SURVIVAL AND CAUSE-SPECIFIC MORTALITY OF NORTHERN BOBWHITES IN WESTERN OKLAHOMA

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Abstract: We present descriptive data on survival and cause-specific mortality of northern bobwhites (*Colinus virginianus*) in western Oklahoma, USA, during 1991–2002. We captured and radiomarked 2,647 bobwhites (286 adult [ad] M, 1,064 juvenile [juv] M, 185 ad F, and 1,049 juv F) to obtain estimates. We estimated that annual survival (Nov–Oct) averaged 0.068 ± 0.018 (SE) and ranged between 0.018 ± 0.048 and 0.211 ± 0.038. We pooled data over the study period and found that sex–age classes survived at similar rates. We estimated average annual isolated rates of bobwhite mortality (rates in the absence of other causes) to be 0.63 ± 0.027 from raptor predation, 0.45 ± 0.021 from mammal predation, and 0.45 ± 0.043 from harvest. Under the additive theorem of probability, the isolated rates translated to an average annual mortality rate of 0.88 ± 0.017. The bobwhite population had variable and sometimes low survival in November–February inclusive. Low monthly survival (<0.5, $n = 7$) during winter was due primarily to harvest (0.57 ± 0.099 losses/known-fate individual) and raptor predation (0.25 ± 0.051 losses/known-fate individual). We discuss evidence indicating that radiotransmitters handicapped bobwhites and resulted in survival estimates biased low and to uncertainty in interpretation of cause-specific mortality.

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Knowledge of survival rates and mortality sources for bobwhite populations possibly can be used to develop management strategies that alter effects of predation, harvest, or both. Predation may be managed through provision of escape cover and adequate food supplies (Leopold 1933:240), timing habitat management practices (e.g., prescribed burning) to minimize exposure of bobwhite quail to predators (Curtis et al. 1988), maintenance of large (keystone) predators to forestall mesopredator release (Henke and Bryant 1999), and direct reduction of predator abundance (Beasom 1974, Tapper et al. 1996).

Management of bobwhite harvest is controversial. Harvest regulations set for broad spatial scales require fine-tuning for optimal harvest management at local scales (Peterson 1996). Evidence is accumulating that harvest of bobwhites on specific areas may increase winter mortality and reduce breeding populations (Roseberry and Klimstra 1984, Curtis et al. 1988, Robinette and Doerr 1993, Guthery 2002) to a degree that cannot be reversed by density-dependent production (Errington 1945). Additional data on bobwhite survival and response to harvest are needed to fully understand these phenomena and properly manage populations.

Although general latitudinal trends (lower survival and higher production in northern latitudes, higher survival and lower production in southern latitudes) in bobwhite demographics are becoming apparent (Guthery 1997), the need remains for site-specific, descriptive data on bobwhite survival and mortality because these basic descriptive data are prerequisite for development of sound management strategies. Accordingly, in 1991 the Oklahoma Department of Wildlife Conservation began a long-term radiomarking project to collect data on survival and cause-specific mortality of northern bobwhites on the Packsaddle Wildlife Management Area in western Oklahoma. We present the results of research conducted on the Packsaddle area during 1991–2002. Our objectives were to assess monthly and annual survival rates, the effects of sex–age class on survival, isolated annual rates of mortality, monthly trends in losses to specific sources, and the nature (additive, compensatory) of harvest mortality.

STUDY AREA AND METHODS

We conducted our study on the Packsaddle Wildlife Management Area (6,475 ha; hereafter, Packsaddle) in southern Ellis County, Oklahoma,

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USA, during October 1991–October 2002. DeMaso et al. (1997) and Townsend et al. (2001) provided information on climate, soils, and vegetation of the study area.

The Packsaddle area had a diverse predator fauna, none of which was the subject of human control measures on site. Common raptors included Cooper's hawks (*Accipiter cooperii*), sharp-shinned hawks (*A. striatus*), red-tailed hawks (*Buteo jamaicensis*), and northern harriers (*Circus cyaneus*; DeMaso et al. 1998). Mammalian predators included bobcats (*Lynx rufus*), coyotes (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), and swift foxes (*Vulpes velox*).

Bobwhite quail were harvested by the public during 1 November–28 February with hunting on Tuesday and Saturday (Parry et al. 1997). The number of hunters in any harvest period averaged 350 (range = 251–443), and the known harvest averaged 1,025 bobwhites (range = 405–1,934).

Capture and Monitoring

We captured bobwhites in baited funnel traps (Stoddard 1931:442) and with night-lighting (Labisky 1968) throughout the study. We classified individuals by sex and age (Rosene 1969:44–54). Additionally, we leg-banded birds and fitted them with mortality-sensing radiotransmitters (Holohil Systems Limited, Carp, Ontario, Canada; Wildlife Materials Inc., Carbondale, Illinois, USA) that weighed <7 g if the bird was >6 weeks old (about 150 g). We attached radiotransmitters with a necklace (Shields et al. 1982).

We monitored birds ≥6 times per week and determined harvest mortality by recovering harvested birds at check stations on the Packsaddle. Otherwise, when we detected a mortality signal, we immediately located the radiotransmitter and assessed proximate cause of mortality. Causes of mortality included entanglement in the necklace, capture (birds that survived <7 days after capture were arbitrarily placed in this class), weather, harvest, mammal predation, raptor predation, and unknown. We used evidence (condition of radiotransmitter, antenna, and carcass; tracks; feathers) at the location of the radiotransmitter (Dumke and Pils 1973, Curtis et al. 1988) to classify type of predation (mammal, raptor).

Statistical Analyses

Parts of the data presented here have been published previously. DeMaso et al. (1998) and Townsend et al. (1999) analyzed survival and cause-specific mortality in association with supplementally fed and control plots on the Packsaddle area. The feeding took place on 4.4% of the study area (283.3 ha). Townsend et al. (1999) reported equivocal effects of supplementation. The annual mortality rates reported in DeMaso et al. (1998) are in error because of a calculation problem. In general, supplementation had neutral effects on Packsaddle bobwhites so we pooled all available data for analyses.

Our study was observational, which limits our approach to analysis and interpretation of data. We rejected using null hypotheses such as "no difference in survival rates between seasons or among years." We made this choice in part because of rather large samples in the pooled data set (all data collected during 1991–2002) that would result in "significant" effects (Johnson 1999). Moreover, doubt no longer exists that phenomena such as survival rates of quails differ among seasons and years. When an effect is known, research becomes a problem of estimating its magnitude (Edwards 1992:2). Hence, we focus on means, standard errors, confidence limits, graphical interpretation of dynamics, and magnitudes of effect.

We used the Kaplan-Meier staggered entry procedure (Pollock et al. 1989) to (1) estimate monthly survival rates, (2) extrapolate from monthly to annual survival rates, and (3) estimate variance associated with annual estimates. We present annual survival rates based on November–October period (e.g., Nov 1991–Oct 1992). We used a 14-day conditioning period (time for recovery from capture and handling and adjustment to the radiotransmitter) because it resulted in higher estimates of annual survival than 0-, 7-, or 21-day conditioning periods. We tested (unpublished data) different conditioning periods because longer periods might reduce the negative bias associated with telemetry-generated estimates of quail survival (i.e., too brief a conditioning period might explain the negative bias; Baker 2002; Guthery and Lusk 2004). In a given month, we censored birds that lost their radiocollars or that disappeared from radio contact.

To further evaluate survival rates, we aged birds killed during the hunting season and estimated the proportion of adults in the population. We used this proportion as an independent check on the survival estimates from radiomarked samples. The average proportion over years provides an estimate of the annual survival rate in a population that is not trending; the annual survival also can be derived from age ratios if a population is changing at a known finite rate. A further assumption is that age classes (juv, ad) are equally vulnerable to harvest. We assumed a nontrending population for estimation. Because of past evidence that juveniles may be more vulnerable to harvest than adults (Shupe et al. 1990, Roseberry and Klimstra 1992), we calculated the mean proportion of adults with raw data and with data adjusted for juvenile vulnerability (juv 1.24 times more vulnerable than ad; Roseberry and Klimstra 1992).

We used the pooled dataset to assess variation in survival among sex–age classes. The dataset was truncated to individuals with known fates (not censored) that survived >14 days. The conditioning period was deducted from total days lived for analysis (birds started at day zero after surviving 14 days). We calculated descriptive statistics for days lived by sex–age class, which we considered an index of comparative survival. We also constructed Kaplan-Meier survival curves by sex–age classes.

We assessed cause-specific mortality in 2 ways. First we estimated isolated annual rates for mortality due to harvest (Q_H), mammal predation (Q_M), and raptor predation (Q_R) by calculating Kaplan-Meier survival and mortality rates for a specific cause and censoring individuals lost to other causes (Pollock et al. 1989, Lee and Wang 2003:354). To estimate total mortality (Q_T) based on these results, we used the additive theorem of probability (Gharhamani 1996:19–20):

$$Q_T = Q_H + Q_M + Q_R - Q_H Q_M - Q_H Q_R - Q_M Q_R + Q_H Q_M Q_R.$$

Failure to apply the additive model would result in $Q_T > 1$. We did not assess losses to other causes because they were infrequent.

Second, to assess the contribution of mortality sources on a monthly basis, we determined cause-specific loss per known-fate individual (monthly probability of death due to a cause). For example, if hunters took 10 of 100 known-fate birds in a given month, the probability of loss due to harvest would be 0.1. We determined the loss-per-known-fate probability for each mortality source for each month of study; we present monthly means and 95% confidence limits for each fate for the duration of the study.

To assess possible interactions between fate and sex–age class, we conducted chi-squared analysis at an arbitrary dichotomy (Burnham and Anderson 2002:27) of $P = 0.05$ with 4 sex–age classes by 4 fates (harvest, mammal, raptor, other). This analysis was conducted using data pooled over the 10-year study.

Following Parry et al. (1997) and expanding their results, we present first-year (direct) recovery rates—an index of harvest rate—for birds banded or radiomarked in November. We calculated the simple binomial probability of recovery, not adjusted for unretrieved loss. The reporting rate was approximately 100% because hunters were required to check in and out of the area.

To assess the nature (compensatory, additive) of harvest mortality, we obtained a sample of radiomarked birds each year that were captured during 1 June–31 October, were alive on 1 November, and had known fates. We determined the fate of these birds for the period 1 November–30 April (6 months) with fates partitioned among survival (S), natural mortality (V), and harvest mortality (K). The relationship between natural and harvest mortality may be described (Anderson and Burnham 1976) as

$$V = V_o + bK,$$

where V_o = the natural mortality rate in the absence of harvest. Anderson and Burnham (1976) show how to estimate the slope parameter (b) and its uncertainty under the additive model of harvest mortality. We used the sample of radiomarked birds to estimate b from the data using simple linear regression. Anderson and Burnham (1976) warned that direct estimation of this relationship was inappropriate for band-recovery data because of sampling correlation. However, we were dealing with known-fate individuals (a population of marked individuals), and we felt justified in conducting regression analyses. Our analysis followed Roseberry and Klimstra (1984:141), who dealt with approximately known populations.

RESULTS

We radiomarked 2,660 bobwhites, and 648 did not survive the 14-day conditioning period. Losses during the conditioning period were attributed to raptor predation (25.9%), slipped radiocollars (21.6%), capture related (17.2%; arbitrarily defined as any bird that survived <7 days), mammal predation (15.8%), harvest (11.2%), and other causes (8.3%). The sample for further analyses included 231 adult males, 827 juvenile males, 149 adult females, 792 juvenile females, and 13 juveniles of unknown sex.

Table 1. Annual survival rates (S; sex–age classes pooled) and proportional frequency (p) of adults in the hunting bag for northern bobwhites on the Packsaddle Wildlife Management Area, Ellis County, Oklahoma, USA, from 1989–1990 to 2000–2001.

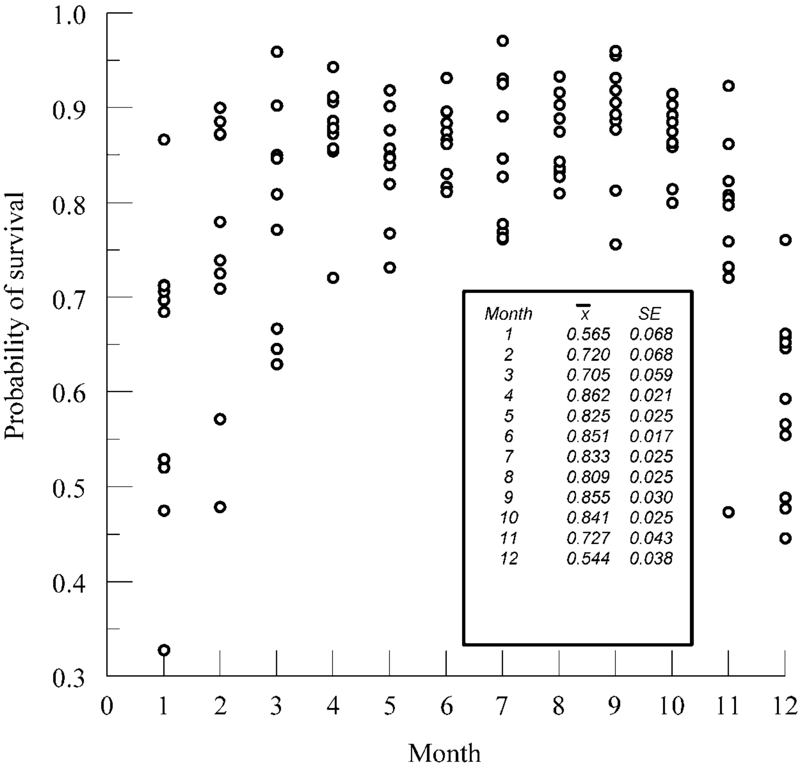
	Annual survival		Proportion adults		
Nov–Oct year	*S*	SE(*S*)	*n*	*p*	SE(*p*)
1989–1990			997	0.157	0.011
1990–1991			1,260	0.135	0.009
1991–1992	0.040	0.0350	1,150	0.138	0.010
1992–1993	0.027	0.0319	778	0.149	0.013
1993–1994	0.072	0.0340	1,249	0.193	0.011
1994–1995	0.053	0.0303	671	0.184	0.015
1995–1996	0.065	0.0389	1,248	0.095	0.008
1996–1997	0.211	0.0384	1,934	0.153	0.008
1997–1998	0.029	0.0653	776	0.255	0.016
1998–1999	0.073	0.0357	648	0.136	0.013
1999–2000	0.092	0.0419	1,188	0.186	0.011
2000–2001	0.019	0.0481	405	0.168	0.019

Survival

Estimated annual survival (Nov–Oct) pooled over sex–age classes ranged between 0.019 ± 0.048 (SE) in 2000–2001 and 0.211 ± 0.038 in 1996–1997 (Table 1; Kaplan-Meier estimates). The mean (n = 10) of annual Kaplan-Meier estimates was 0.068 ± 0.018. Monthly survival was relatively low and variable during cooler months (Nov–Feb) and relatively high and less variable during warmer months (Mar–Oct; Fig. 1).

The raw proportion of adults in the Packsaddle harvest (Table 1) averaged 0.16 ± 0.011 (n = 12; n ≥ 405 birds aged in any year). Upon adjustment for vulnerability, the proportion of adults averaged 0.19 ± 0.013 during the same period. This analysis of the proportion of adults in the population suggested average annual survival rates >2.3 times higher than estimated with radiotelemetry data.

We observed little variation in post-conditioning-period, known-fate survival of sex–age classes as indexed with average days lived. Mean days lived during the study were 115.0 ± 9.27 days for adult males (n = 182), 103.0 ± 4.11 days for juvenile males (n = 692), 98.2 ± 9.23 days for adult females (n = 125), and 101.5 ± 3.79 days for juvenile females (n = 650). Similarity in Kaplan-Meier survival curves (Fig. 2) also indicated similarity in mean days lived.



Month	*x̄*	*SE*
1	*0.565*	*0.068*
2	*0.720*	*0.068*
3	*0.705*	*0.059*
4	*0.862*	*0.021*
5	*0.825*	*0.025*
6	*0.851*	*0.017*
7	*0.833*	*0.025*
8	*0.809*	*0.025*
9	*0.855*	*0.030*
10	*0.841*	*0.025*
11	*0.727*	*0.043*
12	*0.544*	*0.038*

Fig. 1. Monthly (1 = Jan) estimates (Kaplan-Meier) of survival for northern bobwhites, in the Packsaddle Wildlife Management Area, Ellis County, Oklahoma, USA, 1991–2001. The tabulated means represent empirical analyses of the Kaplan-Meier estimates.

Cause-specific Mortality

The highest isolated annual mortality rates were due to raptor predation (Fig. 3) at a mean of 0.63 ± 0.027 during our study period. Mean isolated mortality rates due to harvest were 0.45 ± 0.043 and due to mammal predation were 0.45 ± 0.021. Under the additive model, these isolated rates translated into total annual mortality rates that averaged 0.88 ± 0.017, which were uniformly high except in the year preceding October 1997 (Fig. 3).

Monthly trends in total losses per known-fate individual revealed a relatively stable loss rate from April through October (Fig. 4). From November through February, total mortality rates increased

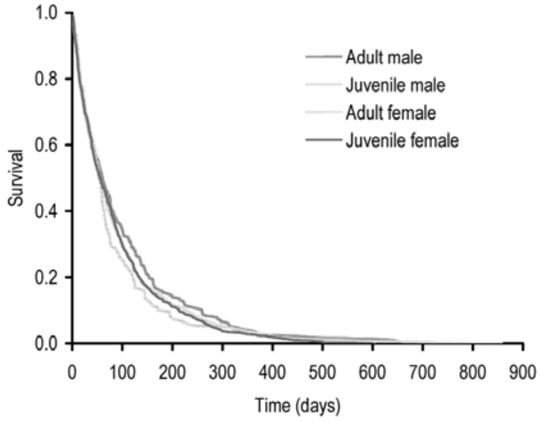


Fig. 2. Kaplan-Meier survival curves for sex–age classes of northern bobwhites, in the Packsaddle Wildlife Management Area, Ellis County, Oklahoma, USA, 1991–2001.

and became noticeably variable during January–February. This annual trend was due largely to the dynamics and variability of mortality due to harvest and raptor predation. Harvest and raptor predation rates were independent ($r = 0.016$, $n = 30$) during months when both occurred. Mortality due to mammal predation was relatively stable throughout the year, with slightly higher rates and more variability during June–August than during other months.

We detected an interaction effect ($\chi^2 = 19.6$, df = 9, $P < 0.025$) between fate and sex–age class (Table 2). The effect arose primarily because more adult males were killed by raptors than expected and fewer were lost to other causes than expected. The proportion of adult males killed by raptors was higher during December–May (0.72 ± 0.043) than during June–November (0.28 ± 0.043). Otherwise, observed and expected frequencies of losses were similar among sex–age classes (Table 2).

Direct recovery rates averaged 0.38 ± 0.046 for banded birds and 0.42 ± 0.053 for radiomarked birds (Table 3). The recovery rate for birds marked during June–October and alive on 1 November averaged 0.27 ± 0.027 (Table 4).

Data used to assess the nature of harvest mortality (Table 4) suggested a theoretical slope (Anderson and Burnham 1976) of –0.57 ± 0.046 (95% CL = –0.662 to –0.478) for the relation between natural mortality (dependent variable)

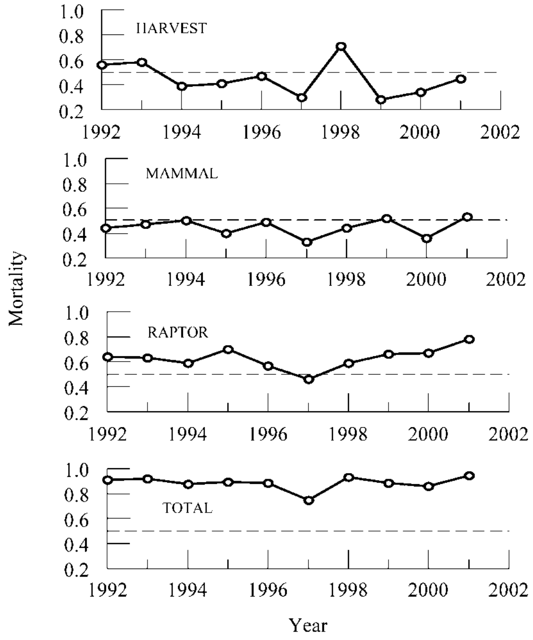


Fig. 3. Annual trends in isolated rates of cause-specific annual mortality (harvest, mammal, raptor) and total mortality (estimated with the additive model) for northern bobwhites, Packsaddle Wildlife Management Area, Ellis County, Oklahoma, USA, 1991–2001. Standard errors for point estimates ranged between 0.035 and 0.055 for harvest mortality, 0.037 and 0.068 for mammal mortality, and 0.025 and 0.057 for raptor mortality. The dashed horizontal lines appear at mortality = 0.5 in each graph to facilitate comparisons among graphs.

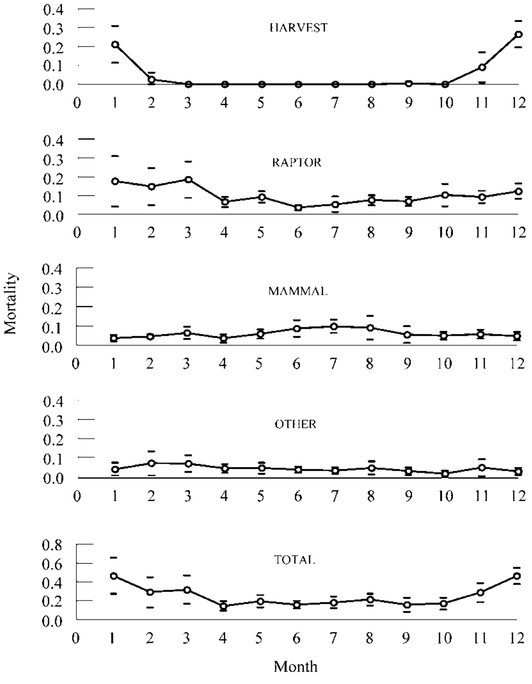


Fig. 4. Monthly (1 = Jan) trends in cause-specific and total rates of loss per known-fate individual for northern bobwhites, Packsaddle Wildlife Management Area, Ellis County, Oklahoma, USA, 1991–2001. The diamonds indicate 95% confidence limits for the associated means (open circles) based on 11 years of data for November and December and 10 years for the remaining months. Known-fate birds exclude those censored from at-risk birds at the end of a month.

Table 2. Chi-squared analysis of the interaction between sex–age class and fate for northern bobwhites on the Packsaddle Wildlife Management Area, Ellis County, Oklahoma, USA, 1991–2001. Ad = Adult, Juv = Juvenile.

	Sex–age class			
Fate	Ad female	Juv female	Ad male	Juv male
Harvest				
Observed	38	221	53	242
Expected	40.5	221.5	61.0	231.0
Chi-square	0.15	0.00	1.05	0.52
Mammal				
Observed	31	176	42	201
Expected	32.9	179.9	49.6	187.6
Chi-square	0.11	0.08	1.16	0.96
Raptor				
Observed	59	290	110	242
Expected	54.5	297.9	82.0	231.0
Chi-square	0.37	0.21	9.56	0.52
Other				
Observed	26	155	27	149
Expected	26.1	142.7	39.3	148.8
Chi-square	0.00	1.06	3.85	0.00

and harvest mortality (independent variable) under the fully additive model. The regression-generated estimate of natural mortality in the absence of harvest was $V_0 = 0.83$ (95% CL = 0.53 to 1.0) and the slope was –0.90 (95% CL = –1.93 to 0.13). Fully compensatory harvest would have a slope of –1 (Anderson and Burnham 1976). The regression estimated slope was closer to –1 than to –0.57, but the variation of the slope was so large as to render the results meaningless concerning compensation and additivity of harvest from November through April.

DISCUSSION

The validity of survival and cause-specific mortality estimates derived from radiotelemetry data depends on satisfaction of assumptions underlying data collection and analysis (Pollock et al. 1989, White and Garrott 1990). Accordingly, we begin by discussing the fit of our results to underlying assumptions. Then we base strength of conclusions on the tenability of assumptions.

Table 3. First-year (direct) harvest-recovery rates (*K*) of northern bobwhites banded or radiomarked in November, Packsaddle Wildlife Management Area, Ellis County, Oklahoma, USA, from 1991–1992 to 1997–1998.

	Banded			Radiomarked		
Year	*n*	*K*	SE(*K*)	*n*	*K*	SE(*K*)
1991–1992	49	0.47	0.07	57	0.53	0.07
1992–1993	147	0.35	0.04	133	0.59	0.04
1993–1994	23	0.30	0.10	61	0.31	0.06
1994–1995	50	0.22	0.06	62	0.32	0.06
1995–1996	26	0.54	0.10	57	0.46	0.07
1997–1997	4	0.50	0.50	19	0.21	0.10
1997–1998	175	0.28	0.03	121	0.51	0.05

Table 4. Six-month (1 Nov–30 Apr) rates of survival (*S*), natural mortality (*V*), and harvest mortality (*K*) for northern bobwhites captured during 1 June–31 October that were alive on 1 November and that experienced a known fate, in the Packsaddle Wildlife Management Area, Ellis County, Oklahoma, USA, 1991–1992 to 2001–2002.

Year	*n*	*S*	*V*	*K*
1991–1992	60	0.117	0.700	0.183
1992–1993	42	0.024	0.738	0.238
1993–1994	46	0.152	0.652	0.196
1994–1995	43	0.140	0.651	0.209
1995–1996	68	0.147	0.485	0.368
1996–1997	26	0.385	0.346	0.269
1997–1998	23	0.000	0.783	0.217
1998–1999	26	0.192	0.385	0.423
1999–2000	50	0.320	0.460	0.222
2000–2001	60	0.017	0.550	0.433
2001–2002	30	0.033	0.700	0.267

Certain assumptions, such as the censoring mechanism is applied randomly (is not related to an animal's fate), are virtually impossible to address. The assumption that survival is independent for different animals may fail for bobwhites during the covey period (i.e., the fate of individuals in a covey may be related). Failure of independence would not bias survival estimates but would bias (reduce) variability associated with the estimates (Pollock et al. 1989). We addressed the assumption that newly radiomarked animals have the same survival function as previously radiomarked animals by employing a 14-day conditioning period. Moreover, we used monthly survival rates, which should tend to make survival functions similar because of short timeframes. We also had evidence of similar survival curves among sex–age classes (Fig. 2). We cannot determine whether our radiomarked sample represented a random sample of the population. If it did not, the effect would arise from differential vulnerability among individuals in the population to trapping or night-lighting.

An assumption rarely discussed is that an appropriate conditioning period is applied. Presumably, bobwhites survive at subnormal rates during adjustment, reach a threshold, and survive at normal rates after passing the threshold. Bobwhite researchers typically use a 7-day conditioning period, but this period is based more on tradition and less on empirical or theoretical justification. We applied a 14-day conditioning period because it resulted in higher estimates of annual survival than 0-, 7-, and 21-day periods. However, we do not know whether some longer conditioning period might have been optimal. Baker (2002) reported an optimal conditioning period of ≥45 days for radiomarked bobwhites in north Texas, USA.

The assumption most troubling to us is that the radiotransmitter package had no debilitating effects on the individual after the conditioning period. Suspected subnormal survival of translocated, radiomarked bobwhites prompted Osborne et al. (1997) to conduct a pen experiment on the effects of radiomarking. With some variation due to attachment style (backpack vs. bib), they observed reduced body and lipid mass, and lower survival up to 12 weeks in radiomarked birds compared to control birds. Likewise, Corteville et al. (2000) observed higher harvest rates and lower rates of mass gain for radiomarked bobwhites in comparison with banded bobwhites. Moreover, 54% of radiomarked birds in the Osborne et al. (1997) study experienced problems with harnesses. We had 23 bobwhites die when they became entangled in the radiocollar or the radiocollar was entangled on vegetation. Burger et al. (1995) reported harness-related mortality for 19 of 1,001 bobwhites. We cannot assess how many mortalities ascribed to predation were in fact associated with harness entanglement.

Generally, telemetry-derived survival rates of bobwhites in the literature are unreasonably low (Guthery and Lusk 2004). We observed normal annual survival (about 0.22; Guthery 1997) for the latitude in 1 of 10 years (1996–1997). The average annual survival rate we observed (0.068) necessitates stabilizing production of 13.7 juv/ad (about 28.5 juv/hen). These levels of production are impossible based on a fairly large empirical record that reports maximum age ratios of about 7 juv/ad for bobwhites, and this level is rare (Guthery et al. 2000). Also, the average annual survival rate estimated from percentage adults exceeded the average annual survival rate estimated from radiotelemetry. Our adjustment for juvenile vulnerability apparently was unnecessary based on the distribution of fates by sex–age class (Table 2).

The direct and circumstantial evidence is compelling that radiotransmitters handicapped bobwhites in the Packsaddle study, thus rendering them more vulnerable to mortality than individuals not radiomarked. This potential bias raises the question as to whether estimates of cause-specific mortality were reliable (Guthery and Lusk 2004).

Cause-specific estimates using telemetry could be taken as an index to the relative magnitude of losses to each loss source. For this index to be valid, meaning that proportional losses to different causes are the same for radiomarked and nonradiomarked bobwhites despite bias imposed by radiotransmitter handicapping, we would have to assume that a radiotransmitter package increases a bobwhite's vulnerability to any loss source by a factor that is constant across all loss sources (Guthery and Lusk 2004). This proportionality seems improbable. More likely is that radiotransmitters will have differential effects on the vulnerability of bobwhites to various loss sources.

The above argument, if true, casts doubt on the use of radiotelemetry to assess bobwhite dynamics and mortality. Nonetheless, radiotelemetry data probably can be taken as a crude index of demographic processes in bobwhite populations because the bias imposed by radiotransmitters may not completely obscure gross trends in population behavior. We continue this discussion under the assumption that the gross trends observed on the Packsaddle area were informative.

Survival for bobwhite populations on the Packsaddle area was lowest and quite variable (Fig. 1) during winter months (Nov–Feb). Low monthly survival during this time was associated with high losses to harvest and to raptors; harvest losses were about twice the magnitude of raptor losses. For example, for months during November–February with an index to survival <0.5 ($n = 7$), harvest averaged 0.57 ± 0.099 losses/known-fate individual, whereas raptor predation averaged 0.25 ± 0.051 losses/known-fate individual. The trends we report in our index were similar to those of Curtis et al. (1988) and Robinette and Doerr (1993) who reported winter and harvest plus raptor losses as times and causes of the most severe annual bobwhite mortality.

Although the additive or compensatory nature of harvest mortality during winter could not be determined because of variability in the data, the direct recovery rates estimated with November-marked birds (Table 3) and June–October-marked birds (Table 4) averaged between 27 and 42%. Factoring in an unretrieved loss rate for the Packsaddle population (12.7%; Parry et al. 1997) leads to estimated average annual harvest rates of 30.9–48.1%. Based on simulation modeling, bobwhite populations in southern latitudes can persist at ≤30% harvest in areas that support ≥700 birds, whereas populations in northern latitudes can persist at ≤40% harvest in areas that support ≥400 birds (Guthery et al. 2000). At 6.475 ha, the Packsaddle area undoubtedly supports populations well above these critical levels. Moreover, productivity of the populations as indexed by age ratios (derivable from the proportion of adults in the population; Table 1) was higher than expected for the latitude (Guthery 2002). The bobwhite population on the Packsaddle area appears sustainable but may exist at the limits of sustainability because of high harvest rates and the associated need for high compensating reproduction.

On an annual basis, however, apparent raptor mortality was of greater importance than harvest mortality (Fig. 3). We caution that the isolated rates of mortality to specific sources, defined as loss to a source in the absence of losses to other sources, would be biased low because of the way we calculated these rates, assuming radiotransmitters did not handicap individuals.

MANAGEMENT IMPLICATIONS

Our findings suggest that bobwhite mortality from raptors and harvest were of greater importance than losses to other sources on the Packsaddle Wildlife Management Area. Presumably, these results would hold approximately for other semi-arid rangeland subject to public hunting in the central plains. Accordingly, management aimed at increasing survival is best directed at these loss sources. Whereas harvest is directly manageable through regulations, the management of raptor losses is problematic. However, if disturbance by harvest exacerbates mortality to raptors, as has been speculated (Curtis et al. 1988, Robinette and Doerr 1993, Smith and Willebrand 1999), then reduced harvest pressure may reduce losses to raptors. However, the data suggested that raptor and harvest losses were independent in months when both occurred. We offer these implications recognizing that our results possibly were biased by radiotelemetry methodology, and that we operated in a competing-risks venue with a species that exhibits density-dependent population responses (survival, production; Errington 1945; Roseberry and Klimstra 1984). Competing risks and density dependence would tend to reduce expected gains accruing from any practice that reduced harvest or raptor losses.

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