

# Wildlife Technical Session

## Northern Bobwhite Survival and Cause-specific Mortality on an Intensively Managed Plantation in Georgia

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*Abstract:* We estimated seasonal and annual survival and cause-specific mortality of northern bobwhite (*Colinus virginianus*) on an intensively managed plantation in Georgia. During 1992-1997, we radio-marked 813 bobwhite and determined causes and temporal patterns of mortality. Annual survival (0.201) did not differ between sexes and was higher than that reported for other populations throughout the Southeast. Yearly variation in annual survival was primarily associated with variation in overwinter mortality. Seasonal survival did not differ between sexes and mortality was equitably distributed throughout the year with fall-spring survival (0.472) similar to spring-fall survival (0.438). Mammalian (0.353) and avian (0.269) predators were the primary sources of mortality. Mean harvest rate on this area was low (0.051). Both overwinter and breeding season survival were higher on our study area than that reported for other populations throughout the Southeast. More importantly, relative to other studies, the seasonal timing of mortality was redistributed from predominantly prebreeding mortality to an equitable distribution between overwinter and breeding seasons. This may have the net effect of increasing breeding population size and total reproductive output. Unlike regional trends, bobwhite populations on this area have remained stable.

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Northern bobwhite populations have declined over most of the species' range during the last 3 decades (Robbins et al. 1986, Droege and Sauer 1990, Brennan 1991, Church et al. 1993). In the southeastern United States, North American Breeding Bird Surveys indicate a 3.5% per year decline from 1966–1996 (Sauer et al. 1997). Of greater concern is that the rate of decline is apparently increasing. Breeding bird surveys from 1966–1979 indicate a 1.8% per year decline, whereas those from 1980–1996 show a 4.9% per year decline (Sauer et al. 1997). Although predators, fire ants, and agrichemicals have been credited with causing this population decline, declines have most frequently been attributed to habitat destruction 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). Land use practices clearly may reduce the quantity of suitable habitat in the landscape (usable space, Guthery 1997). Habitat fragmentation may also alter the quality of remaining habitat thereby influencing the vulnerability of bobwhite to catastrophic weather events, predation, or harvest (Roseberry 1993). In support of the habitat limitation hypothesis, Brennan et al. (1999) reported that although regional bobwhite populations have exhibited declines, populations on intensively managed plantations in the Red Hills region of southern Georgia and northern Florida have been essentially stable during the same time period.

In addition to declining habitat, predator populations (Church et al. 1993) and relative harvest pressure (Brennan and Jacobson 1992) may be greater than in the past. Numerous authors have suggested that former paradigms concerning relationships among predation, harvest, and bobwhite populations might no longer be appropriate (Curtis et al. 1988; Mueller et al. 1988; Pollock et al. 1989a; Robel 1993; Robinette and Doerr 1993; Burger et al. 1994, 1995a; Hurst et al. 1996).

However, habitat management is the most frequent prescription offered by wildlife biologists to halt population declines or enhance local bobwhite populations (Brennan 1991). Considerable resources are expended annually on habitat management regimes designed to increase bobwhite populations by enhancing habitat quality, quantity, and distribution. Intensive habitat management for northern bobwhite is expensive, averaging \$22/ha/year (\$55/acre/year) in a survey of northern bobwhite plantations in the Red Hills Region of north Florida/south Georgia (Snipe 1994). Insofar as declining populations result from mortality consistently exceeding reproduction, the implicit message of the habitat quality/quantity prescription is that increasing habitat quality and/or quantity will enhance survival, reproduction, or both. However, this hypothesis has not been tested.

Guthery (1997) suggested that bobwhite populations exhibit rather invariant mean demographics over a broad range of climatic, landscape, and predator population conditions and stated that little evidence exists to demonstrate a relationship between bobwhite densities and food abundance or habitat interspersion (although he acknowledged that habitat interspersion might provide a limiting condition). From this, he inferred that some operational constancy in habitat quality exists wherever populations persist and postulated that bobwhite density varies in relation to the amount of usable space in a landscape.

Although bobwhite are among the most intensively studied of species (Church and Taylor 1992), only recently have individual-based survival estimates become available. Monthly, seasonal, and annual survival rates have been reported for populations on Fort Bragg Military installation in North Carolina and Tall Timbers Research Station in Florida (Curtis et al. 1988). Robinette and Doerr (1993) also reported over-winter survival of bobwhite on Fort Bragg. Pollock et al. (1989b) reported annual survival and harvest rates for a 15-year interval on Tall Timbers Research Station. Burger et al. (1994, 1995a) reported monthly, seasonal, and annual survival rates for 2 populations on private agricultural lands in Missouri. Puckett et al. (1995) reported breeding season survival for a population inhabiting intensively cropped agricultural lands in North Carolina. Taylor et al. (1999) estimated breeding season survival for a population on a managed area in Central Mississippi and DeVos and Mueller (1993) reported breeding season survival on Tall Timbers Research Station in Florida. Dixon et al. (1996) reported winter survival on a managed plantation in South Carolina.

Despite these recent advances in our understanding of bobwhite population processes, no study has identified the mechanisms through which bobwhite populations respond to habitat management and few studies have examined demographic parameters of a population in an intensively managed landscape. In this paper, we report seasonal and annual survival and cause-specific mortality of bobwhite on an intensively managed plantation in southwest Georgia and test hypotheses concerning the sex-specific nature of seasonal and annual survival and cause-specific mortality. We interpret the significance of cause-specific mortality patterns in the context of a landscape where resources are essentially unlimited for bobwhite.

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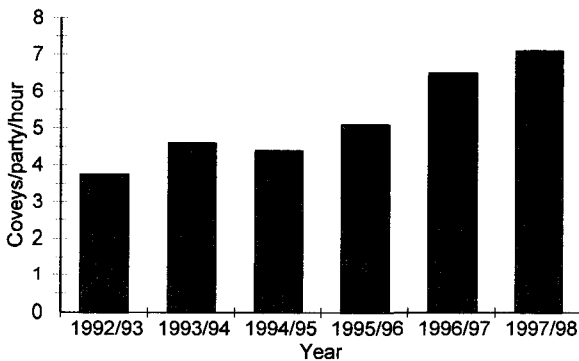
## Methods

From 1 February 1992 to 31 March 1997, we radio-marked bobwhite on portions of an 8,094-ha privately-owned plantation, managed intensively for high density bobwhite populations and quality bobwhite hunting. The plantation is located in a matrix of other quail plantations totaling >80,000 ha under >20 ownerships. This portion of the upper coastal plain is characterized by the Orangeburg-Lucy-Grady soil association (sandy loams, loamy sands, and sandy clays) with slopes from 0%–8%. This property consists primarily of low-basal area, open pine forests (80%) with small (1–4 ha) rotationally-cropped agricultural fields distributed throughout (20%). The forest is predominantly longleaf pine (*Pinus palustris*) or planted slash pine (*P. elliotii*) with interspersed clumps of live oak (*Quercus virginiana*), southern

red oak (*Q. falcata*), water oak (*Q. nigra*) and various understory shrubs. Topography is relatively flat with few wooded drains and no substantial hardwood drains. Forests were maintained in an open pine-grassland structure (9m<sup>2</sup>/14ha) with commercial thinning, annual fire (~70% burned annually), hardwood midstory removal, brush mowing, and disking. The open canopy and frequent disturbance regime has created a herbaceous groundcover dominated by broomsedge (*Andropogon* sp.), annual broad-leaved forbs, and legumes.

Small fields were maintained with rotational agriculture (2-year planted-fallow rotation) and fall disking. Typically, the edges of fields were maintained in corn (*Zea mays*) food plots or the previous year's fallow food plot and the center of the field was disked in October. Bicolor lespedeza was planted down the center or along the edge of fields and occurred in scattered patches throughout the woodlands. During the growing season, the disking regime from the previous fall stimulated development of a lush, herbaceous community dominated by ragweed (*Ambrosia* sp) and partridge pea (*Cassia* sp). Additionally, bobwhite were provided supplemental feed (milo or corn), broadcast biweekly throughout the year. In addition to habitat management and supplemental feeding, the plantation maintained an intensive predator management program, removing as many mammalian nest predators as possible during the regular hunting/trapping season. Estimates of bobwhite density on this plantation during our study were not available. However, from 1992–1998 covey finds/hunting party/hour increased from 3.75 to 7.1, suggesting an increasing population trend (Fig. 1).

During October–November and February–April 1992–1996, we trapped bobwhite with corn-baited funnel traps (Stoddard 1931) and determined age and sex, then weighed, banded, radio-marked, and released them at the capture site. We radio-marked birds with a 6.0–6.5g, pendant-style, activity-sensitive transmitter. We located birds  $\geq 5$  days per week using hand-held Yagi antennas and triangulation or homing (White and Garrott 1990). Upon detection of inactivity we immediately located the



**Figure 1.** Bobwhite population trends indexed by mean number of covey finds/hunting party/hour on an intensively managed plantation in southwest Georgia, 1992–1997.

transmitters and documented the proximate cause of mortality based on sign at the location and damage to the transmitter (Dumke and Pils 1973). We characterized mortalities as attributable to mammalian, avian, harvest, or other causes. Other included hit by vehicles, rattlesnake (*Crotalis horridus*) mortality, and unknown predators. We pooled retrieved and unretrieved kill into "harvest-related mortality."

Monthly, seasonal, and annual survival and cause-specific mortality rates were based on a biological year beginning 1 April and ending 31 March. This annual period was subdivided into 12 calendar months and 2 seasonal intervals for analyses on multiple temporal scales. The spring-fall interval (1 Apr–30 Sep, 183 days) began with covey breakup and initiation of reproduction. The fall-spring interval (1 October–31 Mar, 182 days) began with termination of nesting and formation of coveys.

We estimated seasonal and annual survival using the Kaplan-Meier method (Kaplan and Meier 1958) generalized to the staggered entry case (Pollock et al. 1989a). We assumed birds were randomly sampled, survival times for individuals were independent, left-censored individuals (stagger entered) had survival distributions similar to previously marked birds, censoring mechanisms (i.e., radio failure) were independent of animal fate, and trapping, handling, and radiomarking did not affect survival probability (Pollack et al. 1989a, White and Garrott 1990). Although backpack-mounted radiotransmitters have been shown to adversely affect survival of bobwhite (Taylor et al. 1998), annual survival of bobwhite wearing necklace transmitters was similar to banded birds in a study conducted in Mississippi and Florida (Corteville 1998).

Birds for which fate was unknown because of radio failure or loss, departure from the study area, or survival beyond the period of interest were right-censored. Birds that died or were censored within 7 days of radiomarking were excluded from survival analyses (Kurzejeski et al. 1987, Pollock et al. 1989a). Birds that were radiomarked in one biological year and survived into the next were censored on 30 September and reintroduced as new independent observations on 1 October. Birds censored because of radio failure or loss and subsequently recaptured and again radio-marked were introduced as new independent observations, thus total number of birds used in survival analyses exceeds total number of unique individuals captured.

We estimated monthly, seasonal, and annual cause-specific mortality rates using the Mayfield (1961) approach, generalized by Heisey and Fuller (1985). We defined cause-specific mortality rates as the probability of an animal dying during a given interval due to a specific mortality agent, in the presence of other competing mortality agents (Heisey and Fuller 1985). In addition to the statistical assumptions associated with the Kaplan-Meier approach, we further assumed that daily survival was constant within an interval (Mayfield 1961, Heisey and Fuller 1985). We dealt with censored observations by including radio-days up to the day the animal was censored, but not considering it a mortality (Vangliger and Sheriff 1990). We used the generalized Chi-square hypothesis testing procedures outlined by Sauer and Williams (1989) to test hypotheses of no differences in survival and cause-specific mortality rates among years and to construct contrasts of average survival or cause-specific mortality rates between seasons and sexes.

## Results

From 1 October 1992–30 April 1996, we mounted 831 radio transmitters on 813 different bobwhite. We excluded 16 birds (1.9%) from analyses because they died or were censored less than 7 days after being radio-marked. Of the 815 birds providing useful survival information, 43 were alive 31 March 1997 (the end of the last interval). Observations from 266 birds (32.6%) were right-censored because of radio failure or battery expiration (223), radio loss (36), capture-related mortality (3), or radio-related mortality (antenna or neckloop snagged on vegetation or body-part) (4). We calculated cause-specific mortality rates from 506 natural or harvest-related mortalities.

### Annual and Seasonal Survival

Annual survival was similar ( $\chi^2 = 0.09$ , 1 df,  $P = 0.76$ ) between male ( $S = 0.221$ ,  $SE = 0.018$ ) and female bobwhite ( $S = 0.192$ ,  $SE = 0.017$ ) (Table 1) and mean annual survival (1992–1996) pooled over sexes was 0.201 ( $SE = 0.012$ ). Annual survival varied significantly among years for males ( $\chi^2 = 17.28$ , 4 df,  $P = 0.002$ ), females ( $\chi^2 = 12.12$ , 4 df,  $P = 0.017$ ), and both sexes pooled ( $\chi^2 = 14.3$ , 4 df,  $P = 0.006$ ). Mortality was equitably distributed between seasons. Seasonal survival did not differ between fall-spring and spring-fall intervals for males ( $S_{s-f} = 0.445$ ,  $SE = 0.037$ ;  $S_{f-s} = 0.497$ , 0.033;  $\chi^2 = 1.34$ , 1 df,  $P = 0.247$ ), females ( $S_{s-f} = 0.428$ ,  $SE = 0.035$ ;  $S_{f-s} = 0.449$ , 0.033;  $\chi^2 = 0.46$ , 1 df,  $P = 0.497$ ), or both sexes pooled ( $S_{s-f} = 0.438$ ,  $SE = 0.025$ ;  $S_{f-s} = 0.472$ , 0.023;  $\chi^2 = 2.42$ , 1 df,  $P = 0.119$ ) (Table 1). Seasonal survival did not vary between sexes for the spring-fall ( $\chi^2 = 0.03$ ,

**Table 1.** Seasonal and annual survival of male and female northern bobwhite on an intensively managed plantation in southwest Georgia, 1992–1997.

Year	Season <sup>a</sup>	Male			Female			Pooled		
		N	S	SE	N	S	SE	N	S	SE
1992	Annual	133	0.278	0.032	143	0.173	0.021	276	0.227	0.019
	Spring–fall	54	0.480	0.074	55	0.427	0.081	109	0.458	0.055
	Fall–spring	101	0.574	0.051	104	0.405	0.043	205	0.496	0.034
1993	Annual	146	0.148	0.021	148	0.152	0.021	294	0.148	0.014
	Spring–fall	92	0.324	0.042	87	0.337	0.043	179	0.328	0.030
	Fall–spring	95	0.456	0.051	101	0.450	0.049	196	0.453	0.035
1994	Annual	129	0.183	0.029	125	0.225	0.030	258	0.203	0.021
	Spring–fall	62	0.344	0.093	58	0.486	0.101	120	0.412	0.070
	Fall–spring	76	0.533	0.063	79	0.464	0.052	159	0.493	0.040
1995	Annual	76	0.138	0.025	109	0.273	0.034	186	0.221	0.028
	Spring–fall	33	0.416	0.130	43	0.460	0.094	77	0.448	0.073
	Fall–spring	49	0.331	0.052	79	0.593	0.056	129	0.493	0.041
1996	Annual	59	0.263	0.050	89	0.157	0.030	148	0.193	0.026
	Spring–fall	27	0.515	0.168	49	0.424	0.083	76	0.455	0.072
	Fall–spring	40	0.511	0.080	54	0.371	0.061	94	0.424	0.049
Pooled	Annual	382	0.221	0.018	422	0.192	0.017	808	0.201	0.012
	Spring–fall	171	0.445	0.037	210	0.428	0.035	381	0.438	0.025
	Fall–spring	291	0.497	0.033	297	0.449	0.033	592	0.472	0.023

a. Annual interval = 1 Apr–31 Mar, spring–fall = 1 Apr–30 Sep, and fall–spring = 1 Oct–31 Mar.

1 df,  $P = 0.859$ ) or fall-spring interval ( $\chi^2 = 0.464$ , 1 df,  $P = 0.496$ ). Spring-fall survival did not vary among years for males ( $\chi^2 = 4.36$ , 4 df,  $P = 0.360$ ), females ( $\chi^2 = 3.35$ , 4 df,  $P = 0.501$ ), or both sexes pooled ( $\chi^2 = 7.18$ , 4 df,  $P = 0.127$ ). However, fall-spring survival varied among years for both males ( $\chi^2 = 12.62$ , 4 df,  $P = 0.013$ ), and females ( $\chi^2 = 9.35$ , 4 df,  $P = 0.053$ ).

#### Cause-specific mortality

Annual mortality due to avian predators did not differ between sexes ( $\chi^2 = 1.17$ , 1 df,  $P = 0.280$ ) or among years for males ( $\chi^2 = 5.01$ , 4 df,  $P = 0.286$ ), females ( $\chi^2 = 6.26$ , 4 df,  $P = 0.181$ ), or sexes pooled ( $\chi^2 = 7.41$ , 4 df,  $P = 0.116$ ) (Table 2).

**Table 2.** Seasonal exposure days, cause-specific mortality rates and SE, and survival and SE for male and female northern bobwhite on an intensively managed plantation in southwest Georgia, 1992–1997.

Sex	Year	Interval <sup>a</sup>	Exposure	Mortality event				SE/ Survival
				Mammal	Avian	Other <sup>b</sup>	Harvest	
Male	1992	Spring–fall	5,955	0.219 <sup>c</sup>	0.176	0.154	0.000	0.452
				0.061	0.056	0.053	0.000	0.072
		Fall–spring	10,994	0.275	0.092	0.039	0.026	0.568
	1993	Annual	16,949	0.051	0.033	0.022	0.018	0.056
				0.343	0.217	0.171	0.012	0.257
				0.059	0.056	0.053	0.008	0.048
	1994	Spring–fall	5,657	0.300	0.260	0.120	0.000	0.320
				0.064	0.061	0.046	0.000	0.063
				0.285	0.157	0.028	0.0712	0.459
	1995	Fall–spring	9,193	0.053	0.043	0.020	0.031	0.058
				0.391	0.310	0.129	0.023	0.147
				0.061	0.060	0.046	0.011	0.034
	1996	Annual	14,850	0.228	0.205	0.251	0.000	0.315
				0.063	0.061	0.065	0.000	0.066
				0.220	0.220	0.020	0.020	0.519
	1997	Spring–fall	4,930	0.058	0.058	0.020	0.020	0.069
				0.298	0.275	0.257	0.006	0.164
				0.062	0.060	0.065	0.006	0.041
1998	Fall–spring	6,900	0.272	0.039	0.272	0.000	0.417	
			0.087	0.038	0.087	0.000	0.094	
			0.182	0.254	0.073	0.109	0.383	
1999	Annual	11,830	0.073	0.082	0.049	0.059	0.089	
			0.348	0.145	0.302	0.045	0.160	
			0.085	0.054	0.086	0.027	0.052	
2000	Spring–fall	3,436	0.207	0.165	0.083	0.000	0.546	
			0.082	0.075	0.056	0.000	0.100	
			0.107	0.179	0.107	0.036	0.570	
2001	Fall–spring	4,021	0.056	0.072	0.058	0.035	0.092	
			0.265	0.263	0.141	0.020	0.311	
			0.083	0.079	0.062	0.019	0.076	
Female	1992	Spring–fall	6,205	0.342	0.171	0.021	0.000	0.466
				0.068	0.055	0.021	0.000	0.071
	1993	Fall–spring	7,820	0.415	0.048	0.080	0.048	0.410
				0.061	0.027	0.034	0.027	0.060

	Annual	14,025	0.535	0.193	0.059	0.022	0.191
1993	Spring-fall	7,844	0.061	0.055	0.026	0.013	0.040
			0.229	0.229	0.134	0.000	0.409
			0.058	0.058	0.047	0.000	0.066
	Fall-spring	9,926	0.177	0.177	0.015	0.044	0.588
			0.046	0.046	0.014	0.025	0.059
	Annual	17,770	0.301	0.301	0.140	0.018	0.240
1994	Spring-fall	4,717	0.057	0.057	0.047	0.010	0.045
			0.152	0.279	0.203	0.000	0.366
			0.057	0.071	0.064	0.000	0.071
	Fall-spring	5,763	0.331	0.312	0.040	0.000	0.318
			0.065	0.064	0.027	0.000	0.062
	Annual	10,480	0.273	0.393	0.217	0.000	0.117
1995	Spring-fall	4,887	0.059	0.068	0.063	0.000	0.033
			0.274	0.192	0.055	0.000	0.479
			0.073	0.065	0.038	0.000	0.081
	Fall-spring	5,120	0.175	0.088	0.029	0.0877	0.620
			0.065	0.048	0.029	0.048	0.082
	Annual	10,007	0.358	0.234	0.069	0.042	0.297
1996	Spring-fall	5,617	0.073	0.066	0.040	0.024	0.064
			0.254	0.208	0.093	0.000	0.445
			0.073	0.061	0.044	0.000	0.074
	Fall-spring	5,123	0.124	0.199	0.124	0.124	0.429
			0.052	0.063	0.052	0.052	0.076
	Annual	10,740	0.310	0.296	0.148	0.055	0.191
			0.066	0.063	0.048	0.025	0.046
Pooled 1992	Spring-fall	12,160	0.281	0.173	0.087	0.000	0.459
			0.046	0.039	0.029	0.000	0.051
			0.338	0.072	0.058	0.036	0.496
	Fall-spring	18,814	0.040	0.022	0.020	0.016	0.041
	Annual	30,974	0.437	0.206	0.113	0.017	0.228
1993	Spring-fall	13,501	0.043	0.039	0.030	0.008	0.031
			0.264	0.244	0.127	0.000	0.365
			0.036	0.031	0.012	0.020	0.042
	Fall-spring	19,119	0.231	0.167	0.021	0.058	0.522
			0.036	0.031	0.012	0.020	0.042
	Annual	32,620	0.348	0.305	0.135	0.021	0.191
1994	Spring-fall	9,647	0.042	0.041	0.032	0.008	0.028
			0.192	0.240	0.228	0.000	0.339
			0.043	0.046	0.046	0.000	0.049
	Fall-spring	12,663	0.277	0.268	0.030	0.010	0.416
			0.044	0.044	0.017	0.010	0.048
	Annual	22,310	0.286	0.331	0.238	0.003	0.141
1995	Spring-fall	7,735	0.043	0.046	0.045	0.003	0.026
			0.273	0.129	0.145	0.000	0.453
			0.056	0.042	0.044	0.000	0.061
	Fall-spring	8,456	0.179	0.162	0.049	0.097	0.513
			0.049	0.047	0.027	0.038	0.063
	Annual	16,191	0.354	0.202	0.167	0.044	0.232
1996	Spring-fall	9,053	0.055	0.045	0.045	0.018	0.042
			0.237	0.193	0.089	0.000	0.481
			0.051	0.048	0.035	0.000	0.059
	Fall-spring	9,144	0.117	0.191	0.117	0.088	0.486
			0.039	0.047	0.038	0.034	0.059
	Annual	18,197	0.294	0.285	0.145	0.042	0.234
			0.052	0.049	0.038	0.017	0.041

a. Spring-fall=1 Apr - 30 Sep, Fall-spring=1 Oct - 31 Mar.

b. Other included hit by vehicles, rattlesnake (*Crotalis horridus*) mortality, and unknown.

c. Top number is estimated survival rate and bottom number is variance.



Mean annual avian cause-specific mortality was 0.269 (SE = 0.02) for sexes pooled (Table 3). Avian cause-specific mortality did not differ between fall-spring and spring-fall intervals for males ( $\chi^2 = 0.09$ , 1 df,  $P = 0.736$ ), females ( $\chi^2 = 2.0$ , 1 df,  $P = 0.158$ ), or both sexes pooled ( $\chi^2 = 0.82$ , 1 df,  $P = 0.365$ ). Avian mortality did not differ between sexes during either the spring-fall ( $\chi^2 = 1.5$ , 1 df,  $P = 0.224$ ) or fall-spring ( $\chi^2 = 0.2$ , 1 df,  $P = 0.660$ ) intervals. Mean avian cause-specific mortality for both sexes pooled was 0.201 (SE = 0.02) during spring-fall and 0.164 (SE = 0.015) during fall-spring. Spring-fall avian-related mortality varied among years for males ( $\chi^2 = 12.6$ , 4 df,  $P = 0.014$ ), but not for females ( $\chi^2 = 1.2$ , 4 df,  $P = 0.803$ ). Conversely, fall-spring avian-related mortality varied among years for females ( $\chi^2 = 19.5$ , 4 df,  $P = 0.0006$ ), but not for males ( $\chi^2 = 6.3$ , 4 df,  $P = 0.177$ ). Annual mortality due to mammalian predators did not differ between sexes ( $\chi^2 = 0.35$ , 1 df,  $P = 0.535$ ) or among years for males ( $\chi^2 = 1.95$ , 4 df,  $P = 0.745$ ) or both sexes pooled ( $\chi^2 = 7.44$ , 4 df,  $P = 0.114$ ) (Table 2). However, mammalian cause-specific mortality of females varied among years ( $\chi^2 = 12.0$ , 4 df,  $P = 0.017$ ). Mean annual mammalian mortality was 0.353 (SE = 0.02) for sexes pooled (Table 3). Mammalian cause-specific mortality did not differ between fall-spring and spring-fall intervals for males ( $\chi^2 = 0.49$ , 1 df,  $P = 0.485$ ), females ( $\chi^2 = 0.02$ , 1 df,  $P = 0.883$ ), or both sexes pooled ( $\chi^2 = 0.54$ , 1 df,  $P = 0.461$ ). Mammalian mortality did not differ between sexes during either the spring-fall ( $\chi^2 = 0.01$ , 1 df,  $P = 0.909$ ) or fall-spring

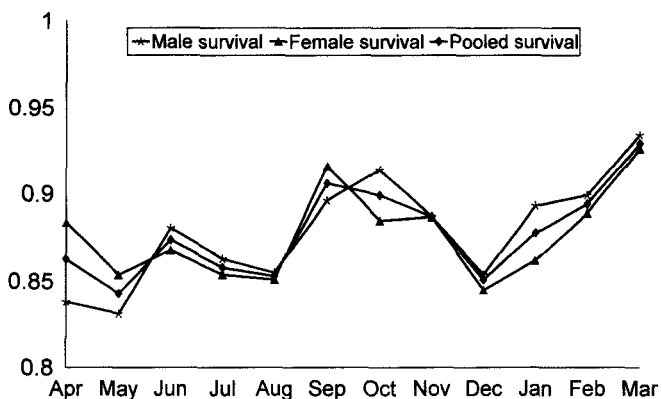
**Table 3.** Seasonal exposure days, cause-specific mortality rates and variances, and survival rate estimation and variances for male and female northern bobwhite, pooled across years, on an intensively managed plantation in southwest Georgia, 1992–1997.

Sex	Interval <sup>a</sup>	Exposure	Mortality event				SE/ Survival
			Mammal	Avian	Other <sup>b</sup>	Harvest	
Male	Spring–fall	23,226	0.249 <sup>c</sup> 0.031	0.185 0.028	0.175 0.028	0.000 0.000	0.391 0.034
	Fall–spring	34,444	0.238 0.027	0.163 0.023	0.044 0.013	0.048 0.013	0.508 0.031
	Annual	57,670	0.342 0.030	0.249 0.028	0.192 0.027	0.019 0.005	0.199 0.021
Female	Spring–fall	29,270	0.252 0.029	0.215 0.028	0.100 0.020	0.000 0.000	0.432 0.033
	Fall–spring	33,752	0.258 0.027	0.164 0.023	0.055 0.014	0.055 0.014	0.468 0.030
	Annual	63,022	0.363 0.029	0.286 0.028	0.124 0.021	0.024 0.006	0.202 0.020
Pooled	Spring–fall	52,496	0.251 0.021	0.201 0.020	0.135 0.017	0.000 0.000	0.413 0.024
	Fall–spring	68,196	0.248 0.019	0.164 0.015	0.049 0.010	0.051 0.010	0.488 0.022
	Annual	120,692	0.353 0.021	0.269 0.020	0.155 0.017	0.021 0.004	0.201 0.015

a. Spring–fall = 1 Apr – 30 Sep, fall–spring = 1 Oct – 31 Mar.

b. Other included hit by vehicles, rattlesnake (*Crotalis horridus*) mortality, and unknown.

c. Top number is estimated survival rate and bottom number is variance.

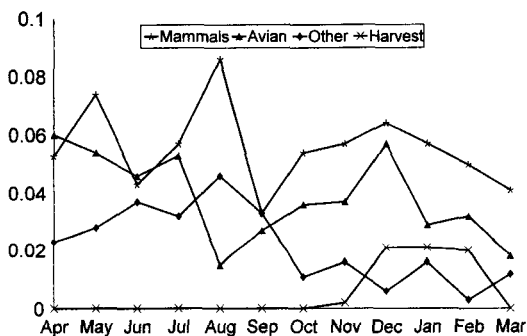


**Figure 2.** Monthly survival for male and female northern bobwhite and both sexes pooled on an intensively managed plantation in southwest Georgia, 1992-1997.

( $\chi^2 = 0.68$ , 1 df,  $P = 0.408$ ) intervals. Mean mammalian cause-specific mortality for both sexes pooled was 0.251 (SE = 0.02) during spring-fall and 0.248 (SE = 0.019) during fall-spring. Spring-fall mammalian-related mortality did not vary among years for males ( $\chi^2 = 1.30$ , 4 df,  $P = 0.861$ ), or females ( $\chi^2 = 4.9$ , 4 df,  $P = 0.295$ ). Fall-spring mammalian-related mortality varied among years for females ( $\chi^2 = 17.8$ , 4 df,  $P = 0.001$ ), but not for males ( $\chi^2 = 7.01$ , 4 df,  $P = 0.135$ ).

Harvest rate for males did not vary among years ( $\chi^2 = 3.75$ , 4 df,  $P = 0.44$ ), however, female harvest rate varied among years ( $\chi^2 = 15.28$ , 4 df,  $P = 0.004$ ) (Table 2). Male (0.048, SE = 0.013) and female (0.055, SE = 0.014) bobwhite were harvested at a similar rate ( $\chi^2 = 0.14$ , 1 df,  $P = 0.73$ ) (Table 3). Harvest rate pooled over sexes and years was 0.51 (SE = 0.01).

Although seasonal survival rate did not differ between spring-fall and fall-spring



**Figure 3.** Monthly cause-specific mortality rates for northern bobwhite on an intensively managed plantation in southwest Georgia, 1992-1997.

intervals, survival varied temporally over the annual cycle (Fig. 2). Survival was lowest during the breeding season (May-Aug). Monthly survival was relatively high from September through November, then declined to a local minima during December. Survival increased steadily from December to an annual high in March. Males and females exhibited similar temporal patterns in monthly survival.

Females experienced the highest avian cause-specific mortality during July. Males were most vulnerable to avian predators during April. Both males and females experienced a peak in avian mortality during December (Fig. 3). Both male and female bobwhite exhibited peaks in mammalian mortality during May and August, and were least vulnerable to mammalian predators during September.

## **Discussion**

Mean annual survival of bobwhite may vary over a relatively narrow range of values throughout the distributional range (Guthery). Summarizing 5 long-term (>12 year) time series on bobwhite age ratios in the harvest, Guthery (1997:292) stated that bobwhite in southern latitudes sustain approximately 70% annual mortality, and those in northern latitudes exhibit > 80% annual mortality and interpreted this narrow range of mean demographics as evidence for “. . . operationally similar habitat quality wherever bobwhite populations persist.” He further inferred that long-term bobwhite density varies most directly in relation to the quantity of usable space in the landscape instead of habitat quality. We studied bobwhite survival on an intensively managed plantation where nesting, brood-rearing, foraging, and winter habitats were meticulously managed at a fine spatial scale. Traditional management practices such as prescribed fire, disking, brush mowing, and rotational agriculture were used to create and maintain a mosaic of early successional plant communities presumably providing the essential structural, seed, and invertebrate resources required by bobwhite. Additionally, bobwhite were regularly provided supplemental feed throughout the year, thus food should be unlimited. Finally, mammalian predators were intensively managed during the period of our study. Despite the scope and intensity of management, mean annual survival of bobwhite during our study (20.1%) was within the range reported by Guthery (1997) and less than the mean suggested for southern latitudes. However, Guthery's (1997) demographic parameters were drawn from studies conducted during previous decades in landscapes that differ markedly from those that occur today. Further, Guthery's (1997) demographic parameters were based on age ratios, instead of individual-based survival estimates. Age ratios are unbiased estimates of survival only for stable and stationary populations and provide no information regarding the timing of mortality (i.e., pre-breeding vs. post-breeding).

Individual-based survival estimates reported from populations in modern, anthropogenically simplified landscapes are considerably lower than suggested by Guthery (1997). However, these differences may be attributable to differences in time, landscape context, or estimators. When compared to recent studies reporting individual-based survival estimates, annual and seasonal survival in our study area

were relatively high. Burger et al. (1994, 1995a) reported 5% annual survival for 2 populations in an agricultural landscape in Missouri. Burger et al (1995a) and Guthery (1997) noted that bobwhite populations could not be maintained under this level of sustained annual mortality. Similar to the Missouri study, Curtis et al. (1988) reported higher survival (25.7%) for an un hunted, radio-marked sample on Tall Timbers Research Station in Florida. Using band recovery models, Pollock et. al (1989a) estimated that annual survival of bobwhite on Tall Timbers Research Station in Florida. Using band recovery models, Pollock et al. (1989a) estimated that annual survival of bobwhite on Tall Timbers Research Station averaged 16.7% over a 15-year period.

Numerous authors have demonstrated or suggested that bobwhite exhibit density-dependent mortality (Roseberry and Klimstra 1984). It is through density-dependent mortality and reproduction that bobwhite populations are able to partially compensate for relatively high harvest rates. However, the mechanisms of density dependence have not been clearly identified. The availability of secure winter ranges, food limitation, and density-dependent predation are potential mechanisms that may contribute to density-dependent mortality. Over the range of population levels achieved on our area during this study, predator, food, and habitat management practices may have effectively resulted in short-term release from some of the effects of density-dependence. In effect, the density level at which density-dependent factors become effective was elevated. Thus, population parameters sensitive to density dependent regulation were high and populations increased. Clearly, as populations continue to increase density dependent mechanisms will have an increasing effect.

A primary difference between our survival estimates and those previously reported relates to the timing of mortality. In Missouri (Burger et al. 1995a) and North Carolina (Curtis et al. 1988) mortality was concentrated during the pre-breeding period with overwinter survival being approximately half that of breeding season survival. During our study, mortality was equitably distributed between pre-breeding and post-breeding intervals. Overwinter survival on our area (47.2%) was considerably higher than that reported in Missouri (15.9%, Burger et al. 1995a), North Carolina (18.5%, Curtis et al. 1988), and South Carolina (28.8%—35.9%, Dixon et al. 1996). Only for 1 un hunted population in Florida (Curtis et al. 1988) has higher winter survival been reported (64.4%).

Numerous factors may have contributed to the high overwinter survival on this area. First, harvest rate during our study (5%) was quite low relative to other populations on private lands (28% in Missouri [Burger et al. 1995a]; 23.3% on Tall Timbers Res. Sta. [Pollock et al. 1989b]; 42.5% on Ill. Private land [Roseberry and Klimstra 1984]) and public wildlife management areas (14% at Fort Bragg, N.C. [Curtis et al. 1988]; 70% on Ill. public wildlife areas [Vance and Ellis 1972]). Roseberry and Klimstra (1984:141) suggested that hunted bobwhite populations experience proportionately more of their total annual mortality prior to the breeding season. In relation to the effects of harvest on overwinter mortality, our population was more similar to un hunted populations. Secondly, the supplemental feeding regime created a situation where food was super-abundant and accessible with minimum energy expenditure.

The benefits of supplemental feeding have not been unequivocally demonstrated for bobwhite. Guthery (1997) reported no irrefutable evidence exists to support the food limitation hypothesis; however, other research in the region has demonstrated that in some years supplemental feeding may increase survival and reproductive output (Sisson et al. 1999, B. Palmer pers. commun.). Supplemental feeding may have reduced the energetic and time requirements for foraging. Similarly, the fine scale at which habitat was managed created a diverse mosaic of plant communities that closely juxtaposed the various seral stages used throughout the diel and seasonal cycle. Reduced foraging time and movements may reduce vulnerability to predation. Finally, mammalian predator populations on our area may have been low because of predator management and avian predator populations may have been low because of relative scarcity of hardwood drain habitats.

The timing of mortality has substantial bearing on population processes insofar as overwinter mortality determines the size of the breeding population. Bobwhite may exhibit density-dependent reproduction (Roseberry and Klimstra 1984:97 and employ a dynamic mating system with numerous components of production that may be sensitive to breeding density (Curtis et al. 1993, Burger et al 1995*b*). Thus, to some degree, bobwhite populations may compensate for lower breeding densities by increased reproductive effort or success. However, as the overwinter rate of mortality increases, it becomes progressively more difficult for populations to compensate for losses with increased reproduction (Roseberry and Klimstra 1984:145). Roseberry and Klimstra (1984:145) stated that for their Illinois study area reproductive capacity of bobwhite would be insufficient to maintain equilibrium if overwinter mortality consistently exceeded 70% (Roseberry and Klimstra 1984:145).

Although annual mortality is clearly an important population parameter, the distribution of mortality between pre-breeding and breeding season intervals can strongly influence population trajectories. Conceivably, 2 populations could have similar annual survival rates, but quite different population trajectories if higher overwinter survival in one population facilitated a larger breeding population and greater participation in production. We observed greater annual variation in overwinter survival than in breeding season survival. Similarly, across all studies conducted throughout the bobwhite range, overwinter mortality fluctuates over a wide range, whereas breeding season survival is relatively invariant across years, geographic locations, and studies. Thus, variation in overwinter mortality may be a primary determinant of annual survival and population growth rates.

Breeding season survival during our study (43.8%) was higher than that reported in Missouri (33.2%, Burger et al. 1995*a*), North Carolina (32.8%, Curtis et al. 1988 and 33%, Puckett et al. 1995), Florida (40%, Curtis et al. 1988), and Mississippi (33.9%, Taylor et al. 1999). Breeding season survival is important to production as it determines the opportunities for nesting, renesting, and double-clutching. Taylor and Burger (1997) reported demographic parameters of a declining bobwhite population on a managed area in Mississippi and suggested that population declines were associated with progressively increasing mammalian-related breeding season mortality (Taylor et al. 1997).

Temporal variation in survival throughout the annual cycle was similar for males and females. Both sexes had relatively low monthly survival during the breeding season (April-August), high survival during September-November, low survival in December and increasing survival from January through March. The low survival during the breeding season likely reflects the cost of reproduction. Burger et al. (1995a) reported that incubating a nest and attending a brood significantly reduces survival relative to non-reproductively active birds. Additionally, advertising for mates by calling may impose a cost on males in increased vulnerability to avian predators (Burger et al. 1994, 1995a). Bobwhite in our study were most vulnerable to mammalian predators during May and August, corresponding to peak nesting and brood-rearing periods, and again in mid-winter. Avian-related mortality was highest during the period April-August, corresponding to reproductive activity, and again in mid-winter when wintering populations of raptors are highest. Although avian predators were an important source of mortality during our study, the absence of substantial hardwood drains on our study area may have resulted in relatively low local densities of accipiters, thereby diminishing the effect of these predators relative to other populations in the Southeast.

Our estimates of mean annual survival on an intensively managed area superficially support Guthery's (1997) observation of relatively invariant mean demographic characteristics across a broad range of landscape, climatic, and predator populations. However, we suggest that mean annual survival rates may provide an incomplete picture of the underlying population processes and may be less important than the distribution and timing of mortality. Unlike regional population trends in the Southeast, populations on our study area increased throughout the study period. Under the intensive habitat and predator management regime characteristic of this plantation, both overwinter and breeding season survival were higher than that reported from other individual-based survival studies. More importantly, relative to other studies the seasonal timing of mortality was redistributed from predominantly pre-breeding mortality to an equitable distribution between overwinter and breeding seasons. This may have the net effect of increasing breeding population size and total reproductive output. We suggest that relationships among habitat management, habitat quality, and population processes will remain poorly understood until researchers explicitly examine habitat quality as measured by habitat-specific population performance (Van Horn 1983). This will require breaking annual demographic parameters down into individual components of production (nesting effort, nest success, renesting rate, double-clutching, male participation, and brood survival) and survival (seasonal and annual survival and cause-specific mortality) and systematically evaluating variation among habitats, landscapes, and predator contexts, and effects on population trajectory.

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