

# PATTERNS IN BOBWHITE MORTALITY AND EFFECTS ON QUAIL POPULATION ECOLOGY

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**Abstract:** In recent decades, bobwhite populations have declined throughout much of their range. In the context of changing landscape patterns and declining habitat quality, a thorough understanding of the causes and temporal distribution of mortality is essential for informed management. In northern Missouri, the relative importance of different mortality agents varied seasonally and between sexes. Mortality is highest during the winter, particularly during the hunting season. Females have lower overwinter survival than males, contributing to sex ratio bias. Avian mortality is highest during winter. Mammalian mortality peaks during the nesting period. Males are particularly vulnerable to avian predation during the peak of calling activity. Incubation and brood-rearing substantially reduce survival. Retrieved (23%) and unretrieved (5%) harvest mortality account for 28% of the fall population. The relative importance of predation and harvest needs to be reexamined in the context of modern landscapes.

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## Introduction

Northern bobwhite (*Colinus virginianus*) populations have been declining throughout most of their range. In recent decades bobwhite populations in many areas have declined precipitously. U.S. Fish and Wildlife Service breeding bird surveys, conducted since 1966, reflect a 2.4%/year decline in bobwhite abundance and the rate of decline is increasing. Population trends from 1966-1979 exhibited a 1%/year decline whereas, trends from 1980-1994 declined 2.8%/year. Throughout much of the range, historically high bobwhite populations were a by-product of land use practices. Primitive agricultural practices, low intensity grazing of native rangelands, and patchwork forest operations created a perfect mosaic of early and mid-successional plant communities to which bobwhite are adapted. Declines have been attributed to many factors, but the most likely are large-scale deterioration of quail habitat quality associated with advanced natural succession, intensive monoculture farming, and intensive forest management (Brennan 1991). Trends in silvicultural and agricultural practices that maximize fiber and commodity production have reduced landscape heterogeneity and habitat suitability for bobwhite throughout much of its range.

Scientific management of bobwhite populations requires information on the demographic processes that determine abundance. The abundance of a population of a given species is a function of recruitment, mortality, ingress, and egress. In order to penetrate bobwhite populations and understand what makes them tick, biologists must have information

on these individual components and their interrelationships. Population declines imply that mortality consistently exceeds production and therefore, a thorough understanding of the causes and temporal distribution of mortality is essential.

Bobwhite inhabiting marginal or isolated habitat may be more vulnerable to catastrophic weather 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 might be exposed to greater predator populations (including hunters) under habitat conditions that favor the predator. Although biologists have historically minimized the importance of predation and harvest on bobwhite populations (Errington 1934, Errington and Hamerstrom 1935), 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. 1989, Robel 1993, Robinette and Doerr 1993). As annual mortality often exceeds production, a thorough understanding of the causes and temporal distribution of mortality of bobwhite in modern landscapes has become increasingly important. Knowledge of the relationships among seasonal biological processes, mortality, exploitation, and production can provide insight into the natural adaptations that bobwhite have and enhance our ability to effectively manage declining bobwhite populations. In this paper, I discuss seasonal patterns in vulnerability of bobwhite to specific predators and compare patterns between sexes. I interpret the significance of these patterns in the context of seasonal biological processes, life history strategies, and changing landscape patterns.

### Study Areas and Methods

To evaluate survival and causes of mortality in a modern agricultural landscape, we initiated research in northern Missouri in 1989. From 1989-1992 we captured, radio marked, and released 1001 wild 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). The agricultural study area (AGSA) was composed of 53.6% row crop, 33.1% pasture/hay, 9.1% woods, and 4.3% old field (>10 yr fallow). Land use practices in the CRP study area (CRPSA) prior to enrollment were 59.6% row crop (44.6% after enrollment), 22.1% pasture/hay, 12.7% woods, and 5.6% old field. Most crop fields in both areas were eligible for enrollment in the CRP. Differences in CRP enrollment between areas were due primarily to land ownership patterns and farmer/owner demographics. Primary crops in both areas were soybeans, corn, wheat, and milo. Topography of both areas was rolling; elevations varied from 229 to 274 m. We monitored radio-marked birds daily to determine date and cause of mortality.

Bobwhite are naturally a short-lived species with high annual mortality. Estimates of annual survival throughout the range have varied from 5-25%. To offset this high mortality rate, bobwhite have tremendous reproductive potential. They are capable of attaining spring to fall increases in excess of 300%. In northern Missouri our radio-marked sample of bobwhite had lower annual survival rate (0.053) than that reported in other studies (0.18, Marsden and Baskett 1958; 0.154, Kabat and Thompson 1963:36; 0.188 based on age ratios, 0.182 based on product of fall-spring and spring-fall survival rates, Roseberry and Klimstra 1984:89). Our estimate, however, was similar to that reported by Curtis et al. (1988) (0.061) for radio-marked bobwhite in North Carolina. A long-term study in northern Florida reported average annual survival of 0.167 (Pollock et al. 1989).

Vulnerability of bobwhite to mortality varies throughout the annual cycle. Survival is lowest during the winter. Fall-spring survival (0.159) was about half that of spring-fall survival (0.332). Other studies have similarly reported that winter is the period of highest mortality (Curtis et al. 1988:267). In addition to seasonal differences in survival, we observed temporal variation within seasons (Fig 1). During the hunting season (November - January) monthly survival of radio-marked bobwhite was 20% lower than during the remainder of the year. This was largely attributable to harvest-related mortality. Monthly harvest mortality was highest in November (21%) and declined to 9% in January. Survival rate during the breeding season (May - September) 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 the form of reduced survival.

Predation was the primary cause of bobwhite mortality in northern Missouri, however, the relative importance of specific mortality agents varied seasonally in relation to predator and prey behavior. In the southeastern United States, the Cooper's hawk (*Accipiter cooperii*) is the dominant avian predator with depredation concentrated during migration (Feb.-Mar.) and nesting (Jun.-Jul.) (Stoddard 1931, Mueller et al. 1988). However, instead of a peak of avian mortality associated with raptor migrations, bobwhite populations in Northern Missouri 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 greathorned 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 greathorned 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 (Fig 2)(Burger et al. 1995c). 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 depredation on males during June-July and differences between sexes in vulnerability to avian depredation support the hypothesis that singing male bobwhite may be vulnerable to predators that hunt by sight (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 might predispose bobwhite to predation by both diurnal and nocturnal avian predators. This form of advertisement likely imposes "costs" of reproduction on males.

Mammalian mortality was high in January, then declined in February (Fig 3). 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 et al. 1995b). Increased mammalian-related mortality during this period may reflect vulnerability of incubating and brood-rearing birds to predators that rely on olfaction to detect prey (Burger et al. 1995a).

Patterns in vulnerability of bobwhite to specific predators differ between sexes. During the reproductive period, male bobwhite were more vulnerable to avian predation than were females. Both male and female bobwhite incubate nests (Klimstra and Roseberry 1975, Burger 1995b, Curtis et al. 1993, DeVos and Mueller 1993, Suchy and Munkel 1993); however, females are twice as likely to incubate a nest and, on average, incubate more nests than males (Burger 1995b). Consequently, females are more affected by mammalian mortality associated with incubation and brood rearing and males are more affected by avian mortality associated with calling activity. We hypothesize that, for bobwhite, the combined cost of displaying and incubation incurred by males approximates the reproduction-related costs incurred by females.

Reproduction reduces survival for both sexes. During the 24 days required to incubate a nest and 21 days to rear chicks, reproductively active birds ( $0.640$ ) had 16% lower survival than non-reproducing birds ( $0.803 \pm 0.014$ ) during the same period. Most of the mortality during the incubation period occurred at the nest. However, birds were at greatest risk during the brood-rearing period. Two-thirds of the total reduction in survival during reproduction was associated with brood rearing. Kabat and Thompson (1963) suggested that the physiological stress of reproduction was the primary factor affecting late summer mortality. Bobwhite may be physiologically stressed following incubation and this could make them more vulnerable to predation. However, we suggest that increased predation while accompanying flightless chicks causes reduced survival during brood-rearing.

Numerous studies have reported a male bias in bobwhite sex ratio, particularly in the



adult segment of the population. Some workers have concluded that this difference results from greater female mortality during incubation (Leopold 1945, Buss et al. 1947, Bennitt 1951). In contrast, Roseberry and Klimstra (1984:136) suggested that adult mortality during incubation was low and that at least some sex bias arose from differential mortality outside the breeding season. Stoddard (1931:94) hypothesized that females experienced higher fall and winter mortality. During our study, overwinter survival of male bobwhite was 4% higher than that of females. Differences between sexes in fall-spring survival may have been due to the cumulative effect of minor differences in vulnerability of females to harvest and predation. Female bobwhite have been reported to be more vulnerable to harvest than are males (Pollock et al. 1989, Shupe et al. 1990, Roseberry and Klimstra 1992). We observed that during nesting females were not more vulnerable to predation than were males, supporting the hypothesis that male bias results from higher fall and winter mortality of females.

Biologists have traditionally assumed that, below some threshold harvest level, hunter kill has little effect on bobwhite survival and breeding densities (Errington and Hamerstrom 1935, Baumgartner 1944, Parmalee 1953, Marsden and Baskett 1958). Numerous recent studies have suggested that harvest mortality, particularly late season harvest (Jan.-Feb.), contributes additively to natural mortality (Roseberry and Klimstra 1984:149, Curtis et al. 1988, Pollock et al. 1989, Robinette and Doerr 1993). The harvest rate observed on our private-land study areas (22.9%) was moderate compared with other reported harvest rates [14% at Fort Bragg, N. C. (Curtis et al. 1988); 23.3% on Tall Timbers Res. Stn. (Pollock et al. 1989), 42.5% on Ill. private land (Roseberry and Klimstra 1984), and 70% on Ill. public wildl. areas (Vance and Ellis 1972)]. The low annual survival rates that we observed, however, were due primarily to low overwinter survival, of which harvest-related mortality contributed about 33%. The real effect of harvest on bobwhite survival, breeding density, production, and fall density will not be understood until replicated, manipulative experiments are conducted (Burger et al. 1994).

Doster et al. (1982) reported that unretrieved kill averaged 28.5% of retrieved kill and 22.2% of total hunting-related mortality over 13 years. Similarly, in our study, unretrieved kill contributed an additional 5.3% mortality (23.2% of the reported harvest and 18.9% of the total hunting-related mortality). Thus, "crippling loss" accounts for a significant portion of the fall populations and studies that report harvest rates not including unretrieved kill may underestimate total hunting-related mortality by 20-25%.

During our study, most annual mortality occurred prior to the reproductive season. Bobwhite may exhibit density-dependent reproduction (Roseberry and Klimstra 1984:145) and can exhibit flexible reproductive strategies to compensate for high annual mortality (Burger 1995*b*, Curtis et al. 1993, Suchy and Munkel 1993). As the rate of prereproductive mortality increases, however, the ability of bobwhite populations to compensate with increased reproductive output diminishes (Roseberry and Klimstra 1984:145, Curtis et al. 1988). Curtis et al. (1988) noted that bobwhite populations in North Carolina, with an annual survival rate of 6.1%, would be unlikely to recover under existing management practices,

suggesting that recovery of bobwhite populations may require reductions in natural and harvest-related mortality. Roseberry and Klimstra (1984:145) hypothesized that bobwhite populations would decline if pre-breeding losses consistently exceeded 70%. Fall-spring mortality on our areas exceeded 70%. Assuming that radio-marked bobwhite survive similarly to unmarked birds, it seems unlikely that bobwhite populations could be maintained if annual mortality consistently remained this high. Declining population and harvest trends observed for this region from 1990 to 1992 are consistent with this observation (e.g., coveys flushed/hr declined 13-14%/yr 1990-92).

### Management Implications

Although low survival and declining bobwhite abundance observed in northern Missouri during our study may reflect a short-term fluctuation, bobwhite populations in the east, southeast, and central portions of North America are exhibiting long-term declines (Brennan 1991) and the rate of decline has increased during the 1980's (Church et al. 1993). Bobwhite populations may not be self-sustaining under existing landscape patterns, predation regimes, and hunter harvest levels (Curtis et al. 1988, Robinette and Doerr 1993). Traditional paradigms regarding the effects of predation and harvest on bobwhite populations may no longer be applicable (Robel 1993, Roseberry 1993). Relationships among harvest, predation, and bobwhite abundance will not be adequately understood until they are viewed as dynamic, complex processes and evaluated with carefully designed, replicated experiments (Burger et al. 1994, Leopold and Hurst 1994). If management objectives of stable or increasing bobwhite populations are to be achieved, aggressive habitat management, suppression of predation levels, and/or reductions in hunting-related mortality may be necessary. We concur with Church et al. (1993) and Brennan (1991) that the design and implementation of a nationally coordinated, comprehensive approach to management and research will be necessary to reverse current bobwhite population trends.

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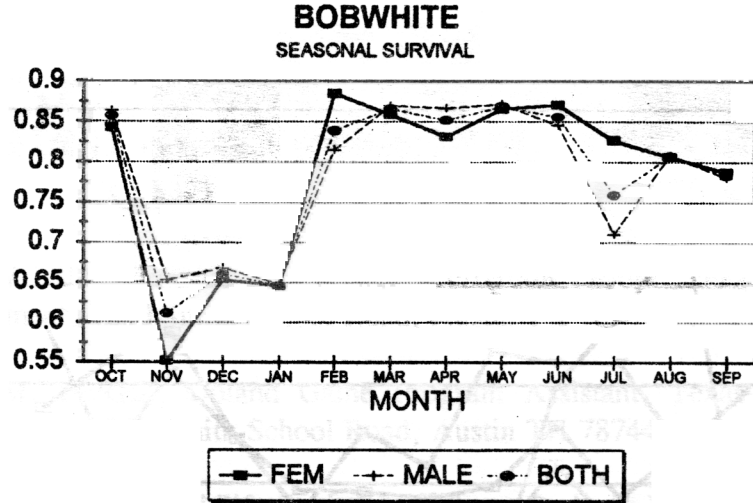


Fig. 1. Monthly survival of male and female bobwhite in northern Missouri, 1989-93.

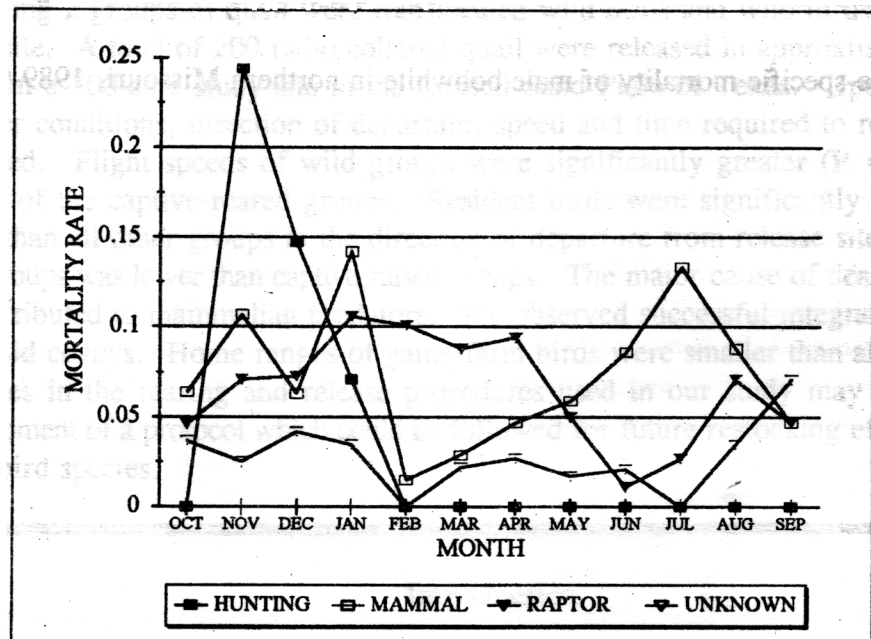


Fig. 2. Cause-specific mortality of female bobwhite in northern Missouri, 1989-1993.

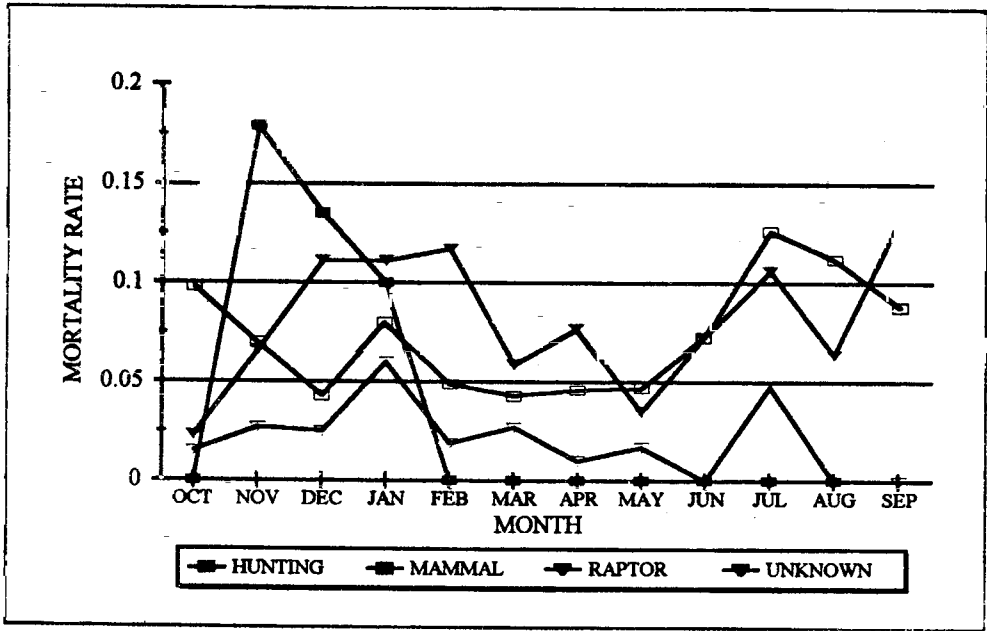


Fig. 3. Cause-specific mortality of male bobwhite in northern Missouri, 1989-93.