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D. Clay Sisson
Albany Quail Project

Theron M. Terhune
University of Georgia

H. Lee Stribling
Auburn University

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Additional Evidence Against Radio-handicapping of Northern Bobwhites

D. Clay Sisson^{1,4}, Theron M. Terhune^{1,2}, H. Lee Stribling³

¹Albany Quail Project, Pineland Plantation, Newton, GA 39870, USA

²D. B. Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602, USA

³School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL 36849, USA

The validity of radio-telemetry to produce reliable information (e.g., survival estimates) has recently been challenged. Radio-telemetry is a widely used technique in studies of numerous species, therefore, concerns regarding potential bias in these estimates warrant further investigation. As such, and as part of a larger study, we investigated 3 aspects of potential radio-bias: 1) variation in survival distributions among treatment (newly radio-tagged) and control (previously radio-tagged) groups; 2) proportion of trapped animals censored during the traditional 7-day censor period; and 3) ramifications to cause-specific mortality through estimation of harvest rate. Kaplan-Meier survival, based on 30-day post trapping, was similar between treatment ($n = 901$) and control ($n = 293$) bobwhites for all but 1 of 8 trapping sessions during 2000-2004. In this case, treatment bobwhites (0.970, SE = 0.015) had higher survival than control birds (0.878, SE = 0.042). We determined the effect of censoring relative to sample size was inconsequential for our analysis because the proportion of bobwhites (18 out of 1,350; 0.013) meeting the criteria for censoring, i.e., dying during the first 7 days, was minimal. Censoring of these data influenced survival estimates by an average of only 0.016 (SE = 0.004; range: 0.00 - 0.04). We evaluated harvest rate by comparing first year recovery rates of banded versus radio-tagged birds during thirteen hunting seasons occurring between 1992 and 2005. Annual recovery rate was not different ($P < 0.05$) for banded birds and radio-tagged birds where harvest averaged 6.68% (range 3.3 - 11.7) and 6.65% (range 3.4 - 11.1), respectively. These findings are consistent with previous research demonstrating that radio-telemetry can provide reliable demographic information. However, we recommend that future researchers test for these potential effects among their data before making biological inferences.

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Key words: *Colinus virginianus*, northern bobwhite, radio-handicapping, southeastern USA, survival, telemetry

Introduction

Over the last two decades, a large amount of demographic and behavioral information has been generated from the use of radio-telemetry on northern bobwhite (hereafter bobwhite; *Colinus virginianus*). The reliability of this information depends on meeting the primary assumption that marking individuals with radio-transmitters does not handicap them in any way and that these individuals are representative of the population at large (Pollock et al. 1989). Recent articles have questioned these underlying assumptions, suggesting that researchers are "radio-handicapping" bobwhites and should therefore, be skeptical of information gener-

ated from these studies (Parry et al. 1997, Cox et al. 2004, Guthery and Lusk 2004). More recent empirical analyses from large-sample and long-term studies by researchers in the southeastern U.S. have addressed these criticisms. In particular, Palmer and Wellendorf (2007) and Terhune et al. (2007) compared survival rates for banded versus radio-tagged birds based on mark-recapture and recovery analysis from a large sample of bobwhites. They found no difference in survival rates between groups and showed that their estimated rates were similar to those derived simultaneously from radio-telemetry. Additionally, Sisson et al. (2009) countered Guthery and Lusk's (2004) argument that telemetry based survival estimates are biased low by presenting

⁴Correspondence: clay@pinelandplantation.com

49 radio-telemetry generated survival estimates for their respective study sites in Georgia and Alabama. This analysis showed that 38 of the 49 (78%) estimates were reasonable according to Guthery and Lusk's (2004) standards, as opposed to only 10 of 58 (17%) in their review of published studies. Collectively, these 3 studies (Palmer and Wellendorf 2007, Terhune et al. 2007, Sisson et al. 2009), produced annual survival rates within the range of what is expected for the region based on the theory of operational constancy in bobwhite demographics (Guthery 1997). In an effort to address this subject more thoroughly, and as part of a larger ongoing study of bobwhite population ecology and management in South Georgia, we examined additional data from our studies for evidence of "radio-handicapping" and discuss anecdotal information in support of this data. We examined the following: 1) variation in survival distributions among treatment (newly radio-tagged) and control (previously radio-tagged) groups; 2) proportion of trapped animals censored during the traditional 7-day censor period; and 3) harvest of banded versus radio-tagged birds. In addition, we present anecdotal information from our studies which provide further support regarding radio-handicapping of bobwhites.

Study Area

Harvest and radio-telemetry generated data for these analyses were collected on three study sites of the Albany Quail Project during 1992-2005. These were privately-owned quail plantations that were contiguous and within a matrix of similar properties each with a similar history and management program. Together, these three encompassed 15,200 ha in Dougherty and Baker Counties near Albany, Georgia. All three were typical of properties in the region as they were characterized by mature old-field pine forests (80%) with a low basal area (3-9 m²/ha) and scattered 1-4 ha fallow fields (20%). Management techniques included maintaining an open canopy through timber thinning and mid-story hardwood removal, frequent prescribed burning, seasonal disking of fields, drum-chopping and

mowing, supplemental feeding, and mammalian predator control. As a result of this management style, quail densities in recent years averaged approximately 5 birds/ha. More detailed descriptions of these sites and their management programs can be found in previous works (Simpson 1976, Yates et al. 1995, Burger et al. 1998, Sisson et al. 2000a,b, 2002b, Hughes et al. 2005, Terhune et al. 2006, 2007).

Methods

All of the studies on these research sites were part of an on-going study by the Albany Quail Project with research protocols similar for all sites and the data pooled by year. Wild bobwhites were trapped on active study sites twice each year (Mar-Apr & Oct-Nov) during 1992-2005 using standard, baited funnel traps (Stoddard 1931). Each bird was classified by age and sex, weighed, leg banded, and a sub-sample was radio-tagged and released at the capture site. Only birds weighing ≥ 132 g were outfitted with pendant style transmitters (6 g; <5% of body weight) equipped with an activity switch (Holohil Systems, Ltd., Ontario, Canada). Trapping, handling, and marking procedures were consistent with the guidelines in the American Ornithologists' Union Report of Committee on the Use of Wild Birds in Research (American Ornithologists' Union 1988) and the protocol was approved by the Auburn University Institutional Animal Care and Use Committee, IACUC.

We monitored all birds at least 2 times weekly using the homing method (White and Garrott 1990) and recorded all locations on aerial photographs. The Kaplan-Meier staggered-entry method was used to produce all survival estimates (Kaplan and Meier 1958, Pollock et al. 1989). Seasonal survival estimates were based on a biological year beginning 1 October and ending 30 September the following year. This annual period was divided into 2 seasonal intervals for analysis as described by Burger et al. (1998). The fall-winter interval (1 Oct - 31 Mar, 182 days) began with termination of nesting and formation of coveys. The spring-summer interval (1 Apr - 30 Sep, 183 days) began with covey breakup and ini-

tiation of mating. An effort was made in every case to insure that birds were evenly distributed across the landscape during trapping and radio-tagging to reduce among covey bias (Pollock et al. 1989, White and Garrott 1990). We used the traditional 7-day conditioning period where birds that died within 7 days of radio-tagging were excluded (i.e. censored) from the analysis (Kurzejeski et al. 1987, Pollock et al. 1989).

The potential effects of capture, handling, and radio-tagging of bobwhites was evaluated by comparing Kaplan-Meier survival distributions for treatment (newly radio-tagged) versus control (previously radio-tagged) bobwhites during 8 post-trapping sessions (i.e., alternating periods of fall-winter and spring-summer) from 2000-2004. A 30-day post-trapping survival curve with no censor period was used for newly tagged birds and was compared to the same time period for birds still being monitored from a previous trapping session. Only previously tagged birds that had been radio-tagged and monitored for a minimum of 90 days were included as controls in this analysis.

The influence of the traditional 7-day censor period on end-point estimates was evaluated by comparing Kaplan-Meier survival distributions for newly radio-tagged individuals for 10 trapping sessions during 2000-2005. The comparison was made between seasonal survival estimates with and without birds that would have been censored during this 7-day period. In addition, we evaluated the magnitude of the effect censoring had on survival estimates if they remained in the analysis, and compared the proportion of birds censored in our analysis to those in previous studies.

Harvest rate was used as a measurable indicator of the effects of transmitters on cause-specific mortality. Following the methods of Parry et al. (1997) and Cox et al. (2004) we present first year (direct) recovery rates, an index to harvest rates, for birds banded or radio-tagged during the fall trapping session immediately prior to the 13 hunting seasons from 1992-2004. Reporting rates for harvest were virtually 100% because these studies were con-

ducted on private property where hunting and harvest were completely controlled, and records of all harvested birds were put into a large research data base (Terhune et al. 2007). Thus, we calculated the simple binomial probability of recovery with no correction for un-retrieved loss.

Results and Discussion

We used a total of 1,194 radio-tagged bobwhites for our survival analysis to compare previously tagged ($n = 293$) versus newly tagged ($n = 901$) individuals. No significant difference ($P < 0.05$) was detected in Kaplan-Meier derived survival estimates for the 30-day post trapping period for all but 1 of 8 sessions during 2000 - 2004 (Table 1). In this case (spring 2003), the newly tagged birds (0.971, SE = 0.015) actually had higher survival than their previously tagged counterparts (0.878, SE = 0.042) (Table 1). This supports the findings of Palmer and Wellendorf (2007) and Terhune et al. (2007) whom also demonstrated no difference in survival between radio-tagged and banded birds. In addition, our analysis did not indicate a negative effect from trapping and handling itself since the control group was from a previous trapping session, was not caught during the current trapping period, and therefore was not susceptible to the potential effects of trapping and handling. Combined, these comparisons provide strong evidence that there were no negative impacts on survival from radio-transmitters for these study areas.

The effect of censoring on Kaplan-Meier survival estimates was negligible. These comparisons were made for 10 seasonal survival estimates from 2000-2005, and no differences ($P < 0.05$) were detected between survival curves with or without this group of birds. Of the 1350 bobwhites newly radio-tagged and added to the sample during this time period, only 18 (1.3%) were censored during the traditional 7-day period. Including these birds in the Kaplan-Meier analysis affected seasonal survival estimates by only an average of 0.016 (SE = 0.005, range 0.00 - 0.04). This is in stark contrast to estimates reported in other studies such as Cox et al. (2004) in

Table 1: Thirty-day Kaplan-Meier survival estimates for previously and newly radio-tagged northern bobwhite quail following 8 trapping sessions on Albany Quail Project study areas in South Georgia during 2000 - 2004.

Season	Previously radio-tagged				Newly radio-tagged			
	n	Surv	SE	95% CI	n	Surv	SE	95% CI
Fall 2000	18	1.000	0.000	1.000-1.000	59	0.983	0.017	0.950-1.000
Spring 2001	29	0.897	0.056	0.788-1.000	132	0.985	0.012	0.964-1.000
Fall 2001	25	1.000	0.000	1.000-1.000	120	0.992	0.008	0.975-1.000
Spring 2002	62	0.949	0.023	0.894-1.000	128	0.948	0.019	0.910-0.985
Fall 2002	24	1.000	0.000	1.000-1.000	116	0.905	0.027	0.853-0.957
Spring 2003	58	0.878	0.042	0.796-0.961	118	0.970 ^a	0.015	0.940-1.000
Fall 2003	21	0.899	0.067	0.768-1.000	119	0.933	0.023	0.889-0.977
Spring 2004	56	0.924	0.036	0.853-0.995	109	0.945	0.023	0.903-0.987

^aSurvival significantly greater ($P < 0.05$) than previously radio-tagged.

which 24.4% of birds radio-tagged did not survive a 14-day conditioning period. Furthermore, Osborne et al. (1997) reported 54% of their radio-tagged sample had trouble with the harness. Our estimates are more consistent with Burger et al. (1995) who reported only 19 of 1,001 birds (1.9%) having trouble with the harness, and Burger et al. (1998) who reported censoring only 16 of 831 (1.9%) from a radio-tagged sample in Georgia during a 7-day censor period. Guthery and Lusk (2004) suggest that the routine application of a censor period was prima facie evidence of at least transient debilitation from radio-tags. We suggest the routine application of the 7-day censor period has been largely due to the recommendation of the original authors publishing the survival analysis technique used (Pollock et al. 1989), and the subsequent necessity of doing so to publish survival information when using this technique. Our analysis, combined with the discontinued use by the AQP and many other researchers studying bobwhite demographics and population ecology in the Southeast (L.W. Burger, W.E. Palmer, J. P. Carroll, personal communication) does not support the notion of an accepted censor period being evidence

of "radio-handicapping".

We examined direct recovery rates for a sample of 3,932 banded and 2,086 radio-tagged birds during 13 hunting seasons from 1992-2004. Annual recovery rate by harvest averaged 6.68% (range: 3.4 - 11.7) for banded birds and 6.65% (range: 3.4 - 11.1) for radio-tagged birds and was not different ($P < 0.05$) between groups during any of the 13 hunting seasons (Table 2). While these harvest rates are admittedly conservative, this analysis does not support the conclusions of previous studies that radio-tags render bobwhites more or less vulnerable to harvest than banded birds. Guthery and Lusk (2004) called into question such inferences obtained from radio-telemetry as the nature and magnitude of cause specific mortality, arguing that if radio-tags effected survival information then it made sense they were affecting other estimates as well. Due to the subjectivity and potential observer error associated with ascribing specific causes of mortalities, this topic has proven difficult to independently verify. However, harvest supplants the inherent observer subjectivity and thus provides a relatively reasonable check. Empirical studies have recently shown no difference

Table 2: First year (direct) harvest recovery rates (K) of banded or radio-tagged northern bobwhites on Albany, GA area Plantations, Baker and Dougherty Counties, Georgia from 1992-93 to 2004-05.

Year	Banded			Radio-tagged		
	n	K	SE(K)	n	K	SE(K)
1992-93	200	0.065	0.017	112	0.045	0.020
1993-94	422	0.047	0.010	282	0.067	0.015
1994-95	115	0.070	0.024	227	0.066	0.016
1995-96	98	0.112	0.032	126	0.103	0.027
1996-97	93	0.075	0.027	179	0.095	0.022
1997-98	111	0.117	0.031	190	0.111	0.023
1998-99	238	0.067	0.016	149	0.067	0.020
1999-00	652	0.041	0.008	125	0.072	0.023
2000-01	434	0.060	0.011	117	0.034	0.017
2001-02	494	0.059	0.011	189	0.042	0.015
2002-03	602	0.038	0.008	110	0.055	0.022
2003-04	234	0.034	0.012	147	0.048	0.018
2004-05	239	0.084	0.018	133	0.060	0.021
TOTAL	3,932	0.067		2,086	0.067	

in harvest rates between banded and radio-tagged birds (Palmer and Wellendorf 2007, Terhune et al. 2007) whereas other studies have produced mixed results ranging from marginally higher (Corteville et al. 2000, Cox et al. 2004) to significantly lower (Parry et al. 1997) harvest of radio-tagged compared to banded birds. This was a concern to us at the inception of our project in 1992; therefore we have tracked radio-tagged and banded birds during harvest time periods for the duration of our research program. Our results re-enforce the conclusion that radio-tagging quail does not affect their vulnerability to harvest on our study sites.

Guthery and Lusk (2004) used anecdotal evidence to explain abnormal behavior of radio-tagged bobwhites. Such accounts included radio-tagged birds less likely to flush than the non-tagged members of a covey, as well as the observation of radio-tagged birds dying in fires while non-tagged birds

escaped. These observations can be countered with innumerable observations from monitoring over 8,000 radio-tagged birds over the last 14 years on our study sites in Georgia. Our combined experiences during the course of these studies have never led us to these same conclusions. Parry et al. (1997) documented radio-tagged birds being less vulnerable to harvest on their study site in Oklahoma, and proposed this was due to their habituation to humans and reluctance to fly when encountered by hunters. Our field staff has never made such observations, nor do our studies of encounters between hunters and radio-tagged coveys support these observations (Sisson 1996, Sisson et al. 2000c, Sisson 2005). During these studies, our field staff monitored over 1,100 encounters with radio-tagged coveys over an 8-year period without making any observations that radio-tagged birds behaved abnormally while being hunted.

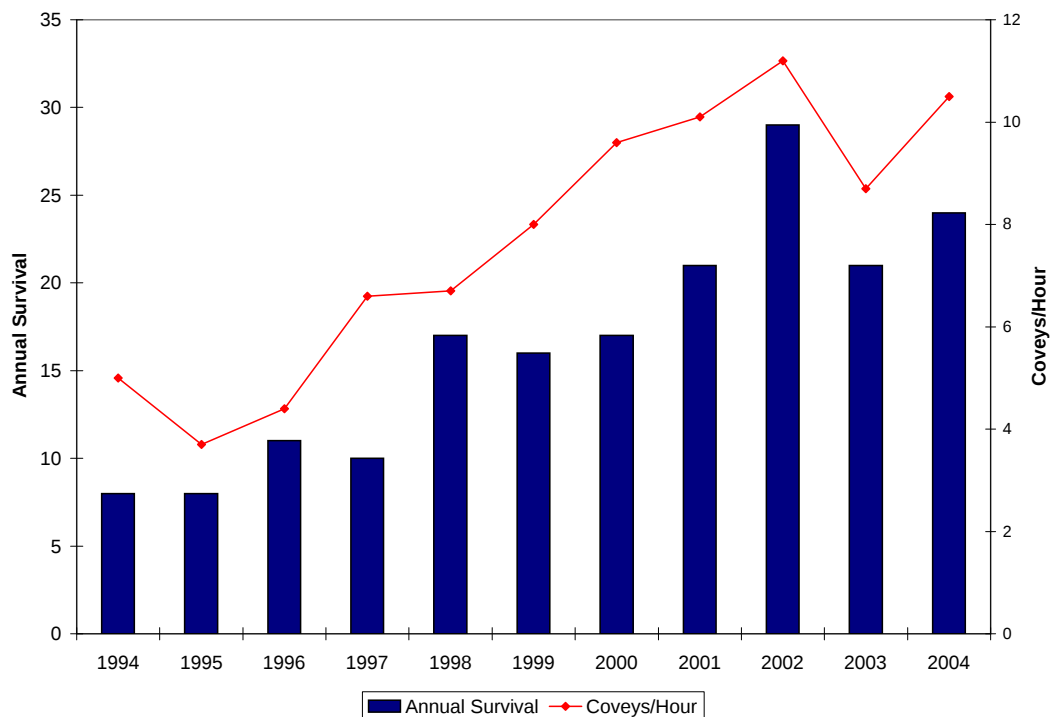


Figure 1: Kaplan-Meier annual survival estimates and coveys seen per hour hunted for one of the long-term study sites of the Albany Quail Project in Dougherty and Baker, Counties Georgia during 1993 - 2004.

Perhaps the best testament to the reliability of telemetry-generated data is whether it accurately reflects population performance of the population at large under study. Guthery and Lusk (2004) pointed out the paucity of investigations on the demographic consequences of the reported survival rates based on telemetry. Results from our study indicate that telemetry-based estimates of population parameters represent those of the population under study. This can best be illustrated by examining a case study: consider the population dynamics of one of our long-term study sites during the 11 years it was monitored year round with radio-tagged birds. We used coveys observed per hour as an index to population density (Palmer et al. 2002). Figure 1 illustrates how this population was closely associated with annual survival during the preceding year. The first 3 years of this study (1993-94 through 1995-96) were used in the meta-analysis by Guthery and Lusk (2004) as evidence of radio-handicapping due to an-

nual survival estimates averaging only 9% during this time period (Sisson et al. 2000a). Annual survival rates have clearly recovered since then with a corresponding response in population density and hunting success (Figure 1). Further evaluation highlights the problem of using individual years or a short series of years (i.e., 2-4 years) in these type analyses. Four of the 11 annual survival estimates in Figure 1 are below the threshold of 0.125 proposed by Guthery and Lusk (2004) for the maintenance of population stability, while the long-term average is well above it. Very different conclusions could be drawn from these data depending on which years the population was under study. In reality, during the initial years of the study the population was declining (Sisson et al. 2000b,a), during the middle years it was responding to habitat improvements (Sisson et al. 2002a) and currently is relatively high and stable (Stribling and Sisson 2009).

We are uncertain at this point why "radio-

handicapping" appears to be problematic for some areas and not others, but we suspect it may be related to a combination of regional differences in habitat conditions, climate, harvest pressure, and trapping and handling techniques. We agree with Guthery's interpretation of Bro et al. (1999) that the influence of radio-tagging on a species might depend on the environmental context of the population. The populations we have studied were intensively managed properties, in a region of mild climate, and subjected to a conservative harvest. In addition, our analyses were based on a large sample of birds over many years, leading to a more powerful inference about the effects of radio-telemetry on survival. We believe the direct and circumstantial evidence is compelling that we conclude that no radio-handicapping existed on our study sites and advise other researchers to follow similar approaches before drawing inferences about population parameters from radio-telemetry data.

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