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# SURVIVAL RATES FOR NORTHERN BOBWHITES ON TWO AREAS WITH DIFFERENT LEVELS OF HARVEST

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## ABSTRACT

We estimated survival rates for radio-marked northern bobwhites (*Colinus virginianus*) in south-central Iowa from 1984 to 1988. Survival rates and survival functions were calculated for 2 areas that received different and varied amounts of hunting pressure. Survival from fall-spring averaged  $17.1\% \pm 6.9\%$  on the Brown's Slough study area (BSSA) and  $20.1\% \pm 5.7\%$  on the Millerton study area (MSA). Although these estimates were not different ( $P = 0.898$ ), the survival functions did differ between the 2 areas ( $\chi^2 = 25.82$ ,  $P < 0.001$ ). Mortality due to hunting averaged  $27.7\% \pm 8.2\%$  on the BSSA during the fall-spring period and  $12.3\% \pm 4.9\%$  on the MSA. Predators accounted for 52% of fall-spring mortality on the BSSA and 79% of the mortality on the MSA. The BSSA had much lower rates of predation the 2 months following the hunting season. Survival rates during both the spring-fall period and annually did not differ between the 2 areas ( $P = 0.395$  and  $P = 0.979$ ). Hunting did not appear to be a limiting factor for quail numbers on these areas during the study.

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## INTRODUCTION

Many studies have examined the life history and various population dynamics of the northern bobwhite (e.g., Stoddard 1931, Roseberry and Klimstra 1984). Most of the studies in Iowa on quail have focused on censusing populations (Kozicky and Hendrickson 1952, Kozicky et al. 1956, Kozicky 1957, Stempel 1962). Many of these early studies utilized methodology that produced variable results. Since the 1960's quail populations have declined in Iowa (Suchy et al. 1991) and throughout most of their range (Church et al. 1993). The advent of radio-telemetry makes it possible to collect detailed demographic information unattainable by earlier methods. Detailed information on survival could potentially help identify causes of the decline and, more importantly, provide insight into management practices that could mitigate the factors responsible.

The primary objective of this study was to evaluate the impact that hunting has on survival rates on 2 areas that receive different levels of hunting pressure. The Brown's Slough study area (BSSA) was centered around a state wildlife management area which traditionally received heavy hunting pressure. The Millerton study area (MSA) was a similar area of privately owned land with lower hunting pressure (Suchy and Munkel 1993). Causes of hunting and natural mortality were estimated using radio-marked quail captured on both study areas. We compare the causes of non-hunting mortality as well as the overall timing of all sources of mortality to evaluate the apparent impact hunting had on quail numbers on these areas.

## METHODS

### Study Area

The BSSA (1,960 acres) and MSA (2,315 acres) consist of some of the best northern bobwhite habitat in Iowa. Seventeen habitat types were identified and measured on each study area. The proportion of cropland, grassland, woodland and strip cover on the BSSA averaged 24.6%, 45.2%, 10.9% and 17.8% from 1984–88 while the MSA averaged 38.9%, 35.8%, 9.3% and 15.8%. The biggest specific difference in land use was that soybeans were planted on an average of 20.5% of the MSA but only 5.3% of the BSSA. The percent of cropland on the MSA was reduced by about 25% during 1987 and 1988 due to enrollment in the Conservation Reserve Program. The amount of each cover type on the BSSA was more consistent, although some intermittent flooding occurred when nearby Rathbun Reservoir rose above normal pool levels.

During the period of the study, the mean number of quail observed on the annual August roadside survey increased from 2.4 to 14.5 birds per 30 miles in the southern Iowa region (Suchy et al. 1991). Flush counts conducted prior to the hunting season each year averaged 37 birds per square mile on the BSSA and 42 birds per square mile on the MSA.

### Capture Methods

We captured birds by bait-trapping in September, October, February and March (Stoddard 1931:442) and night-lighting in May–October (Bartholomew 1967),

attached radio-transmitters and numbered leg bands and released them. Birds were aged as either juvenile or adults and their sex was recorded (Rosene 1969: 44–54). Backpack style transmitters (5–6 grams, AVM Instrument Co. Ltd., Livermore, CA) were attached using wing loops to all quail weighing  $\geq 150$  g. Birds were located  $>3$  times per week using truck-mounted and hand-held Yagi antennas. An attempt was made to determine the proximate cause of death (Dumke and Pils 1973) when a mortality was suspected based on inactivity of the marked bird.

### Hunting Pressure

Hunter bag-checks were conducted on each study area using a stratified design to sample the number of parties on each area. The number of vehicles on each area was counted at the beginning and end of each survey period. Hunter interviews were conducted to determine whether the party was hunting quail, the number of hours each party hunted, the number of coveys flushed, the number of quail retrieved and the number hit but not retrieved for as many of the parties as possible. The hunting season was divided into 3 periods: the first 9 days (quail and pheasant open concurrently), the remainder of the pheasant season, and the remainder of the quail season. The pheasant season opened on November 3, 2, 1 and October 31 and closed on January 1, 5, 4, 3 in 1984 to 1988, respectively. The quail season opened the same day as the pheasant season and ended on January 31 each year.

### Survival and Mortality Rates

We calculated survival rates for 2 periods, the fall-spring period from October 1 to March 31 (182 days), and the spring-fall period from April 1 to September 30 (183 days). The fall-spring period begins when coveys are formed and most juvenile birds are large enough to carry transmitters, includes the hunting season, and ends when coveys begin to break up in the spring. The spring-fall season coincides with the nesting season. Annual rates were calculated by combining the 2 periods. We used the staggered entry technique (Pollock et al. 1989b) to produce Kaplan-Meier survival estimates (Kaplan and Meier 1958). The assumptions required are that radio-marked birds are selected randomly from the population, survival rates are independent, left-censored birds had similar survival rates, censoring was random and trapping and tagging did not affect survival. If tagging does affect survival then our estimates will be negatively biased; however, we believe the comparisons between the 2 areas would still be valid, because potential differences in survival would be relative.

Birds were right-censored if they survived past the end of a period, or if their fate was unknown due to radio failure or loss or movement off the study area. Birds that died or were censured within 7 days of being radio-marked (Pollock et al. 1989b) were excluded from analyses to minimize the impact of capture. Birds surviving to the next period were treated as new, independent observations. Log-rank tests were used to

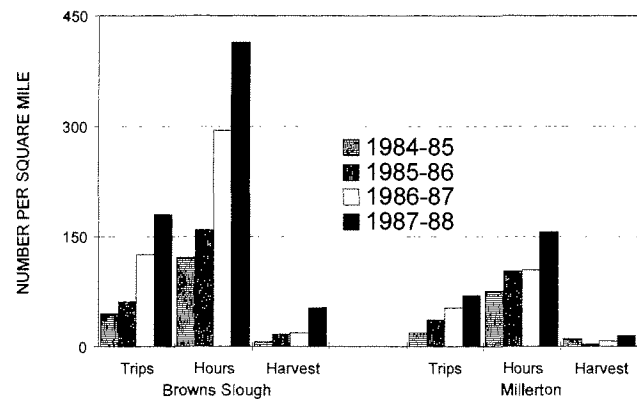


Fig. 1. The estimated number of trips, hours spent afield and harvest on the BSSA and MSA, 1984–1988 based upon hunter interviews. Trips are the number of hunters going afield on a day, hours are the number of hunters multiplied times the number of hours each hunter spent hunting and harvest is the number of birds retrieved.

compare survival functions between age, sex and study areas (White and Garrot 1990). Z-tests were used to determine if survival estimates differed between age, sex and study areas after any period (Pollock et al. 1989b). A generalized Chi-square hypothesis testing procedure was used to determine if survival rates differed between study areas and years (Sauer and Williams 1989). A 5% level of significance was used for all comparisons.

Cause-specific mortality rates (Heisey and Fuller 1985) were calculated for each period on each study area. This assumes that survival rates are constant within the period. A generalized Chi-square hypothesis testing procedure was used to determine if cause-specific harvest mortality rates differed between areas and years (Sauer and Williams 1989). Cause-specific rates were calculated by month for each study area during the fall-spring period.

## RESULTS

We captured 822 quail from 1984–1988. Radio transmitters were placed on 628 birds. We excluded 14 birds (2.2%) from analyses because they died or were censured within 7 days after release.

### Hunting Pressure

The number of hunter trips, hunter hours and the number of quail killed varied considerably on the BSSA and MSA during the study (Figure 1). Hunting pressure, in general, increased as the study progressed. The number of hunter trips increased from 137 to 551 on the BSSA and from 68 to 252 on the MSA between the 1984–1985 and 1987–1988 hunting seasons. Hunting pressure was consistently higher on the BSSA. Hunter trips, hunter hours and harvest were, on average, twice as high on the BSSA. The reported crippling rate on the BSSA averaged 28% of the harvest and was higher than on the MSA, which averaged 17% of the harvest. Hunters reported flushing an average of

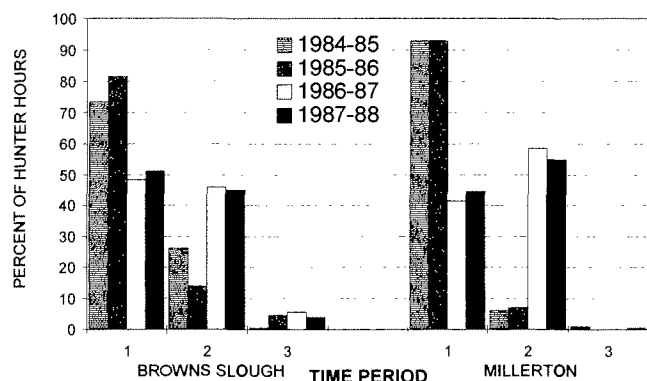


Fig. 2. The estimated number of hunter hours on the BSSA and the MSA from 1984-1988. Period 1 was the first 9 days of the season. Period 2 was from the end of Period 1 to the end of the pheasant season in early January. Period 3 was from the end of Period 2 to the end of the hunting season on January 31.

0.08 coveys per hunter hour on both areas. The number of coveys flushed per hunter hour increased from 0.05 to 0.12 on the BSSA and from 0.06 to 0.10 on the MSA during the study.

The distribution of the hunting pressure during the season also changed as the study progressed (Figure 2). During the first 2 years over 70% of the hunter trips occurred during the first 9 days of the season. During the last 2 years this fell to 40 to 50% as more hunters spent more time hunting later during the season. Less than 5% of the trips occurred during January (Period 3) when the pheasant season was closed. Although there were fewer hunters afield during this period they were, on average, more successful.

#### Cause-Specific Mortality

We estimated cause-specific mortality rates from observed mortalities of 392 radio-marked bobwhites. Avian and mammalian predators were the largest known source of mortality (24.1%) during the fall-spring period on the MSA, while harvest (27.7%) was the largest source of mortality on the BSSA when all

years are pooled (Table 1). During the spring-fall period mammals were the largest source of mortality on both study areas. Annually, harvest (27.7%) was the largest source of mortality on the BSSA, while predation due to mammals (29.1%) was slightly greater than predation by raptors (27.7%) on the MSA.

Mortality due to harvest during the fall-spring period (Table 2) was similar between years on each study area ( $P > 0.079$ ) but differed significantly between the 2 areas ( $\chi^2 = 5.46$ , 1 df,  $P = 0.020$ ).

When we compare estimates of cause-specific mortality by month on each study area (Figure 3) we see that most hunting mortality occurred during November and December and was higher on the BSSA. Mortality due to other causes were similar on both areas until February and March when mortality due to predation was much higher on the MSA.

#### Survival Estimates

Survival rate estimates were similar for males and females on both areas during the fall-spring period, except in 1987-1988 on the MSA, and for all periods during the spring-fall period. Estimates ranged from 9.5% to 40.1% for males and from 5.0% to 34.5% for females during the fall-spring period and from 25.3% to 60.5% for males and 16.2% to 55.6% for females during the spring-fall period. When data for the 2 study areas were pooled, survival rate estimates did not differ between the sexes during any period ( $P > 0.137$ ); therefore, sexes were pooled for all comparisons.

Survival rate estimates were similar for juveniles and adults on both areas during the fall-spring period, except in 1986-1987 on the BSSA and for all periods during the spring-fall period except in 1986 on the BSSA. Estimates ranged from 9.4% to 34.6% for juveniles and from 5.4% to 43.8% for adults during the fall-spring period and from 23.0% to 61.6% for juveniles and 18.7% to 87.5% for females during the spring-fall period. When data for the 2 study areas were pooled, survival rate estimates did not differ be-

Table 1. Fall-spring (1 October-31 March), spring-fall (1 April-30 September) and annual (1 October-30 September) cause-specific mortality rates (M) (Heisey and Fuller 1985) of radio-marked northern bobwhite pooled for all years, 1984-1988.

| Interval    | Cause            | Brown's Slough |    |       |       | Millerton  |    |       |       |
|-------------|------------------|----------------|----|-------|-------|------------|----|-------|-------|
|             |                  | Radio-days     | n  | M     | SE    | Radio-days | n  | M     | SE    |
| Fall-Spring | Raptor           | 10,141         | 22 | 0.197 | 0.037 | 16,153     | 41 | 0.241 | 0.033 |
|             | Mammal           |                | 14 | 0.125 | 0.031 |            | 41 | 0.241 | 0.033 |
|             | Harvest          |                | 31 | 0.277 | 0.042 |            | 21 | 0.123 | 0.025 |
|             | Unknown Predator |                | 10 | 0.089 | 0.027 |            | 21 | 0.123 | 0.025 |
|             | Other            |                | 12 | 0.107 | 0.029 |            | 7  | 0.041 | 0.015 |
| Spring-Fall | Raptor           | 13,522         | 18 | 0.154 | 0.033 | 16,614     | 23 | 0.155 | 0.030 |
|             | Mammal           |                | 21 | 0.179 | 0.035 |            | 32 | 0.215 | 0.033 |
|             | Harvest          |                |    |       |       |            |    |       |       |
|             | Unknown Predator |                | 19 | 0.162 | 0.034 |            | 22 | 0.148 | 0.029 |
|             | Other            |                | 16 | 0.137 | 0.032 |            | 21 | 0.141 | 0.028 |
| Annual      | Raptor           | 23,663         | 40 | 0.228 | 0.037 | 32,767     | 64 | 0.277 | 0.032 |
|             | Mammal           |                | 35 | 0.162 | 0.032 |            | 73 | 0.291 | 0.032 |
|             | Harvest          |                | 31 | 0.277 | 0.042 |            | 21 | 0.123 | 0.025 |
|             | Unknown Predator |                | 29 | 0.123 | 0.028 |            | 43 | 0.157 | 0.026 |
|             | Other            |                | 28 | 0.135 | 0.030 |            | 28 | 0.074 | 0.017 |

Table 2. Cause-specific mortality rates (M) (Heisey and Fuller 1985) of radio-marked northern bobwhites during the fall-spring period (1 October–31 March), 1984–1988.

| Year      | Cause            | Brown's Slough |    |       |       | Millerton  |    |       |       |
|-----------|------------------|----------------|----|-------|-------|------------|----|-------|-------|
|           |                  | Radio-days     | n  | M     | SE    | Radio-days | n  | M     | SE    |
| 1984–1985 | Raptor           | 1,028          | 1  | 0.083 | 0.079 | 4,277      | 10 | 0.211 | 0.059 |
|           | Mammal           |                | 1  | 0.083 | 0.079 |            | 19 | 0.400 | 0.070 |
|           | Harvest          |                | 4  | 0.331 | 0.134 |            | 3  | 0.063 | 0.035 |
|           | Unknown Predator |                | 2  | 0.166 | 0.116 |            | 6  | 0.126 | 0.048 |
|           | Other            |                | 2  | 0.166 | 0.116 |            | 0  | 0.000 | 0.000 |
| 1985–1986 | Raptor           | 2,692          | 3  | 0.127 | 0.068 | 2,977      | 8  | 0.262 | 0.079 |
|           | Mammal           |                | 6  | 0.255 | 0.089 |            | 3  | 0.098 | 0.054 |
|           | Harvest          |                | 4  | 0.170 | 0.077 |            | 5  | 0.164 | 0.067 |
|           | Unknown Predator |                | 1  | 0.042 | 0.041 |            | 5  | 0.164 | 0.067 |
|           | Other            |                | 1  | 0.042 | 0.041 |            | 2  | 0.066 | 0.045 |
| 1986–1987 | Raptor           | 1,988          | 4  | 0.192 | 0.086 | 4,176      | 5  | 0.143 | 0.059 |
|           | Mammal           |                | 1  | 0.048 | 0.047 |            | 6  | 0.171 | 0.063 |
|           | Harvest          |                | 3  | 0.144 | 0.077 |            | 5  | 0.143 | 0.059 |
|           | Unknown Predator |                | 2  | 0.096 | 0.064 |            | 3  | 0.086 | 0.047 |
|           | Other            |                | 6  | 0.288 | 0.098 |            | 2  | 0.057 | 0.039 |
| 1987–1988 | Raptor           | 4,433          | 14 | 0.251 | 0.058 | 4,723      | 18 | 0.311 | 0.060 |
|           | Mammal           |                | 6  | 0.107 | 0.041 |            | 13 | 0.225 | 0.055 |
|           | Harvest          |                | 20 | 0.358 | 0.063 |            | 8  | 0.138 | 0.045 |
|           | Unknown Predator |                | 5  | 0.089 | 0.038 |            | 7  | 0.121 | 0.043 |
|           | Other            |                | 3  | 0.054 | 0.030 |            | 3  | 0.052 | 0.029 |

tween the ages during any period ( $P > 0.110$ ); therefore, ages were pooled for all comparisons.

Survival rate estimates did not differ significantly between the 2 study areas during any year for any period or annually (Table 3). Survival rates did not differ between years for either study area except for the spring-fall period in 1985 on the MSA ( $P = 0.001$ ). Survival rates for the fall-spring period ranged from 12 to 28% on the BSSA and from 15 to 40% on the MSA. Spring-fall survival rates were higher and ranged from 32 to 39% on the BSSA and 24 to 62% on the MSA. Annual survival rates ranged from 4 to 10% on the BSSA and from 5 to 13% on the MSA.

Survival estimates with ages and sexes pooled did not differ between years for either study area during the fall-spring or spring-fall period or for the whole year. Survival rates also did not differ between the study areas in any year for any time period.

#### Survival Functions

Although the point estimates for the above comparisons were similar for the study areas, the survival functions differed between the 2 study areas for all periods except the fall-spring period in 1987–1988, the spring-fall period in 1988 and annually for 1987–1988. The survival functions for both areas declined rapidly during the early portion of the hunting season for each year of the study (Figure 4). After these initial losses, the functions were more variable and depended upon the number of birds harvested during the hunting season. Although hunting pressure and harvest increased throughout the study (Figure 1), the proportion of radio-marked birds that died due to hunting was more variable (Table 2). Losses due to hunting were higher on the BSSA in 1984–1985 and 1987–1988 than on the 2 years in between. Mortality on the MSA was low in 1984–1985 and then remained constant. As a result, mortality due to hunting on the BSSA was 5 times higher than on the MSA in 1984–1985, about 3 times higher in 1987–1988 but very similar in the other 2 years.

Pooling birds for all years on each study area allows for a more detailed examination of the influence of harvest on the survival functions (Figure 5). Both curves are very similar until mid-November, which coincides with the end of the initial period of heavy harvest. After this, the survival curve for the BSSA falls below the MSA and stays lower throughout the rest of the hunting season. Hunting mortality on the BSSA during this period is about twice that on the MSA (Figure 3). After the end of the hunting season on January 31 the survival curve on the MSA declines while little additional mortality occurs on the BSSA during this period (Figure 3). By the end of March the difference between the 2 areas becomes statistically non-significant.

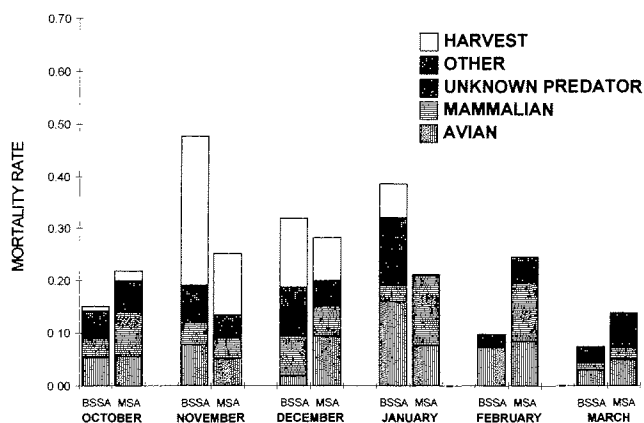


Fig. 3. Monthly estimates of cause-specific mortality (Heisey and Fuller 1985) during the fall-spring period for radio-marked bobwhites on the BSSA and MSA, 1984–1988.

Table 3. Fall-to-spring (1 October–31 March), spring-to-fall (1 April–30 September) and annual (1 October–30 September) survival (S) Kaplan and Meier 1958) of radio-marked northern bobwhite quail in south-central Iowa, 1984–1988.

|             |           | Brown's Slough |       |       | Millerton |       |       | P-value                    |                     |
|-------------|-----------|----------------|-------|-------|-----------|-------|-------|----------------------------|---------------------|
|             |           | n              | S     | SE    | n         | S     | SE    | log-rank test <sup>a</sup> | Z-test <sup>b</sup> |
| Fall–Spring | 1984–1985 | 17             | 0.219 | 0.113 | 68        | 0.203 | 0.056 | 0.000                      | 0.898               |
|             | 1985–1986 | 44             | 0.276 | 0.106 | 46        | 0.220 | 0.077 | 0.068                      | 0.670               |
|             | 1986–1987 | 56             | 0.283 | 0.109 | 62        | 0.397 | 0.084 | 0.013                      | 0.403               |
|             | 1987–1988 | 83             | 0.118 | 0.042 | 92        | 0.145 | 0.044 | 0.875                      | 0.651               |
|             | Pooled    | 219            | 0.173 | 0.035 | 277       | 0.201 | 0.029 | 0.000                      | 0.533               |
| Spring–Fall | 1985      | 25             | 0.394 | 0.179 | 41        | 0.624 | 0.095 | 0.001                      | 0.257               |
|             | 1986      | 34             | 0.364 | 0.090 | 42        | 0.267 | 0.073 | 0.185                      | 0.400               |
|             | 1987      | 52             | 0.321 | 0.071 | 66        | 0.240 | 0.058 | 0.070                      | 0.375               |
|             | 1988      | 54             | 0.371 | 0.083 | 51        | 0.334 | 0.077 | 0.447                      | 0.741               |
|             | Pooled    | 165            | 0.367 | 0.044 | 196       | 0.318 | 0.038 | 0.002                      | 0.395               |
| Annual      | 1984–1985 | 39             | 0.086 | 0.059 | 81        | 0.126 | 0.040 | 0.000                      | 0.573               |
|             | 1985–1986 | 56             | 0.101 | 0.046 | 67        | 0.059 | 0.026 | 0.027                      | 0.428               |
|             | 1986–1987 | 82             | 0.091 | 0.040 | 94        | 0.095 | 0.030 | 0.003                      | 0.924               |
|             | 1987–1988 | 113            | 0.044 | 0.018 | 109       | 0.048 | 0.018 | 0.576                      | 0.856               |
|             | Pooled    | 273            | 0.064 | 0.015 | 341       | 0.064 | 0.012 | 0.000                      | 0.979               |

<sup>a</sup> comparison of survival distributions (White and Garrot 1990).<sup>b</sup> comparison of survival rate estimates at end of period (Pollock et al. 1989b).

## DISCUSSION

The primary objective of this study was to evaluate the impact that hunting has on quail numbers. The intent was to evaluate 2 areas of similar habitats with differing harvest rates for a period of 4 years and compare results. The study design did not anticipate that hunting pressure would change as markedly as is indicated in Figures 1 and 2. Although this variability complicates the interpretation, conclusions about the effect of hunting can still be drawn from the comparisons.

Hunting was not the major source of mortality re-

corded for our radio-marked birds on either study area. Predation from all sources accounted for 52% of the mortality during the fall-spring period and 55% of the annual mortality on the BSSA while hunting accounted for 35% of the mortality during the fall-spring period and 30% annually. On the MSA, predation accounted for 79% of the mortality during both the fall-spring period and annually. Hunting accounted for 16% of the mortality during the fall-spring period and 13% annually.

Despite these large differences in the sources of mortality, the survival estimates were nearly identical, 17.3% on the BSSA and 20.1% on the MSA by the

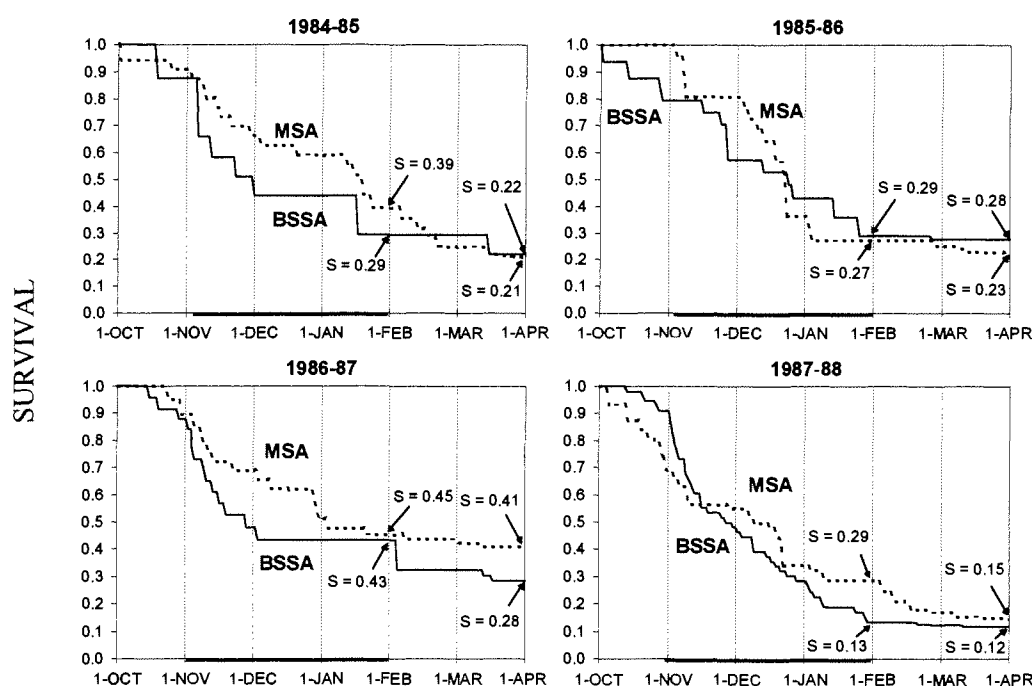


Fig. 4. Kaplan-Meier survival functions for radio-marked bobwhite on the BSSA and the MSA for the fall-spring period for each year of the study. The shaded bar represents the open hunting season and survival estimates are given for each area at the end of the hunting season and the end of the fall-spring period.

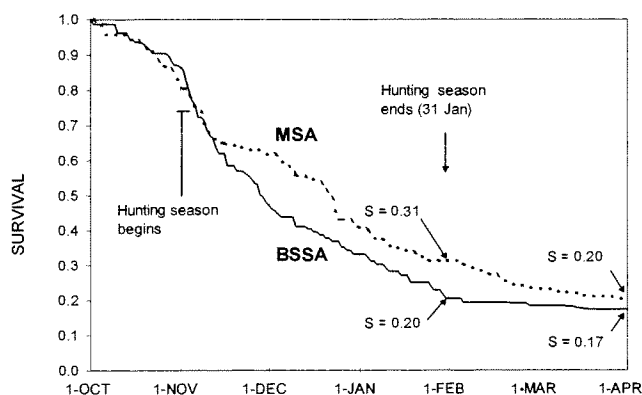


Fig. 5. Kaplan-Meier survival functions for radio-marked bobwhite on the BSSA and the MSA. Birds were pooled for each study area over all 4 years of the study. Survival estimates are given for each area at the end of the hunting season and the end of the fall-spring period.

end of the fall-spring period and were the same (6.4%) on both areas annually.

These survival rates are similar to those reported for radio-marked birds on private land in Missouri for the fall-spring (0.159) and annually (0.053) (Burger et al. 1995) and in North Carolina annually (0.061) (Curtis et al. 1988)). They are much lower than reported from studies which used flush counts or age-ratio data (0.18, Marsden and Baskett 1958; 0.154, Kabat and Thompson 1963; 0.188 and 0.182, Roseberry and Klimstra 1984) or from band recoveries (0.167, Pollock 1989a). Vance and Ellis (1972) reported similar survival estimates (0.215 and 0.233) from flush counts on public land in Illinois during the fall and winter.

Although crippling losses based upon hunter surveys was estimated to be about 28% and 17% of the reported kill on the 2 areas according to our hunter bag surveys, this mortality source was only detected in our radio-marked birds a total of 3 times or about 5% of the harvest mortality. This mortality source may be reported as predation in our study if wounded quail were killed or scavenged by predators. This would increase our estimate of hunting mortality to about 49% on the BSSA and 17% on the MSA during the fall. The survival rate estimates, however, would be unchanged.

The level of harvest on the MSA is similar to what Burger et al. (1995) found on private land in Missouri (22.9%) but lower than on private land in Illinois (42.5%) (Roseberry and Klimstra 1984). The level of harvest on the BSSA was lower than the 70% that Vance and Ellis (1972) found on public land in Illinois.

Most hunting regulations for quail are based upon the assumptions that harvest mortality simply replaces natural mortality (Errington and Hamerstrom 1935, Baumgartner 1944, Marsden and Baskett 1958). Some recent studies suggest that harvest above a threshold level, particularly in January and February, can be additive (Roseberry and Klimstra 1984, Curtis et al. 1988, Pollock et al. 1989a, Robinette and Doerr 1993). The low survival rates in our study appear to be related to predation, not harvest. This is similar to what Bur-

ger et al. (1995) found in Missouri. Results from our study indicate that little hunting pressure and even less kill (< 5%) occurred during the later part of the quail season. Even in years when hunter kill was low (1985–1986 and 1986–1987), survival rates were not significantly higher than the years when the kill was high. Hunting pressure and harvests were twice as high on the BSSA compared to the MSA, yet by 1 April the survival estimates for the 2 areas were very similar. This is vividly illustrated in Figure 4 where it appears that hunting simply removed birds that would have been lost to predators later during the fall-spring period. The survival functions for the 2 areas differ, mainly due to the additional harvest in November to January on the BSSA (Figure 5), but the net number of birds remaining in the population to begin the nesting season are similar. The apparent reason is that predation is low after the hunting season closes on the BSSA while on the MSA, predation remained higher.

Our results and their interpretation assume that the birds with radio-transmitters have the same survival rates and behavior as the rest of the population. If this assumption is not true then our conclusions may be inappropriate.

## MANAGEMENT IMPLICATIONS

There is little evidence that hunting at the level measured on the MSA and BSSA impacted the number of quail on our study areas. Although the fall-spring period is a time of heavy mortality, predation appears to be the most important factor limiting quail numbers on these 2 areas. Additionally, little harvest occurred late in the season with 40% or more of the harvest occurring during the first 9 days of the season in all years. Most of the birds taken at this time probably would not have survived till spring anyway. Survival functions derived for the 2 study areas seem to indicate that even when harvest is low, the final survival rate does not change. We agree with Burger et al. (1995) that relationships among harvest, predation, productivity and abundance must be viewed dynamically. Careful evaluation of the relationships between these factors is needed if we hope to be able to manage for stable populations.

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