Radiotelemetry studies: are we radio-handicapping northern bobwhites?

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Abstract Having become suspicious of telemetry-based survival rates reported for northern bobwhites (*Colinus virginianus*), we surveyed the published record to determine whether reported survival rates were consistent with empirical expectations of production, for which there exists a vast database. If the production (juvenile/adult) required to stabilize a population at a reported or inferred annual survival rate was ≤7, we deemed the reported survival rate reasonable; otherwise, we deemed it not reasonable. We obtained 58 estimates of survival rates for unique points in space and time; 83% of these were not reasonable (apparently biased low). These results and supporting information strongly suggest (but do not necessarily prove) that radio packages (harness, transmitter, antenna) somehow handicap bobwhites. We recommend that researchers be extremely skeptical of telemetry data, plan telemetry studies such that independent data on population performance are available for comparison with telemetry estimates, and discuss the demographic implications of telemetry estimates. We also suggest that radiotelemetry might not always be appropriate for a given research question and that alternative methods be employed whenever possible.

Key words *Colinus virginianus*, demographic consequences, northern bobwhite, radio-handicapping, survival estimates, telemetry

Perhaps the fundamental assumption in radiotelemetry methodology is that radiotagged animals perform (behave, survive, reproduce) in a manner similar to animals not radioed. Expressed differently, the assumption means that a radio package (harness, transmitter, antenna) does not debilitate a radioed animal relative to an animal not radioed. If the assumption fails, then information derived from a radioed sample does not apply to the population not radioed, the object of inference and interest.

We have observed that telemetry-derived survival estimates of northern bobwhites (*Colinus virginianus*) often are low. Indeed, the rates occasionally are alarmingly low, implying, for example, that a population would go extinct during a 3-year study, given expected production. This led us to question the assumption of null effects of a radio package on bobwhite performance.

We recognize that certain research results support null effects of radio packages on the study species. Survival rates for spruce grouse (*Canachites canadensis*) did not differ between radiomarked and nonradiomarked groups (Herzog 1979). Similarly, juvenile blue grouse (*Dendragapus obscurus*) survived at the same rate, based on subsequent resightings, regardless of whether they were banded or radiotagged (Hines and Zwickel 1985). Red grouse (*Lagopus lagopus scoticus*) fitted with dummy transmitters had the same recovery rate as grouse fitted only with patagial tags (Thirgood et al. 1995). The addition of radiotransmitters between 2.4 and 5.8% of body weight did not affect the survival rates of juvenile great (*Parus major*) and coal tits (*P. ater*) when compared to untagged birds (Naef-Daenzer et al. 2001). With regard to bobwhites, Mueller et al. (1988) reported that bobwhite males outfitted with radiotags

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survived at a rate similar to those without transmitters. Corteville (1998) fitted bobwhites with dummy transmitters or leg bands and determined survival from hunter recoveries. She found no difference in the survival of bobwhites between radioed and banded birds. However, it is possible that radiotransmitters affected these species and the effects were undetected. That is, the effects of radiotransmitters might be sub-lethal. Such sub-lethal effects will be of critical importance when results of radiotelemetry studies are employed in estimating parameters for models of population dynamics, especially those associated with population viability analysis. Subtle, sub-lethal effects could influence parameter estimation and lead to improper management actions.

Other researchers have questioned and in some cases tested the assumption that radiotags have no effect, and their results tend to support our thesis. The effects of transmitters and their magnitude often vary among species (Samuel and Fuller 1994, Withey et al. 2001). Warner and Etter (1983) reported that survival decreased with increasing radio-package weight for female ring-necked pheasants (*Phasianus colchicus*) in central Illinois. Marcström et al. (1989) reported that the type of transmitter influenced survival rate for female pheasants in Sweden. Only backpack-style transmitters reduced female survival; there was no difference in survival among banded and necklace-style transmitters (Marcström et al. 1989). Male rock ptarmigan (*Lagopus mutus*) fitted with radiotags had lower survival than males without tags (Cotter and Gratto 1995). The effects of transmitters on the body weight of gray partridge (*Perdix perdix*) were apparent for only the first 2 weeks after attachment (Schulz and Upgren 1977).

The effects of transmitter attachment might also vary in time. Bro et al. (1999), studying the effects of 2 types of radiotransmitters on gray partridge in France, reported no effect of transmitter attachment on survival in 1995, but a significant effect in 1996. Further, the effects of radiotransmitters varied among populations in 1996 and were correlated with weather and predator abundance. Although the results of Bro et al. (1999) require further verification, they suggest that the influence of radiotagging on a species might depend on the environmental context of the population.

However, none of the studies cited above has investigated the demographic consequences of the reported survival rates. Accordingly, we gathered published information on survival rates of bobwhites as estimated with radiotelemetry and determined the demographic implications of the reported rates. Based on our working hypothesis that radio packages debilitate bobwhites, we expected to find a preponderance of telemetry-estimated survival rates that were too low to permit population persistence. We judged whether the rates were too low with reference to the vast empirical database on bobwhite age ratios (see Guthery et al. [2000] for summary data) and to known relations between annual survival, age ratios, and population behavior (Guthery 2002). Herein we report circumstantial evidence that radio packages handicap bobwhites, leading to unreliable estimates of survival and possibly to biased information on cause-specific mortality.

Methods

We conducted a comprehensive search of the peer-reviewed literature to obtain the studies used for this analysis. We interpreted published, telemetry-derived survival rates of bobwhites according to these protocols. We determined the interval (number of days, d) for a reported survival rate (S) and estimated daily survival rate (S_d) as

$$S_d = \exp[\ln(S)/d].$$

We then estimated annual survival rate (S_a) as

$$S_a = S_d^{365}.$$

The latter manipulation operates under the unrealistic assumption of a constant daily survival rate through the year. However, the manipulation was necessary to standardize results among studies, which reported survival rates for different seasons and time frames. We assessed the implications of the assumption by comparing general results with those from studies that reported annual survival rates (no manipulation of data was necessary).

We assessed the demographic implications of a reported or derived annual survival rate by determining the age ratio (R, juv/ad) that would lead to population stability (finite growth multiplier = 1.0) given the reported survival-rate estimate (Guthery 2002):

$$R = \frac{1}{S_a} - 1.$$

We chose $R = 7$ as a conservative benchmark to determine whether telemetry-derived survival rates were reasonable: if $R \leq 7$, the rates were deemed reasonable, whereas if $R > 7$, the rates were deemed not reasonable. The age-ratio cutpoint (7) we used is conservative (i.e., biased in favor of the legitimacy of telemetry-derived survival rates) because age ratios this high are rarely observed in bobwhite populations. For example, an age ratio of 7 is 2.36 SDs from the mean for bobwhites in southern Illinois (Roseberry and Klimstra 1984), indicating that a higher age ratio would occur with a probability of 0.0091. Roseberry and Klimstra (1984) did not observe an age ratio ≥ 7 in 30 years of record. Likewise, the benchmark age ratio is 2.8 SDs from the mean for bobwhites in south Texas (Lehmann 1984), indicating that a higher age ratio would occur with a probability of 0.0026.

To add statistical rigor to our assessment, we used bootstrapping to compare the stabilizing age ratios calculated from published survival rates (Table 1) with harvest age ratios of nonradioed birds (Roseberry and Klimstra 1984 [$n = 29$], unpublished data [$n = 12$]). We used SYSTAT (v10.2, Systat Software, Inc. 2002) for generating distributions of mean age ratios. We generated 1,000 bootstrap means each for stabilizing (Table 1) and harvest age ratios and used 95% confidence limits to test for significance (Mooney and Duval 1993).

Results and discussion

We obtained data from 58 points in space and time (Table 1). The data suggested that 17% of survival rates were reasonable, given our benchmark age ratio (7 juv/ad), whereas 83% were unreasonable (too low). Indeed, 71% of the age ratios required for population stability were outlandish ($R \geq 10$). Such ratios are ≥ 9.1 SDs from the mean for the relatively productive population studied by Roseberry and Klimstra (1984). Again, the age ratio cutpoint favored finding estimated survival rates reasonable. Bootstrapped means for harvest age ratios (95% CL: 4.85–5.48) did not overlap with the bootstrapped-mean age ratios from Table 1 (95% CL: 49.77–849.85). Therefore, age ratios calculated from radiotelemetry-derived survival estimates differed significantly from empirically derived age ratios.

When we used data from studies that reported annual survival rates, thus eliminating concern about extrapolating constant daily survival rates, we

Table 1. Reported interval (S), daily (S_d), and annual survival rates (S_a) and stabilizing production (age ratio) based on the annual survival rate for radio-tagged northern bobwhites. The entries (S_d, S_a, stabilizing production) were rounded for presentation, whereas estimates were based on figures not rounded.

Source Interval Treatment Year	S	S_d	S_a	Stabilizing age ratio (juv/ad)
Curtis et al. (1988)				
Spring–winter (365 days)				
Fort Bragg, Hunted				
1985	0.0400	0.9912	0.0400	24.0
1986	0.0270	0.9902	0.0270	36.0
1987	0.0640	0.9925	0.0640	14.6
Tall Timbers, not hunted				
1984–1988	0.2570	0.9963	0.2570	2.9
Pollack et al. (1989*b*)				
31 Mar–21 Jun (91 days)				
Area 1				
1985	0.6462	0.9952	0.1735	4.8
17 Nov–15 Mar (119 days)				
Area 2				
1985–1986	0.1455	0.9837	0.0025	401.6
Robinette and Doerr (1993)				
Winter (91 days)				
Hunted				
1987–1988	0.0380	0.9871	0.0088	111.6
1988–1989	0.6290	0.9949	0.1557	5.4
Not hunted				
1987–1988	0.5930	0.9943	0.1229	7.1
1988–1989	0.7370	0.9966	0.2940	2.4
Burger et al. (1995)				
1 Oct–30 Sep (365 days)				
Area 1				
1989–1990	0.0610	0.9924	0.0610	15.4
1990–1991	0.0430	0.9914	0.0430	22.3
1991–1992	0.0530	0.9920	0.0530	17.9
Corteville (1998)				
1 Oct–30 Sep (365 days)				
Divided Section WMA				
1995–1996	0.068	0.9926	0.068	13.7
1996–1997	0.078	0.9930	0.078	11.8
1997–1998	0.012	0.9880	0.012	82.3
Taylor et al. (1999)				
24 Apr–20 Aug (119 days)				
Area 1				
1991–1994	0.2600	0.9887	0.0161	61.3
Area 2[a]				
1991–1994	0.4629	0.9935	0.0942	9.6

(*Continued*)

[a] Survival calculated as a weighted average of males and females.

Table 1 (*continued*). Reported interval (S), daily (S_d), and annual survival rates (S_a) and stabilizing production (age ratio) based on the annual survival rate for radio-tagged northern bobwhites. The entries (S_d, S_a, stabilizing production) were rounded for presentation, whereas estimates were based on figures not rounded.

Source Interval Treatment Year	S	S_d	S_a	Stabilizing age ratio (juv/ad)
Townsend et al. (1999)				
Nov–Mar (151 days)				
Experimental control				
1992–1993	0.0304	0.9771	0.0002	4,646.6
1993–1994	0.1259	0.9864	0.0067	148.8
1994–1995	0.2200	0.9900	0.0257	37.9
1995–1996	0.2251	0.9902	0.0272	35.8
Supplementally fed				
1992–1993	0.1886	0.9890	0.0177	55.4
1993–1994	0.3050	0.9922	0.0567	16.6
1994–1995	0.1069	0.9853	0.0045	221.4
1995–1996	0.1562	0.9878	0.0112	87.9
Liu et al. (2000)				
May–Jul (63 or 77 days)				
Resident birds				
1990	0.2734	0.9796	0.0005	1,831.0
1991	0.3489	0.9864	0.0068	146.3
1992	0.3869	0.9877	0.0111	89.1
Translocated residents				
1990	0.6972	0.9943	0.1237	7.1
1991	0.7721	0.9966	0.2935	2.4
1992	0.4643	0.9900	0.0263	36.0
Translocated immigrants				
1990	0.4859	0.9886	0.0153	64.5
1991	0.3414	0.9861	0.0061	162.1
1992	0.1400	0.9748	<0.000	>11,157.7
Sisson et al. (2000)				
Nov–Mar (154 days)				
Wild birds only				
1993–1994	0.4820	0.9952	0.1772	4.6
1994–1995	0.3490	0.9932	0.0825	11.1
1995–1996	0.3160	0.9926	0.0667	14.0
Wild birds and liberated birds				
1993–1994	0.1830	0.9890	0.0179	55.0
1994–1995	0.2220	0.9903	0.0282	34.4
1995–1996	0.1800	0.9989	0.0172	57.2
Taylor et al. (2000)				
1 Apr–27 Sep (180 days)				
Area 1				
1993	0.5090	0.9962	0.2543	2.9
1994	0.3620	0.9944	0.1274	6.8
1995	0.3380	0.9940	0.1109	8.0
1996	0.1670	0.9901	0.0265	36.6

(*Continued*)

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[a] Survival calculated as a weighted average of males and females.

Table 1(*continued*). Reported interval (S), daily (S_d), and annual survival rates (S_a) and stabilizing production (age ratio) based on the annual survival rate for radio-tagged northern bobwhites. The entries (S_d, S_a, stabilizing production) were rounded for presentation, whereas estimates were based on figures not rounded.

Source Interval Treatment Year	S	S_d	S_a	Stabilizing age ratio (juv/ad)
Suchy and Munkel (2000)				
Annual (365 days)				
Area 1				
1984–1985	0.0860	0.9933	0.0860	10.6
1985–1986	0.1010	0.9937	0.1010	8.9
1986–1987	0.0910	0.9935	0.0910	10.0
1987–1988	0.0440	0.9915	0.0440	21.7
Area 2				
1984–1985	0.1260	0.9943	0.1260	6.9
1985–1986	0.0590	0.9923	0.0590	15.9
1986–1987	0.0950	0.9936	0.0950	9.5
1987–1988	0.0480	0.9917	0.0480	19.8
Williams et al. (2000)				
11 Nov–31 Jan (82 days)				
Area 1				
1993–1996	0.4700	0.9908	0.0347	27.8
Area 2				
1993–1996	0.4629	0.9850	0.0040	246.2
Williams (2001)				
9 Nov–31 Jan (84 days)				
Not hunted				
1997–1998	0.5810	0.9936	0.0945	9.6
1998–1999	0.6540	0.9950	0.1580	5.3
1999–2000	0.4290	0.9900	0.0253	38.5

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[a] Survival calculated as a weighted average of males and females.

found that 2 of 18 (11.1%) survival estimates were reasonable, whereas the balance (88.9%) were not reasonable. The assumption of constant daily survival rate did not seem to have a large impact on interpretation of the available data (Table 1).

To further examine demographic consequences of reported survival rates, we estimated the level of production necessary to achieve a stabilizing age-ratio (R). We can estimate the mean clutch size (c) necessary, assuming multiple brooding, to achieve R (Guthery 2002: 73):

$$c = \frac{R}{nwz\left(1-q\right)},$$

where n is the number of nesting attempts (3), w is the proportion of hens in the breeding population

(0.45), z is the proportion of hens that lay (1.0), and q is the probability of nest failure on any given nesting attempt (0.70) (Guthery 2002). Using data from those studies reporting annual survival to calculate mean R, we find that the average clutch size would have to be 465.9 eggs. This is obviously impossible. Burger et al. (1995) assumed the inordinately low survival estimates obtained from radiotelemetry studies were true and posited that the bobwhite breeding system allowed them to maintain stable populations. Whereas this might be true to some extent, the production demanded by the reported annual survival rates we used above (Table 1) is inconsistent with the production capabilities of bobwhites.

Our estimation of the production required for population stability operated under the assumption that survival data were drawn from a stable, nontrending population (finite growth-multiplier = λ = 1.0). This assumption is not necessary, however. Manipulation of an equation provided by Guthery (2002) reveals that the age ratio consistent with estimated survival in a population experiencing a known finite rate of increase or decrease can be expressed

$$R = \frac{\lambda}{S} - 1.$$

For example, Burger et al. (1995) observed average annual survival of 0.053 in a bobwhite population declining at $\lambda \approx 0.86$. Insertion of these values into the above equation indicates a compatible age ratio of 15.2 juv/ad, which is unlikely.

Thus, the published record suggests, but does not prove, that survival rates of bobwhites estimated with radiotelemetry are biased low. This supposition would not hold if nearly all authors happened by chance to conduct survival experiments in areas and times with low natural survival (i.e., the estimated survival rates are unbiased). This happenstance seems improbable. It is more likely that a few of the survival estimates we deemed not reasonable actually were reasonable. Bro et al. (1999) suggested that survival estimates could vary in time and space with environmental factors. For example, severe winters may reduce annual survival to low levels (Leopold 1937, Errington 1945). This would suggest that within-year variation in survival and the effects of radiotagging on survival could bias low the annual survival estimates. Further, Liu et al.'s (2000) experiments with bobwhites translocated to areas where they were not adapted (semi-arid south Texas to mesic east Texas) provide an example of a case where low survival was expected. But on the other hand, some or all of the survival estimates we deemed reasonable could in fact have been biased low.

Limited anecdotal and research results support the hypothesis of radio-handicapping in bobwhites. Biologists routinely apply a censor period (typically 7 days) to provide bobwhites time to adjust to capture and handling and adapt to the radio package. The censor period is *prima facie* evidence of at least transient debilitation. Although Tsai et al. (1999) stated the short-term effects of radiotagging on survival could be eliminated by having a conditioning (i.e., censor) period of 7–14 days, no one knows whether the 7-day censor period is appropriate. Its application is based on tradition.

Deaths ascribed to radiopackage-related causes (e.g., entanglement of appendages in the harness or entanglement of the harness on vegetation) are irrefutable examples of debilitation associated with radiotagging. Burger et al. (1995) reported 19 such losses in a sample of 1,001 radioed bobwhites. It seems likely that losses of birds entangled and subsequently depredated would be ascribed to predation, which would lead to overestimates of predation rates and underestimates of survival in the nonradioed population. Osborne et al. (1997) observed harness-related problems in 54% of radioed bobwhites in an *ex situ*, controlled experiment. They also observed loss of body and fat mass and lower survival in radioed than in nonradioed bobwhites up to 12 weeks after radioing. However, Corteville (1998) found no effect of radio transmitters on the body mass or fat content of bobwhites in Mississippi.

Condition effects (loss of mass, fat) may explain anecdotal evidence that radioed bobwhites behave abnormally. They are least likely to flush and most likely to be caught during night lighting (J. S. Taylor, Nebraska Game and Parks Commission, personal communication). Our research team also has observed this effect. R. M. Whiting (Stephen F. Austin State University, personal communication) observed that radioed bobwhites in a covey are typically the last to flush, a behavior that might render them vulnerable to predation. Our research team observed a radioed bobwhite, the last to flush in a covey, catch fire during a prescribed burn, whereas other members of the covey flew to safety.

Comparing survival rates derived from radiotelemetry with those derived from independent sources also tends to indict telemetry estimates.

Based on a banding study, bobwhite males in Florida survived at an annual rate of 18.7±1.2%, whereas females survived at 14.3±1.2% (Pollock et al. 1989*a*). Rosene (1969) reported average annual survival rates ranging between 20.2 and 33.7% for bobwhites on southern plantations. These estimates were derived from count data. Corteville (1998) reported survival rates for banded birds that were not significantly different from those of radio-tagged bobwhites in Mississippi measured from harvest returns. However, the survival rates of the banded birds were too low to allow population persistence at reasonable production levels. In a study of nonhunted bobwhites in Kansas, overwinter survival for radiotagged individuals was 53.7% compared with 63.5% estimated from continuous covey counts (C. K. Williams, University of Wisconsin at Madison, personal communication).

Survival rates derived from age ratios have long been used to assess bobwhite demographics. In a stable (i.e., nontrending) population, the average proportion of adults in the fall population estimates the average annual survival rate. Survival rates so estimated follow a latitudinal pattern and range between about 0.2 in northern latitudes and 0.3 in southern latitudes (Guthery 1997). Only 4 of 58 (7.5%) annual survival rates we observed or estimated were >0.2 (Table 1).

The direct and circumstantial evidence that radio packages handicap bobwhites is compelling. This outcome draws into question other inferences obtained from radiotelemetry data, such as the nature and magnitude of cause-specific mortality. Although based on a small sample, radiotagged red grouse had twice the predation mortality of nonradioed birds (7 radiotagged vs. 3 banded birds) despite similar estimated survival rates (Thirgood et al. 1995). Data on cause-specific mortality in a radioed population are unbiased for a nonradioed population if radiotagging increases vulnerability to all loss sources by a constant factor. Suppose that we are interested in proportional losses (P_i) to loss source i, where L_i represents total losses to source i. Then

$$P_i = \frac{L_i}{\sum L_i}.$$

Now, suppose that radio-handicapping increases the vulnerability of a bobwhite to all loss sources by a constant multiple k, where $k > 1.0$. Then

$$P_i = \frac{kL_i}{\sum kL_i} = \frac{L_i}{\sum L_i},$$

which is identical to proportional loss in the absence of radio-handicapping. However, an expectation that radio packages handicap bobwhites constantly across mortality sources (raptors, mammalian predators, hunters, reptilian predators, weather catastrophes) seems unwarranted. If one accepts that radio packages handicap bobwhites, one is compelled to suspect that information on cause-specific losses derived from radiotelemetry is blemished.

Our results pertain to the use of radiotelemetry for estimating survival. Although we have not investigated the effects of radiotransmitters on behavior and habitat use, we suspect that such effects are likely. However, whether radiotagging affects behavior and habitat use will depend on how radiotagging affects the bird. If radiotagging makes bobwhites more visually conspicuous to predators compared to untagged birds, then bobwhite behavior might be unaffected. Again, our analysis did not address possible effects on behavior and habitat use, and we encourage researchers in these areas to rigorously test for such effects, particularly because many management decisions are based on studies of habitat use.

Although attachment method is known to affect factors such as survival and production (Markström et al. 1989, Taylor 1997), we did not explicitly consider this in our evaluations. We acknowledge that such effects exist, but the fact that they do does not alter our conclusion that radiotagging has detrimental effects for bobwhites. For example, Taylor (1997) reported lower productivity rates for female bobwhites tagged with backpack-style transmitters than those with necklace-style transmitters but did not investigate whether backpack and necklace transmitters resulted in lower production than that found in nontagged hens. Although some attachment methods are less detrimental than others, the use of radiotransmitters affects the tagged individual. For example, Hubbard et al. (1998) studied the effects of radio-attachment method on the growth of wild turkey poults (*Meleagris gallopavo*). Whereas wing growth-rate was higher for poults carrying subcutaneous implants than for those with backpack-style transmitters, the untreated control poults had the highest wing growth-rate.

We conclude with an admonition and recommendations. Research biologists should be skeptical of information on bobwhite demographics obtained with radiotelemetry. This includes information in the published record as well as information that will become a part of the published record. Further, our results do not necessarily apply only to bobwhite research. We suspect that radiotransmitters affect a wide variety of species at some level. For example, Tuyttens et al. (2002) reported lower body-condition scores for European badgers (*Meles meles*) tagged between 1 and 100 days, but not after 100 days. These effects need not be lethal; subtle, sub-lethal effects might also influence results. Therefore, researchers should anticipate bias and take measures to counteract or at least understand it. This will entail independent measures of population performance as determined with counts, age ratios in the population, and other indices obtained simultaneously with the collection of radiotelemetry data. The basic purpose is to determine whether the radioed population is performing similar to the nonradioed population regardless of whether one is interested in survival, habitat use, or behavior. We believe it is imperative that the demographic implications of telemetry-estimated survival rates are addressed in discussing results and that these implications are compared with what is known about productivity and survival in populations not radioed. The value of such assessments is tremendous when radiotelemetry data are to be used in management of endangered and threatened species, especially in population viability analyses.

Our intent is to make wildlife researchers aware of the potential bias elicited by telemetry techniques so that they become more skeptical when evaluating the results of their own research, as well as that appearing in the literature. Further, we suspect that the relative ease of radiotelemetry techniques has led to its overuse. We encourage researchers, in light of the possible biases we highlighted above, to critically assess whether radiotelemetry is necessary to address their particular research questions and to consider alternative methods of data collection whenever possible.

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