder (*Acer negundo*) and green ash (*Fraxinus pennsylvanica*) dominated moist areas in fields adjacent to Trim Cane Creek, and areas of poor drainage throughout the study area.

During 1992, TCWA was divided into 50 fields, averaging 6.5 ha in size (Manley 1994) and 1 of 4 management regimes (prescribed burning, strip-disking, burn-disk combinations, control) was randomly assigned to each field. Control areas were allowed to succeed naturally; these areas rapidly developed into a shrub/sapling community dominated by green ash, box elder, eastern baccharis (*Baccharis halimifolia*), or loblolly pine (*Pinus taeda*) (Manley 1994). During the period 1993 to 1996, habitat composition of TCWA and associated private lands used by radio-marked bobwhite averaged 9.1% control, 18.4% burned, 13.5% disked, 14.7% burn/disked, 11.5% pasture, 9.5% rowcrop, 22.6% woody shrubs.

METHODS

We trapped bobwhites with walk-in funnel traps baited with commercial 3-grain chicken scratch or cracked corn (Stoddard 1931). Bobwhites were aged, sexed, weighed to the nearest 1 g, banded with a #7 aluminum leg band, radio-instrumented with a 5–6 g pendant-style transmitter, and released at the capture site. Radio-transmitters operated on the 148.000 to

149.999 MHz band and included a mortality sensor switch and a 25-cm antenna. Trapping began in late winter and continued well into the breeding season to maintain an appropriate sample size.

We located radio-marked birds ≥ 5 days/week using a programmable scanning receiver and handheld Yagi, or H-series antennas. Fixed-wing aircraft were used to locate individuals that dispersed great distances from the study area. Upon detecting a mortality signal, transmitters were located immediately. Evidence at the recovery site, along with transmitter condition, was used to determine the proximate cause of mortality (Dumke and Pils 1973). If signs of both avian and mammalian predators were present, or if no obvious signs were detected, the mortality factor was recorded as unknown.

We based breeding season survival rates on a 180-day interval (1 Apr–27 Sep) which began with covey breakup and initiation of reproduction (Burger et al. 1995). We used the Kaplan-Meier method (Kaplan and Meier 1958) generalized to the staggered entry case (Pollock et al. 1989b,c) to estimate seasonal survival. We made the following assumptions: (1) birds were randomly sampled; (2) survival times were independent among individuals; (3) censoring mechanisms (i.e., radio-failure, emigration) were random; (4) left-censored individuals (entered at staggered intervals) had survival distributions similar to previously marked birds; and (5) survival probability was not affected by trapping, handling, or radio-marking (Pollock et al. 1989b,c; White and Garrott 1990; Burger et al. 1995).

Birds with an unknown fate (radio-loss, radio-failure, emigration from study area, or survival past 27 September) were right-censored. Birds were allowed a 7-day period of adjustment following radio-marking, and all censored and dead observations during this period were excluded from survival analysis (Kurzejeski et al. 1987; Curtis et al. 1988; Pollock et al. 1989b,c; Burger et al. 1995).

We used the program STAGKAM (Kulowiec 1989) to estimate breeding season survival (Pollock et al. 1989b). We used the program CONTRAST (Sauer and Williams 1989) to test hypotheses of no differences in overall survival between ages, sexes, and years. We used the program MICROMORT (Heisey 1985) to calculate cause-specific mortality rates for breeding bobwhite, assuming that daily survival is constant during intervals. Cause-specific mortality rates are represented as the probability of an individual dying from a specific mortality agent during the 180-day breeding season interval, given that other competing mortality agents were present (Heisey and Fuller 1985, Burger et al. 1995). We assumed that censoring mechanisms were random, and censored observations were not considered dead or alive (Pollock et al. 1989b). We compared cause-specific mortality rates between years, ages, and sexes using a likelihood-ratio goodness-of-fit test (Sauer and Williams 1989).

During the second week of June, 1992 to 1996, we conducted 5-minute counts of calling males on each of 3 mornings from 11 permanent stations distributed throughout the study area. Counts were com-

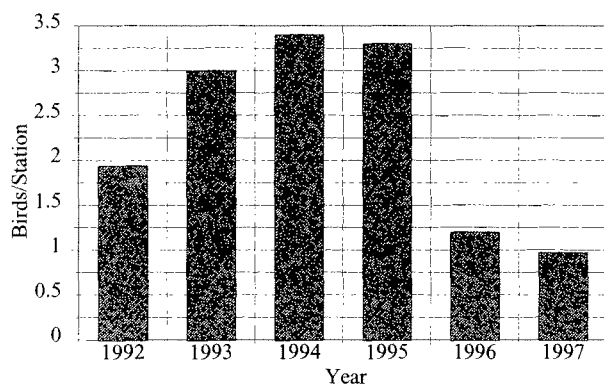


Fig. 1. Mean number of northern bobwhite males calling per station in managed old-field habitats on Trim Cane Wildlife Research and Demonstration Area, MS, 1992 to 1997.

pleted during the first 3 hours after sunrise, and mean number of whistling males/station was used as an index to breeding season density.

RESULTS

We radio-marked 194 bobwhites from 1993 to 1996 (55, 51, 57, and 31, respectively). We excluded 27 birds (13.8%) from analysis because they died or were censored within 7 days of capture (3 in 1993, 11 in 1994, 8 in 1995, and 5 in 1996). Of the remaining 167 marked individuals, 43 were alive at the end of the breeding seasons (24 in 1993, 6 in 1994, 10 in 1995, and 3 in 1996). We right-censored 40 of these 167 individuals (23.3%) due to radio-failure or emigration (27), radio-loss (5), trap-related mortality (5), or radio-related mortality (3).

Relative Abundance

Following initiation of burning and disking management practices on TCWA, mean number of whistling males/station increased from 1992 to 1994 (Figure 1). Relative abundance peaked in 1994, then declined after 1995.

Seasonal Survival

Breeding season survival of bobwhites differed among years ($S_{1993} = 0.509$, $S_{1994} = 0.362$, $S_{1995} = 0.338$, $S_{1996} = 0.167$; $X^2 = 10.54$, 3 df, $P = 0.01$; Table 1) and declined from 1993 to 1996. Survival differed between sexes ($X^2 = 23.04$, 6 df, $P < 0.001$), with females exhibiting higher breeding season survival. Breeding season survival was similar between age classes ($S_{adults} = 0.304$, $S_{sub-adults} = 0.417$; $X^2 = 11.30$, 6 df, $P = 0.08$).

Cause-Specific Mortality

We used observed mortalities of 84 bobwhites to estimate cause-specific mortality rates during the breeding season. Cause-specific mortality rates differed among years ($X^2 = 34$, 14 df, $P < 0.01$). Avian, mammalian, and unknown predators accounted for

Table 1. Breeding season survival of radio-tagged northern bobwhite in managed old-field habitats at Trim Cane Wildlife Research and Demonstration Area, MS, 1 April to 27 September, 1993 to 1996.

Year	N	S ^a	95% C.I. ^b
1993	52	0.509	±0.143
1994	40	0.362	±0.253
1995	49	0.338	±0.171
1996	26	0.167	±0.150

^a Survival rate.

^b 95% confidence interval on survival rates.

most of the natural mortality, whereas mortality directly related to severe weather and accidents (automobile-related mortality) was low (Table 2). Mammalian mortality rate increased significantly from 1993 to 1996 ($X^2 = 13.51$, 3 df, $P < 0.01$; Table 2). Avian mortality rates were stochastic and differed among years ($X^2 = 8.3$, 3 df, $P = 0.04$), while unknown mortality rates were similar across years ($X^2 = 5.74$, 3 df, $P = 0.13$). Cause-specific mortality rates among years differed by sex ($X^2 = 50$, df = 24, $P < 0.01$) and age ($X^2 = 45$, df = 24, $P < 0.01$).

DISCUSSION

Habitat manipulations initiated in 1992 converted grass-bound broomsedge fields into a mosaic of early successional habitat patches that were used by radio-marked bobwhites for nesting, brood-rearing, foraging, loafing and roosting (Taylor and Burger, *this volume*). These management practices were conducted during each year, at the same intervals, with the same intensity. Bobwhite populations on TWCA apparently responded to these practices insofar as breeding season indices of relative abundance increased from 1992–1994. Breeding season survival (51%) during the 2nd year of management was well above that typically reported throughout the Southeast (Curtis et al. 1988, Burger et al. 1995, 1998). In the 2nd and 3rd years of

Table 2. Breeding season cause-specific mortality of radio-tagged northern bobwhite in managed old-field habitats at Trim Cane Wildlife Research and Demonstration Area, MS, 1 April to 27 September, 1993 to 1996.

Year	Cause	Radio-days	N ^a	M ^b	95% C.I. ^c
1993	Mammal	5,239	7	0.1665	±0.112
	Raptor		4	0.0951	±0.088
	Unknown		11	0.2616	±0.132
	Car		1	0.0238	±0.046
1994	Mammal	2,779	4	0.1660	±0.148
	Raptor		9	0.3735	±0.191
	Unknown		2	0.0830	±0.110
	Weather		2	0.0488	±0.066
1995	Mammal	4,534	12	0.2928	±0.138
	Raptor		3	0.0731	±0.080
	Unknown		10	0.2440	±0.131
	Weather		2	0.0488	±0.066
1996	Mammal	1,359	12	0.5815	±0.208
	Raptor		2	0.0969	±0.127
	Unknown		5	0.2423	±0.184

^a Mortalities during season due to specific agent.

^b Cause-specific mortality rate.

^c 95% confidence interval on survival rates.

the study breeding season survival declined. Breeding season survival on TCWA, 1994–95, (0.339) was similar to that of radio-marked bobwhite in Missouri (0.332, Burger et al. 1995), North Carolina (0.328) and Florida (0.40) (Curtis et al. 1988). Mean survival from 1993 to 1996 (0.368) was also similar to other populations reported in the literature; however, pooling over years obscures the temporally declining pattern. Breeding season relative abundance peaked in 1994, following the high breeding season survival observed in 1993. Relative abundance began to decline in 1995, and declined precipitously in 1996. Two years of high breeding season mortality and associated low reproductive success (Taylor and Burger 1997) may have contributed to reduced breeding populations in 1996.

Predation was the primary cause of mortality during the breeding season. Cooper's hawks (*Accipiter cooperi*) and great-horned owls (*Buteo virginianus*) were likely responsible for most avian depredation, whereas most mammalian depredation was attributed to feral cats. Predation may limit, regulate, or have little effect on prey populations. Predation may simply be the proximate mechanism that brings populations down to a level limited by habitat availability (Errington 1934). Predation has been defined as limiting when it prevents or slows a rise in population levels. Newton (1993) defined predation as limiting when it "measurably depresses prey breeding numbers below what the habitat could otherwise sustain." Although predation on nests and young is the primary cause of reproductive failure for many avian species and can influence recruitment and fall population size (Cote and Sutherland 1997), predation on adults is most likely to affect subsequent breeding populations (Newton 1993). Newton (1993) identified several types of predator-prey interactions that might depress breeding bird populations below levels that the habitat would support. He suggested that density-dependent predation can regulate numbers around an equilibrium level below that which habitat would support. The nature of the density-dependent relationship may be mitigated by the quantity and quality of breeding habitat. Further, density-independent predation can in some circumstances result in depression of prey breeding populations and in rare cases, local extirpation.

Predation is generally thought to act in a density-dependent fashion with predators accounting for a smaller proportion of a prey population at low prey densities than at high. Conversely, the rate of predation from a given type of predator should decline as prey populations decline. During our study, predation by avian predators seemingly behaved in a density-dependent fashion, with avian cause-specific mortality generally tracking breeding season relative abundance. This may represent a functional response of avian predators to bobwhite abundance. Keith et al. (1977) similarly reported a functional response of great-horned owls and red-tailed hawks to snowshoe hare abundance. Alternatively, because of the great mobility of avian predators, this may have represented a numerical response of hawks and owls concentrating in an area of high prey density (Newton 1993). In con-

trast, mammalian cause-specific mortality remained relatively constant from 1993 to 1994 as breeding abundance increased. Any mammalian density-dependent response to increasing bobwhite populations from 1992 to 1994 lagged 1 to 2 years behind. Less mobile mammalian predators might be slower to respond to density than avian predators because any numerical response is more dependent on reproduction than immigration (Newton 1993). After the bobwhite population began declining in 1995, predation by mammalian predators was insensitive to bobwhite abundance, doubling each year from 1994 to 1996, despite declining bobwhite abundance. Mammalian cause-specific mortality seemed to drive declining breeding season survival and subsequent year breeding populations, instead of being responsive to bobwhite abundance in a density-dependent fashion.

MANAGEMENT IMPLICATIONS

During our study, we witnessed changes in breeding season survival and rates of cause-specific mortality over a 4-year period on a non-hunted bobwhite population. While our estimates of low survival and high mortality may reflect short-term fluctuations in an isolated portion of east-central Mississippi, bobwhite populations at landscape and regional levels are exhibiting long-term declines. Furthermore, these rates of decline have increased within the past decade, suggesting that current landscape patterns may not allow bobwhite populations to sustain themselves under current habitat conditions, depredation regimes, and hunter harvest rates (Curtis et al. 1988, Burger 1994, 1995). Relationships among bobwhite abundance, landscape composition and complexity, and predation will not be understood until viewed as a dynamic process and evaluated with carefully designed, replicated experiments (Burger et al. 1994, 1995, Leopold and Hurst 1994). Thus, design must include estimates of density and availability of all prey species (Craighead and Craighead 1956); density estimates of the predator community (Latham 1951); and replication across spatial and temporal scales (Miller and Speake 1978).

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