

# Temporal Patterns in Cause-specific Mortality of Northern Bobwhite in Northern Missouri

Loren W. Burger, Jr.,<sup>1</sup> *The School of Natural Resources, University of Missouri, Columbia, MO 65211*

Mark R. Ryan, *The School of Natural Resources, University of Missouri, Columbia, MO 65211*

Thomas V. Dailey, *Missouri Department of Conservation, 1110 S. College Ave. Columbia, MO 65201*

Eric W. Kurzejeski, *Missouri Department of Conservation, 1110 S. College Ave. Columbia, MO 65201*

---

*Abstract:* Northern bobwhite populations have been declining throughout most of their range. Population declines imply that mortality consistently exceeds production and therefore a thorough understanding of the causes and temporal distribution of mortality is important. We present Heisey-Fuller estimates of monthly survival and cause-specific mortality rates of 1,001 radio-marked bobwhite on private lands in northern Missouri during 1989–1992. Monthly survival rate was lowest during the hunting season (November–January) ( $\bar{x} = 0.639$ ), intermediate during the breeding season (May–September) ( $\bar{x} = 0.815$ ) and highest during the remainder of the year (October, March–April) ( $\bar{x} = 0.858$ ). Females had significantly lower ( $P = 0.027$ ) survival rate (0.552) than males (0.653) during the first month of the hunting season. Males had lower ( $P = 0.06$ ) survival rate than females during July (0.710 vs. 0.887). Avian and mammalian predators were primary causes of natural mortality. Avian mortality was highest during December, January, and February, then declined through May. However, avian mortality increased during the breeding season for male bobwhite. During June, males experienced greater ( $P = 0.012$ ) avian mortality (0.073) than did females (0.025). This corresponds to the peak in whistling activity in Missouri and may represent a cost of “advertising” by males. Mammalian-caused mortality of bobwhites increased from March through July, reaching a maximum during the peak reproductive period and is associated with increased vulnerability of nesting and brood-rearing birds to olfactory predators.

Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 48:208–219

---

<sup>1</sup> Present address: Department of Wildlife and Fisheries, Mississippi State University, Box 9690, Mississippi State, MS 39762.

Northern bobwhite (*Colinus virginianus*) populations are declining over much of their range (Robbins et al. 1986, Droege and Sauer 1990, Brennan 1991, Church et al. 1993). In many areas, rate of decline has increased during the last decade (Church et al. 1993). These declines are typically attributed to habitat destruction from 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 may reduce the quality of remaining habitat through fragmentation. Bobwhite inhabiting marginal or isolated habitat may be more vulnerable to catastrophic climatic events, predation, or harvest (Roseberry 1993).

Concurrent with reductions in bobwhite habitat quantity and quality, predator populations (Petersen et al. 1988, Church et al. 1993) and relative harvest pressure (Roseberry and Klimstra 1993, Brennan and Jacobson 1992) have increased. In modern landscapes, smaller bobwhite populations may be exposed to greater predator populations (including hunters) under habitat conditions that favor the predator. Although biologists have historically minimized effects of predation and harvest on bobwhite populations (Errington 1934, Errington and Hamerstrom 1935) former paradigms concerning relationships among predation, harvest, and bobwhite populations may no longer be applicable (Curtis et al. 1988, Mueller et al. 1988, Pollock et al. 1989b, Robel 1993, Robinette and Doerr 1993). As average annual mortality consistently exceeds production, a thorough understanding of the causes and temporal distribution of mortality of bobwhite in modern landscapes has become increasingly important.

Although bobwhite have been studied extensively, seasonal variation in survival and mortality factors has received little attention. Curtis et al. (1988) reported monthly, seasonal, and annual survival rates for a hunted population in North Carolina and an unhunted population in Florida. Robinette and Doerr (1993) monitored overwinter survival of bobwhite in North Carolina. Burger et al. (1995a) reported seasonal and annual survival rates and seasonal cause-specific mortality of bobwhite in northern Missouri. However, the temporal distribution of cause-specific mortality has not been reported for any bobwhite population.

Knowledge of the relationships among seasonal processes, mortality, exploitation, and population performance can provide insight into the adaptive significance of observed life history strategies and enhance our ability to effectively manage declining bobwhite populations. In this paper, we report seasonal patterns in cause-specific mortality of bobwhite and test hypotheses concerning the sex-specific nature of seasonal cause-specific mortality. We interpret the significance of cause-specific mortality patterns in the context of seasonal biological processes and life history strategies within the context of changing landscape patterns.

We thank T. H. Burger, R. S. Fuller, R. H. Fergusson, C. Gatlin, K. E. Laves, C. Mason, T. D. McCoy, L. H. Neher, P. Reynolds, and G. E. Shurvington for assisting in data collection. L. D. Burger provided constructive review.

This research was funded by The Missouri Department of Conservation, Federal Aid in Wildlife Restoration Project W-13-R-44, the University of Missouri, and Missouri Chapters of Quail Unlimited. This paper is a contribution of the Missouri Agricultural Experiment Station, Journal series 12407 and the Missouri Cooperative Fish and Wildlife Research Unit (U.S. Fish and Wildl. Serv., Mo. Dep. Conserv., and Univ. Mo. at Columbia, cooperating).

## Methods

We radio-marked bobwhite on 2 23-km<sup>2</sup> study areas in Macon and Knox counties in north-central Missouri. These areas were 4.8 km apart and similar in land use except that 15% of 1 study area (25% of the total cropland) was enrolled in the Conservation Reserve Program (CRP). Primary land use on the 2 study areas was a combination of rowcrop, pasture/hay, and CRP. Study areas were described by Burger et al. (1995a).

We trapped bobwhite with baited funnel traps (Stoddard 1931) during October, February, and March 1989–1992 and supplementally captured additional birds throughout the year by netting roosting coveys with 6- × 9-m 1.9-cm mesh, knotless nylon net. We determined age, sex, and weight; then banded, radio-marked, and released bobwhite at the capture site. We radio-marked birds weighing >150g with a 6.5–6.9g, pendant-style, mortality-mode transmitter (Burger 1995a).

We used truck-mounted and hand-held Yagi antennas to locate birds  $\geq 5$  days per week and aircraft to locate widely-dispersed individuals. We located transmitters immediately following a mortality signal and determined the proximate cause of mortality (Dumke and Pils 1973). Carcasses recovered intact with no apparent cause of mortality were radiographed and necropsied at the Veterinary Medical Diagnostic Laboratory, University of Missouri. We pooled retrieved and unretrieved kill into “harvest-related mortality” for estimates of monthly cause-specific mortality rate.

### Survival and Cause-specific Mortality Rates

Monthly survival and cause-specific mortality rates were based on a biological year beginning 1 October and ending 30 September. We used the Mayfield (1961) approach, generalized by Heisey and Fuller (1985), to estimate monthly survival and cause-specific mortality rates. Monthly cause-specific mortality rates are the probability of an animal dying during a given interval from a specific mortality agent in the presence of other competing mortality agents (Heisey and Fuller 1985). We assumed that survival times for individuals were independent, each animal radio-day was an independent event, daily survival rate was constant within a month, left-censored individuals (staggered entry) had survival distributions similar to previously marked birds, and censoring mechanisms (i.e., radio-failure) were independent of the fate of the animal. We further assumed that birds were randomly sampled, and that trapping, handling,

and radio-marking did not affect survival probability (Heisey and Fuller 1985; Pollock et al. 1989a,c; White and Garrott 1990). We censored birds with unknown fates due to radio failure or loss. We excluded birds that died or were censored within 7 days of radio-marking (Kurzejeski et al. 1987, Pollock et al. 1989a, c). We dealt with censored observations by including radio-days up to the day an animal was censored but not considering it a mortality (Vangilder and Sheriff 1990). Survival and seasonal cause-specific mortality rates did not differ among years or between areas (Burger et al. 1995); therefore, we pooled survival and mortality data from both areas and all 3 years to examine seasonal patterns. We used *z*-tests to compare monthly survival and cause-specific mortality rates between sexes (Heisey and Fuller 1985). 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 months and to construct contrasts of average monthly survival or cause-specific mortality rates among the hunting season, breeding season, and the remainder of the year.

Birds radio-marked in 1 biological year and surviving into the next were censored on 30 September and reintroduced as new independent observations on 1 October. Birds that were censored and later recaptured and again radio-marked were introduced as new independent observations. We included birds that were radio-marked when they were too young to accurately determine sex in overall survival estimates, but not in sex-specific survival estimation.

## Results

From 1 October 1989–30 September 1992, we radio-marked 1,001 bobwhite; 97 (9.7%) were excluded from analyses because they died or were censored within 7 days of radio-marking. We censored 227 of the remaining 904 birds (25.1%) due to radio-failure or battery expiration (132), radio loss (67), capture-related mortality (9), or radio-related mortality (antenna or neckloop snagged on vegetation or body part, 19). On an annual basis, raptors, harvest, and mammals were primary sources of mortality.

For both sexes pooled, monthly survival rates ranged from 0.611–0.869. Survival rates varied among months (Table 1) ( $X^2 = 160.12$ , 11 df,  $P < 0.001$ ). In Missouri, the hunting season extended from 1 November–15 January. For males, females, and both sexes pooled, survival during November–January was lower than survival during the breeding season (May–Sept.) ( $P < 0.001$ ) or survival during the remainder of the year (Oct, Feb–Apr) ( $P < 0.001$ ). Breeding season survival of males ( $X^2 = 4.20$ , 1 df,  $P = 0.04$ ) and both sexes pooled ( $X^2 = 4.52$ , 1 df,  $P = 0.03$ ) was lower than that outside the hunting and breeding seasons (Oct, Feb–Apr). During November, females had lower survival rate (0.552) than males (0.653) ( $Z = 2.21$ ,  $P = 0.027$ ) (Table 1). During July, male survival rate (0.710) was less than female survival rate (0.827) ( $Z = 1.88$ ,  $P = 0.06$ ).

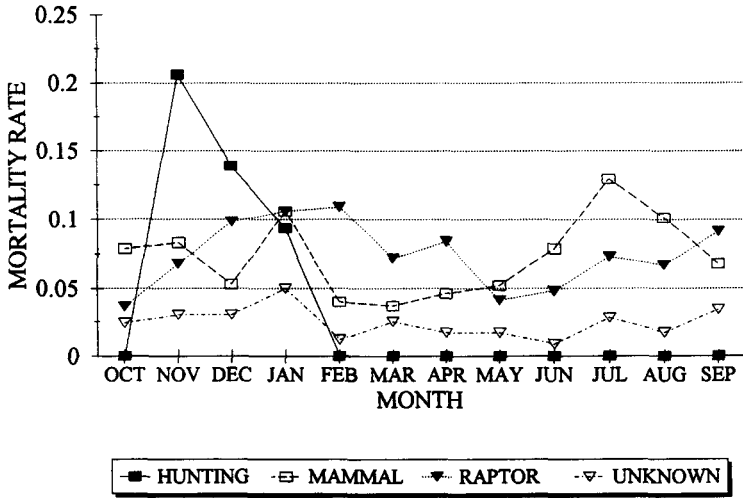
**Table 1.** Monthly survival rate of female and male northern bobwhite in northern Missouri, 1 October 1989–30 September 1992.

Month	Female			Male			Pooled		
	<i>N</i>	Survival rate	SE	<i>N</i>	Survival rate	SE	<i>N</i>	Survival rate	SE
Oct	225	0.843	0.035	276	0.864	0.030	519	0.857	0.022
Nov	212	0.552	0.035	278	0.653	0.029	509	0.611	0.022
Dec	101	0.654	0.048	166	0.668	0.037	275	0.661	0.029
Jan	62	0.645	0.063	111	0.648	0.047	177	0.646	0.037
Feb	110	0.885	0.038	162	0.815	0.038	275	0.839	0.028
Mar	170	0.859	0.030	227	0.870	0.025	397	0.866	0.019
Apr	152	0.831	0.031	204	0.867	0.024	356	0.852	0.019
May	124	0.866	0.031	180	0.872	0.025	304	0.869	0.020
Jun	96	0.871	0.034	147	0.846	0.031	243	0.856	0.023
Jul	79	0.827	0.044	109	0.710	0.044	188	0.759	0.032
Aug	57	0.806	0.052	68	0.808	0.050	125	0.807	0.036
Sep	51	0.787	0.063	70	0.780	0.061	129	0.783	0.044
Annual	404	0.050	0.009	534	0.049	0.010	968	0.050	0.007

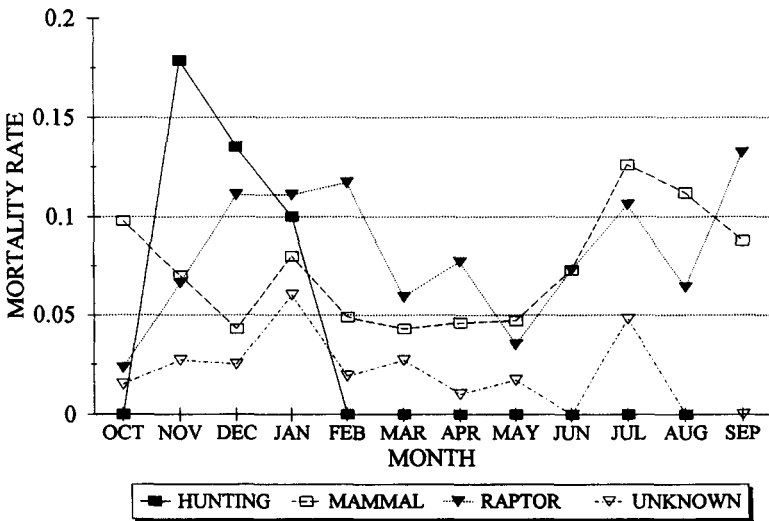
During November and December, hunting was the primary source of mortality (Fig. 1). During January, mortality was equally distributed among harvest, mammalian, and avian predators (Fig. 1). In November, females had marginally higher harvest-related mortality (0.244) than males (0.179) ( $Z = 1.68$ ,  $P = 0.09$ ). Avian mortality was highest during December–February, then declined through May (Fig. 1). However, male bobwhite avian cause-specific mortality increased from May through July (Fig. 2). During June, males (0.073) experienced greater avian mortality than did females (0.025) ( $Z = 2.50$ ,  $P = 0.012$ ). Mammalian mortality was high in January, declined in February, and increased from March through July, reaching a maximum during the middle of the reproductive period (Fig. 1). However, mammalian mortality for females began increasing in March (Fig. 3), whereas mammalian mortality for males did not begin increasing until June (Fig. 2).

## Discussion

Numerous researchers, using several techniques to estimate survival, have reported that northern bobwhite experience high annual mortality (Marsden and Baskett 1958, Kabat and Thompson 1963, Snyder 1978, Roseberry and Klimstra 1984, Curtis et al. 1988, Robinette and Doerr 1993, Burger et al. 1995a). Greatest mortality generally occurs in winter. Kabat and Thompson (1963) reported that in Wisconsin, November–December was the period of highest mortality. In North Carolina, Robinette and Doerr (1993) observed declining survival from the onset of hunting season in 2 hunted areas and sharply declining survival in hunted and unhunted areas during mid-winter. Curtis et al. (1988) reported lowest survival rate during December–February in a hunted area in North Carolina and low survival rate from February–April in an un-



**Figure 1.** Monthly cause-specific mortality of radio-marked bobwhite in northern Missouri, 1989–1992.



**Figure 2.** Monthly cause-specific mortality of radio-marked male bobwhite in northern Missouri, 1989–1992.

hunted area in northern Florida. Burger et al. (1995a) reported that in northern Missouri, fall-spring survival rate was approximately half that of spring-fall survival. All of these studies demonstrate that winter survival is lower than breeding season survival; however, little information is available regarding the temporal distribution of cause-specific mortality within these seasonal intervals. We

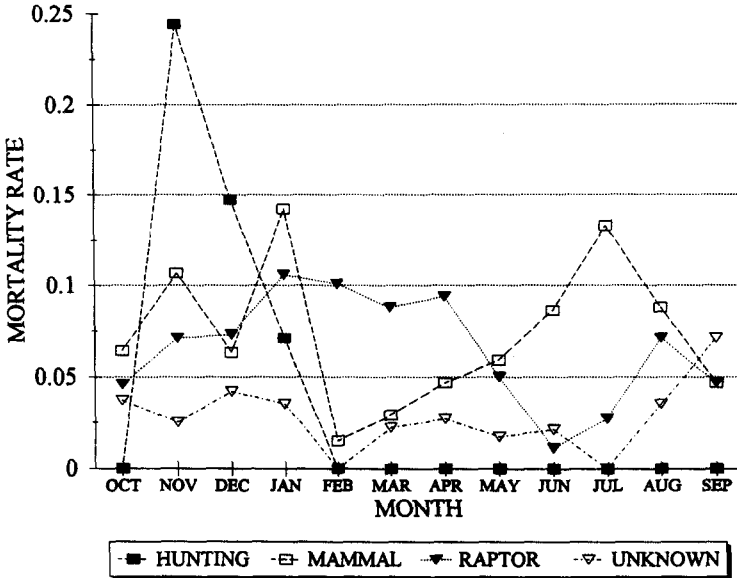


Figure 3. Monthly cause-specific mortality of radio-marked female bobwhite in northern Missouri, 1989–1992.

observed that during the hunting season, monthly survival of radio-marked bobwhite was approximately 20% lower than during the remainder of the year. Monthly harvest mortality was highest in November (21%) and declined to 9% in January. Survival rate during the breeding season (May–Sep) was lower than survival rate outside breeding and hunting seasons, particularly for males. This suggests that both harvest and reproduction pose some cost to the population in reduced survival.

Although Stoddard (1931) suggested that harvest might be additive to natural mortality, biologists and managers have traditionally assumed that, below some threshold, harvest has little effect on bobwhite survival and breeding densities (Errington and Hamerstrom 1935, Baumgartner 1944, Parmalee 1953, Marsden and Baskett 1958). Vance and Ellis (1972) suggested that bobwhite populations on public hunting areas in Illinois may sustain harvest rates as high as 70%. However, Robinette and Doerr (1993) reported that hunted populations in North Carolina exhibited lower overwinter survival rates than unhunted populations. Similarly, Curtis et al. (1988) reported that a hunted population in North Carolina experienced lower survival rates than an unhunted population in northern Florida. Pollock et al. (1989b) and Roseberry and Klimstra (1984) demonstrated that harvest mortality, particularly late season harvest, may contribute additively to natural mortality. The low survival rates that we observed during the hunting season was largely attributable to harvest related-mortality.

Our data suggests that under current habitat and predation regimes, even

moderate levels of harvest may comprise a substantial portion of total mortality (30% of total annual mortality). Harvest may directly depress breeding densities. However, under sustained yield harvest theory, reductions in breeding density are not an unexpected consequence of harvest (Roseberry and Klimstra 1984, Robertson and Rosenberg 1988). If remaining individuals have enhanced survival and the population exhibits density-dependent reproduction, the annual growth increment may be harvested on a sustained basis with little appreciable effect on fall density (Roseberry and Klimstra 1984). However, as Roseberry and Klimstra (1984) stated, it is clear that the traditional "annual surplus" view is an inadequate basis for scientific management of bobwhite populations. Scientific harvest theory must be applied to bobwhite population management. Yet the nature of relationships among harvest, survival, breeding density and production will not be adequately understood for bobwhite until carefully designed, replicated, manipulative experiments are conducted (Burger et al. 1994).

Male bias in bobwhite sex ratios has been reported throughout the range of the bobwhite, particularly for the adult segment of the population. Although this bias has been attributed to female mortality during incubation (Leopold 1945, Bennitt 1951, Buss et al. 1947), Roseberry and Klimstra (1984) suggested that some of the sex bias arose from differential mortality outside the breeding season. Stoddard (1931) believed that females experienced higher fall and winter mortality. Burger et al. (1995a) reported that female bobwhite in Missouri exhibited 4% lower overwinter survival rate than males. Studies in Florida (Pollock et al. 1989b), Texas (Shupe et al. 1990), and Illinois (Roseberry and Klimstra 1992) demonstrate that females are more vulnerable to harvest. During November, radio-tagged female bobwhite in our study areas experienced higher harvest mortality than males. This harvest bias may result from behavioral or physical differences between sexes. Flight speed or willingness to flush may differ between sexes (Stoddard 1931:94). Differential vulnerability to harvest could contribute to differential overwinter survival rate (Burger et al. 1995a) and produce the observed skewed sex ratios.

Although the effect of predators on bobwhite populations has been discounted in the past (Errington 1934), predation was the primary cause of mortality of radio-marked bobwhite during our study. Our observations of high natural mortality are consistent with results from other recent radio-telemetry studies (Curtis et al. 1988, Robinette and Doerr 1993). However, if radio-marking predisposes bobwhite to predation or hunter harvest, our estimates of survival rate and those of Curtis et al. (1988) and Robinette and Doerr (1993) would be biased.

In our study, relative importance of specific mortality agents varied seasonally in relation to predator and prey life history attributes. In the southeastern United States, the Cooper's hawk (*Accipiter cooperii*) is the most frequent avian predator and may cause substantial bobwhite mortality during migration (Feb-Mar) and the nesting season (Jun-Jul) (Stoddard 1931, Mueller et al. 1988). However, instead of a peak of avian mortality associated with raptor migra-



tions, bobwhite populations in our study areas experienced sustained high avian depredation from December–April. Although Cooper’s and sharp shinned hawks (*A. striatus*) were responsible for some mortality during our study, much of the avian depredation in northern Missouri was attributable to resident great-horned owls (*Bubo virginianus*). Additionally, numerous red-tailed hawks (*Buteo lineatus*) and northern harriers (*Circus cyaneus*) wintered on our study areas and were documented as bobwhite predators (Burger pers. observ.). Errington (1934) similarly reported that great-horned owls were responsible for most of the mortality in his Wisconsin study areas. In Missouri, avian depredation declined from February through May, then increased sharply in June and July for male bobwhite. During June, male bobwhite in Missouri were more vulnerable to avian predation than were females. Mid-June corresponds to peak bobwhite nesting in Missouri. Male bobwhite solicit females by singing from exposed perches. Increased avian mortality on males during June–July and the between sex difference in vulnerability to avian depredation support the hypothesis that singing male bobwhite may be vulnerable to visual predators (Burger et al. 1995a). Kabat and Thompson (1963) reported that bobwhite calling intensity peaked between 0430 and 0530 hours, varied sporadically throughout the day, then increased slightly 30 minutes before sunset. Peak calling activity during crepuscular periods may predispose bobwhite to predation by both diurnal and nocturnal avian predators. This form of advertisement likely imposes “costs” of reproduction on males that are typically not addressed in evolutionary models (Reznick 1985).

Mammalian mortality was high in January, then declined in February. This may reflect vulnerability of bobwhite to mammalian predators during severe snow and ice conditions typical of northern Missouri during January. Similar to Curtis et al. (1988), we observed increasing mammalian depredation during the reproductive season. Mammalian depredation increased gradually in April and May, then increased sharply, peaking in July. The peak in mammalian predation corresponded with the middle of the nesting period (Burger 1995b). Increased mammalian-related mortality during this period may reflect vulnerability of incubating and brood-rearing birds to predators with olfactory senses (Burger et al. 1995a). During incubation and early broodrearing, bobwhite are 15% more vulnerable to predation than birds that are not actively nesting or broodrearing (Burger et al. 1995a).

Errington (1934) stated that “kinds and numbers of wild predators, migrant or resident, had no measurable impact on carrying capacity.” As a profession we have assumed that humans act like predators and that harvest of small game is completely compensatory (Roseberry and Klimstra 1984, Robel 1993). However, recent studies have suggested that predation and harvest may have substantial effects on bobwhite populations. Many bobwhite populations may not be self-sustaining under existing habitat conditions, depredation regimes, and harvest levels. We concur with Robel (1993), Roseberry (1993), and Church et al. (1993) that former paradigms regarding mechanisms of bobwhite population

regulation need to be re-examined in the context of changing landscape patterns. We support Leopold and Hurst's (1994) contention that effects of predation will not be adequately understood if studied only from the standpoint of mortality on the prey species. Scientific management of bobwhite populations will not follow until predation and harvest are viewed as dynamic, complex processes and evaluated with carefully designed, replicated experiments (Burger et al. 1994, Leopold and Hurst 1994).

## Literature Cited

- Baumgartner, F. M. 1944. Bobwhite quail populations on hunted vs. protected areas. *J. Wildl. Manage.* 8:259–260.
- Bennett, R. 1951. Some aspects of Missouri quail and quail hunting 1938–1948. *Missouri Conserv. Comm. Tech. Bull. No. 2.* 51pp.
- Brennan, L. A. 1991. How can we reverse the northern bobwhite population decline? *Wildl. Soc. Bul.* 19:544–555.
- and H. A. Jacobson. 1992. Northern bobwhite (*Colinus virginianus*) hunter use of public wildlife areas: the need for proactive management. *Gibier Faune Sauvage* 9:847–858.
- Burger, L. W., Jr., T. V. Dailey, E. W. Kurzejeski, and M. R. Ryan. 1995a. Seasonal and annual survival and cause-specific mortality of northern bobwhite in Missouri. *J. Wildl. Manage.* 59:401–410.
- , E. W. Kurzejeski, L. D. Vangilder, T. V. Dailey, and J. H. Shultz. 1994. Effects of harvest on population dynamics of upland birds: are bobwhite the model? *Trans. N. Am. Wildl. and Nat. Resour. Conf.* 59:466–476.
- , M. R. Ryan, T. V. Dailey, and E. W. Kurzejeski 1995b. Reproductive strategies, success, and mating systems of northern bobwhite in northern Missouri. *J. Wildl. Manage.* 59:417–426.
- Buss, I. O., H. Mattison, and F. M. Kozlik. 1947. The bobwhite quail in Dunn County, Wisconsin. *Wis. Conserv. Bul.* 12:6–13.
- Church, K. E., J. R. Sauer, and S. Droege. 1993. Population trends of quails in North America. Pages 44–54 in K. E. Church, and T. V. Dailey, eds. *Quail III: Natl. Quail Symp. Kans. Dep. Wildl. and Parks, Pratt.*
- Curtis, P. D., B. S. Mueller, P. D. Doerr, and C. F. Robinette. 1988. Seasonal survival of radio-marked northern bobwhite quail from hunted and non-hunted populations. *Biotelemetry X: Internatl. Radio-telemetry Symp.* 10:263–275.
- Droege, S. and J. R. Sauer. 1990. Northern bobwhite, gray partridge, and ring-necked pheasant population trends (1966–1988) from the North American Breeding Bird Survey. Pages 2–20 in K. E. Church, R. E. Warner, and S. J. Brady, eds. *Perdix V: gray partridge and ring-necked pheasant workshop. Kans. Dep. Wildl. and Parks, Emporia.*
- Dumke, R. T. and C. M. Pils. 1973. Mortality of radio-tagged pheasants on the Waterloo Wildlife Area. *Wis. Dep. Nat. Resour. Tech. Bul. No. 72.* 52pp.
- Errington, P. L. 1934. Vulnerability of bobwhite populations to predation. *Ecology* 15:110–127.
- and F. N. Hamerstrom, Jr. 1935. Bobwhite winter survival on experimentally shot and unshot areas. *Iowa State Coll. J. Sci.* 9:625–639.

- Exum, J. H., R. W. Dimmick, and B. L. Deardon. 1982. Land use and bobwhite populations in an agricultural system in west Tennessee. Pages 6–12 in F. Schitosky Jr., E. C. Schitosky, and L. G. Talent, eds. Proc. Second Natl. Bobwhite Quail Symp. Okla. State Univ., Stillwater.
- Heisey, D. M. and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. *J. Wildl. Manage.* 49:668–674.
- Kabat, C. and D. R. Thompson. 1963. Wisconsin quail, 1834–1962.—population dynamics and habitat management. *Wis. Conserv. Dep. Tech. Bul. No. 30.* 136pp.
- Klimstra, W. D. 1982. Bobwhite quail and changing landuse. Pages 1–5 in F. Schitosky, Jr., E. C. Schitosky, L. G. Talent, eds. Proc. Second Natl. Bobwhite Quail Symp. Okla. State Univ., Stillwater.
- Kurzejeski, E. W., L. D. Vangilder, and J. B. Lewis. 1987. Survival of wild turkey hens in north Missouri. *J. Wild. Manage.* 51:188–193.
- Leopold, A. S. 1945. Sex and age ratios among bobwhite quail in southern Missouri. *J. Wildl. Manage* 9:30–34.
- Leopold, B. D. and G. A. Hurst. 1994. Experimental designs for assessing the impacts of predators on gamebird populations. *Trans. N. Am. Wildl. and Nat. Resour. Conf.* 59:(In press).
- Marsden, H. M. and T. S. Baskett. 1958. Annual mortality in a banded bobwhite population. *J. Wildl. Manage.* 22:414–419.
- Mayfield, H. 1961. Nesting success calculated from exposure. *Wilson Bul.* 73:255–261.
- Mueller, B. D., J. B. Atkinson, Jr., and T. DeVos. 1988. Evaluation of post-fire cover to mortality of northern bobwhites. *Biotelemetry X: Internatl. Radio-telemetry Symp.* 10:254–262.
- Parmalee, P. W. 1953. Hunting pressure and its effect on bobwhite quail populations in east-central Texas. *J. Wildl. Manage.* 17:341–345.
- Petersen, L. R., R. T. Dumke, and J. M. Gates. 1988. Pheasant survival and the role of predation. Pages 165–196 in D. L. Hallett, W. R. Edwards and G. V. Burger, eds., *Pheasants: symptoms of wildlife problems on agricultural lands.* North Cent. Sect. Wildl. Soc., Bloomington, Ind.
- Pollock, C. M. Winterstein, S. R., Bunck, and P. D. Curtis. 1989a. Survival analysis in telemetry studies: the staggered entry approach. *J Wildl. Manage.* 53:7–14.
- , C. T. Moore, W. R. Davidson, F. E. Kellogg, and G. L. Doster. 1989b. Survival rates of bobwhite quail based on band recovery analysis. *J. Wild. Manage.* 53:1–6.
- , S. R. Winterstein, and M. J. Conroy. 1989c. Estimation of analysis of survival distributions for radio-tagged animals. *Biometrics* 45:99–109.
- Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. *Oikos.* 44:257–267.
- Robbins, C. S., D. Bystrak, and P. H. Geissler. 1986. The breeding bird survey: its first fifteen years, 1965–1979. *U.S. Fish and Wildl. Serv., Resour. Publ.* 157. 196pp.
- Robel, R. J. 1993. Symposium wrap-up: what is missing? Pages 156–158 in K. E. Church and T. V. Dailey, eds. *Quail III: Natl. Quail Symp.* Kans. Dep. Wildl. and Parks, Pratt.
- Robertson, P. A. and A. A. Rosenberg. 1988. Pages 177–201 in *Ecology and management of game birds.* P. J. Hudson and M. R. W. Rands, eds. Blackwell Sci. Publ., Ltd. Oxford, Engl.
- Robinette, C. F. and P. D. Doerr. 1993. Survival of northern bobwhite on hunted and nonhunted study areas in the North Carolina Sandhills. Pages 74–78 in K. E.

- Church, and T. V. Dailey, eds. Quail III: Natl. Quail Symp., Kans. Dep. Wildl. and Parks, Pratt.
- Roseberry, J. L. 1993. Bobwhite and the "new" biology. Pages 16–20 in K. E. Church, and T. V. Dailey, eds. Quail III: Natl. Quail Symp. Kans. Dep. Wildl. and Parks, Pratt.
- and W. D. Klimstra. 1984. Population ecology of the bobwhite. So. Ill. Univ. Press. Carbondale, Ill. 259pp.
- and ———. 1992. Further evidence of differential harvest rates among bobwhite sex-age groups. Wildl. Soc. Bul. 20:91–93.
- and ———. 1993. Attitudes of a select group of Illinois quail hunters. Pages 34–42 in K. E. Church, and T. V. Dailey, eds. Quail III: Natl. Quail Symp. Kans. Dep. Wildl. and Parks, Pratt.
- , B. G. Peterjohn, and W. D. Klimstra. 1979. Dynamics of and unexploited bobwhite population in deteriorating habitat. *J. Wildl. Manage* 43:306–315.
- Sauer, J. R. and B. K. Williams. 1989. Generalized procedures for testing hypotheses about survival or recovery rates. *J. Wild. Manage.* 53:137–142.
- Shupe, T. E., F. S. Guthery, and R. L. Bingham. 1990. Vulnerability of bobwhite sex and age classes to harvest. Wildl. Soc. Bul. 18:24–26.
- Stoddard, H. L. 1931. The bobwhite quail: its habits, preservation, and increase. Charles Scribners Sons, New York, N.Y. 559pp.
- Snyder, W. D., 1978. The bobwhite in eastern Colorado. Colo. Div. Wildl. Tech. Publ. 32. 88pp.
- Vance, D. R. 1976. Changes in land-use and wildlife populations in southeastern Illinois. Wildl. Soc. Bul. 4:11–15.
- and J. A. Ellis. 1972. Bobwhite populations and hunting on Illinois public hunting areas. Pages 165–173 in J. A. Morrison, and J. C. Lewis, eds. Proc. First Natl. Bobwhite Symp., Okla. State Univ., Stillwater.
- Vangilder, L. D. and S. L. Sheriff. 1990. Survival estimation when the fates of some animals are unknown. *Trans. Mo. Acad. Sci.* 24:57–68.
- White, G. C. and R. A. Garrott. 1990. Analysis of radio-tracking data. Acad. Press, Inc., San Diego, Calif. 383pp.