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Radiotelemetry Survival Estimates of Lesser Prairie-Chickens in Kansas: Are There Transmitter Biases?

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Abstract

*Radiotelemetry has provided wildlife biologists with a tool to estimate survival where fates of individuals likely are known. Analyses of known-fate data can yield accurate survival estimates if 5 assumptions are met. Two of these assumptions are rarely tested: that transmitters have no effect on survival of study animals and that right-censoring (i.e., any animal not located is as likely to be alive as dead) is random with respect to the survival of study animals. Using joint-models originally developed for live-encounter and dead-recovery data, we examined the potential for bias in survival estimates of radiomarked male lesser prairie-chickens (*Tympanuchus pallidicinctus*) in a 3-year study in southwestern Kansas, USA. Additionally, we examined the potential bias of right-censoring by comparing the return rates of known-fate and right-censored individuals. We captured 216 male lesser prairie-chickens and marked them with a combination of leg bands and a radio (*n *= 72) or leg bands only (*n *= 144). We applied joint-models to capture histories based on live-capture and telemetry data. The model best supported by the data indicated that 6-month survival was constant ($\hat{S}_c = 0.679$, SE = 0.050) across radiomarked and banded birds. Eight of 16 (50%, SE = 12.5%) right-censored birds not detected because of radio failure were subsequently recaptured, which was not different from the return rates for known-fate birds (23 of 59; 39%, SE = 6.3%). Survival estimates of male lesser prairie-chickens in this study were not measurably biased by radiomarking, as their survival was greater than or equal to those of banded birds, and right-censored birds had similar return rates to those of known-fate individuals. Our results are encouraging because they indicate that 2 critical assumptions underlying analyses of known-fate data can be met with radiotransmitters and attachment techniques currently used in field studies of wild populations of lesser prairie-chickens.* (WILDLIFE SOCIETY BULLETIN 34(4):1064–1069; 2006)

Key words

Kansas, lesser prairie-chicken, live-recapture dead-recovery models, necklace, radiotelemetry, right-censoring, transmitter, Tympanuchus pallidicinctus.

Radiotelemetry is widely used to collect data for estimating survival of observational or experimental groups in wildlife studies. Unbiased survival estimation from known-fate data requires meeting several assumptions: 1) radiomarked animals are representative random and independent samples of the population of interest, 2) observation periods are independent, 3) working radios are always located, 4) right-censoring is random (i.e., any animal lost is as likely to be alive as dead), and 5) radios do not impact survival of marked individuals (Winterstein et al. 2001). Assumptions 1, 2, and 3 can be addressed by implementing the appropriate research design or statistical model (Winterstein et al. 2001). A general problem in telemetry studies is that fates are sometimes unknown (assumptions 3 and 4) because of animals losing radios or radio failure. Individuals undetected because of vagaries of equipment or dispersal will be right-censored for a given period. Right-censoring occurs when an individual cannot be located either temporarily or permanently and the fate of the individual is unknown. In practice animals are right-censored when there is radio failure, detection rates are <1, or there is emigration from the study area. Assumptions 4 and 5 are less controllable because of radio failure and behavior of individual animals cannot be accounted for entirely in project design. Generally, appropriate controls for studies of attachment techniques can be difficult to identify (Esler et al. 2000).

Effects of radiotransmitters on survival of game birds have been investigated, but the results have been inconclusive (Thirgood et al. 1995). Most studies suffer from a lack of a suitable control group and rigorous estimates of survival. Typically, studies examined differences in return rates or daily survival of birds marked with 2 or more types of harness configuration or transmitter mass (Withey et al. 2001). Radios with external attachments (e.g., poncho, necklace, and backpack) have had negative impacts on survival of upland game birds (Withey et al. 2001). Handling effects (i.e., increased mortality immediately after handling) occurred with early radio designs of backpack-style and wing-loops (Marks and Marks 1987, Pekins 1988). In contrast, studies comparing other attachment techniques found no measurable effects of radios on survival or other vital rates (Hines and Zwickel 1985, Cotter and Gratto 1995, Thirgood et al. 1995, Bro et al. 1999). Most of the preceding studies used return rates, the number of previously

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marked and reencountered at time t/number marked at time $t - 1$, as an estimate of survival. This approach is problematic because return rates are the product of 4 probabilities: true survival (S), site fidelity (F), site propensity (γ), and detection (p). Hence, differences in return rates between control and experimental groups may be due to demographic processes other than true survival. Mark–recapture models can provide local survival estimates while accounting for site propensity and detection rates, whereas recovery models give estimates of true survival. We know of no study to date that has examined effects of radiomarking on game birds using contemporary models for analyses of capture–recapture data.

Our objectives were to determine potential effects of radiomarking on survival of male lesser prairie-chickens (*Tympanuchus pallidicinctus*) and the possible bias of right-censoring on survival probabilities. Joint-analyses of live encounters and dead recoveries have been applied to banded individuals marked on breeding grounds and recovered during the hunting season (Burnham 1993). We used this joint-model in a novel way by applying it to encounter histories based on live encounter information and dead recoveries of hunter-harvested and radiomarked individuals. Last, we examined the potential bias of right-censoring by comparing the return rates of known-fate and right-censored individuals.

Methods

Field Methods

We conducted this study in native sand sagebrush (*Artemisia filifolia*) prairie south of Garden City, Kansas, USA (37°52′N, 100°59′W), from spring 1998 to spring 2000. We captured male lesser prairie-chickens over 3-week periods using walk-in funnel traps at display sites (leks) during late March to early April and late September to early October (Haukos et al. 1990, Salter and Robel 2000). To ensure equal sampling across the study site (approx. 5,000 ha), we trapped birds at all leks with >2 males ($n = 11$, total leks = 13). We identified birds as yearling (approx. 10 months) or adult (≥22 months) based on shape, wear, and coloration of the ninth and tenth primaries (Amman 1944, Copelin 1963). We fitted all captured birds with serially numbered aluminum leg bands. We opportunistically marked a subset of yearling and adult males in similar proportions with necklace-style radios (Model 7-PN; Advanced Telemetry Systems, Isanti, Minnesota). These radios had a mass ≤12 g which were ≤1.7% of a male's body mass ($\bar{x} = 788$ g, SD = 42 g, $n = 71$). Each radiotransmitter had a 6-month battery life, a whip antenna, and an 8-hour mortality switch. We did not left-censor radiomarked individuals that died during the 2-week postcapture acclimation period (Winterstein et al. 2001). This approach allowed for potential acute effects of transmitters to be included in the parameter estimates. We monitored radiomarked birds daily using a truck-mounted null-peak antenna system to track movements and determine their status (live or dead). For the purposes of this study, the observation period was 6 months for radiomarked and banded birds. Research procedures were approved by the Institutional Animal Care and Use Committee at Kansas State University (IACUC# 2609).

Data Analysis

We used data from radiomarked and banded birds using live-encounter–dead-recovery models (hereafter joint-models; Burnham 1993) to examine effects of radiomarking on lesser prairie-chicken survival. Joint-models of survival allow for combination of multiple sources of information (Burnham 1993, Barker and White 2001). If study areas are relatively small, then S is effectively apparent survival (i.e., ϕ as estimated from live recapture data) because losses to mortality and emigration are confounded. If the study area is large enough that emigration is unlikely or animals are highly philopatric, then S is effectively true survival. Joint-models extend standard Cormack–Jolly–Seber models of live capture–recapture data (Burnham 1993) and estimate additional parameters. The 4 parameters of the Burnham model and their definitions are as follows:

$S_i =$ The probability of survival; an animal that is alive at time i, is again alive at time $i + 1$.

$p_i =$ The probability of detection; an animal that is alive, is at risk of detection at occasion i, and is detected.

$r_i =$ The probability of reporting; a marked animal that is alive at time i dies and is reported at time $i + 1$.

$F_i =$ The probability of site fidelity; an animal that is at risk of capture at trapping occasion i and is again at risk of capture at time $i + 1$.

In our study, sources of live encounter information came from 5 standard marking periods of banded birds and "resighting" periods of live radiomarked individuals (once every 6 months). Dead recovery data came from 5 reporting periods (r) of both banded and radiomarked birds. Because there were only 5 encounters, we considered time (t) a nuisance parameter. We expected consistently unequal detection probabilities, p, in spring and autumn trapping periods because lek activity varies (Salter and Robel 2000). Thus, we pooled the 2 autumn and 3 spring encounters into 2 seasonal periods, "spring" and "autumn," respectively. The subscript "season" referred to the temporal effect on a parameter, and we estimated survival for 2 6-month periods.

We right-censored from the radiomarked group individuals that survived a given interval and had their radios removed at recapture ($n = 6$) and added them to the banded group, and the opposite was true for banded birds that received a radio at a subsequent interval ($n = 9$). We coded individual capture histories using the "live–dead" format (LD) in which we recorded 2 values for each sampling occasion. Live encounters included captures of banded bird and telemetry detections of a radiomarked bird. A code of 1 1 = a marked individual encountered but recovered dead; 1 0 = a prairie-chicken encountered and not recovered dead; 0 1 = an individual not encountered alive at the beginning of

Table 1. Joint-models estimating 6-month survival probabilities of radiomarked and banded lesser prairie-chickens in Finney County, Kansas, USA, 1998–2000.

Model structure[a]				**Model statistic**[b]			
S	***p***	***r***	***F***	**ΔQAIC$_c$**	**w_i**	***K***	***Dev***
constant(*c*)	marker + season	marker	fixed(*x*)	0.00	0.44	6	137.796
season	marker + season	marker	fixed(*x*)	1.59	0.20	7	137.298
marker	marker + season	marker	fixed(*x*)	1.83	0.18	7	137.537
marker + season	marker + season	marker	fixed(*x*)	3.36	0.08	8	136.956
marker × season	marker + season	marker	fixed(*x*)	3.91	0.06	9	135.389
marker × season	marker × season	marker	fixed(*x*)	5.79	0.02	10	135.137
marker × season	marker × season	marker + season	fixed(*x*)	7.93	0.01	11	135.128
marker × season	marker × season	marker × season	fixed(*x*)	8.03	0.01	12	133.068
marker × season	marker × season	marker × season	constant(*c*)	9.89	0.00	13	132.759
marker × season	marker × season	marker × season	marker	12.08	0.00	14	132.759
marker × season	marker	marker	fixed(*x*)	20.85	0.00	7	156.549
marker × time	marker × time	marker × time	marker × time	42.15	0.00	34	115.773

[a] Models were structured to separate survival ($\hat{S}$) for marker effect (marker) for radiomarked and banded males. Parameter estimates include survival (*S*), detection rate (*p*), and reporting rate (*r*). Site fidelity (*F*) was fixed at 0.993.

[b] Model fit is described by deviance (*Dev*), the number of parameters (*K*), QAIC$_c$ weights (w_i), the difference in quasi-Akaike's Information Criterion ($\hat{c} = 1.53$) corrected for small sample size (ΔQAIC$_c$), and QAIC$_c$ = 422.08 for the best model.

the interval but recovered dead during the interval; and 0 0 = a prairie-chicken not detected during an interval.

We analyzed joint-models of survival of banded and radiomarked individuals following 3 steps: 1) selection of the global model, 2) goodness-of-fit testing of the global model, and 3) development of less-parameterized models and model selection. We based model selection on quasi-likelihood corrected Akaike's Information Criterion adjusted for small sample sizes and over-dispersion (QAIC$_c$; Burnham and Anderson 1998). We used Program MARK 4.0 for model selection and parameter estimation (Cooch and White 2004).

We developed an a priori set of candidate models (Table 1) that allowed us to examine the potential for effects of radiomarking. Our primary interest was evaluating survival (*S*); thus, we treated recapture (*p*), reporting (*r*), and fidelity (*F*) as nuisance parameters. Subscripts following parameters indicate explanatory variables (e.g., $S_{\text{marker}\times t}$ describes a model that includes both marker effect (i.e., marker = banded or radiomarked) and time-dependence (i.e., survival varies by encounter occasion) in survival. Last, we used the subscript (*c*) to describe parameters modeled as a constant rate (e.g., S_c describes a model where one survival probability is estimated for all time periods and groups). We fitted alternative structures of *F*, *r*, and *p* from the global model ($S_{\text{marker}\times t}$, $p_{\text{marker}\times t}$, $r_{\text{marker}\times t}$, $F_{\text{marker}\times t}$) that were biologically and practically meaningful. The parameter *F* was fixed at 0.993 and denoted as F_x because only 2 of 95 ($0.979^{0.33}$) radiomarked males were known to have permanently emigrated. We expected seasonal differences in behavior to yield consistently unequal detection probabilities, *p*, in spring and autumn trapping periods (Salter and Robel 2000). We fitted a factorial time structure (marker × season) to *p* and *r* and selected the best structure based on minimum QAIC$_c$ values. We assumed the probabilities *p* and *r* for radiotelemetry (~1) and banding data (<1) would be unequal, and we did not model *p* and *r* as constant rates. The simplest form was with a marker effect only. We examined survival of radiomarked and banded birds as a group effect (S_{marker}) against the alternatives S_{season} and S_c; if support was greater for the latter 2 model structures, then we concluded that transmitter effects were not measurably different between radiomarked and banded birds.

We assessed the overall goodness-of-fit test of the global model using a Pearson χ^2 statistic from the residuals of the global model as estimated in MARK (G. C. White, Colorado State University, personal communication). We used the pooled χ^2 divided by model degrees of freedom (df) to estimate the degree of over-dispersion ($\hat{c}$). We calculated parameter estimates from the best-fit model; where there was more than one parsimonious model (ΔQAIC$_c$ < 2), we used the model-averaging procedure in MARK (Cooch and White 2004). This procedure calculated a weighted-average parameter estimate from all models in the candidate set, using the Akaike weights (w_i) specific to each model.

We examined the assumption of random censoring by comparing return rates of known-fate individuals (no. alive and recaptured/no. alive + no. dead) to the proportion of birds that were right-censored but were recaptured or reported later (no. censored and recaptured/total no. censored). We used a likelihood ratio test (G^2) and constructed a 95% confidence interval around the difference ($\bar{d}$) of these proportions to determine if it was different from zero (Agresti 1996). We report sample sizes and standard errors along with the effect size ($\bar{d}$).

Results

We captured and marked 216 male lesser prairie-chickens. We fitted 72 of these birds with leg bands and a radio and 144 with leg bands only. Because body mass and age can affect survival, we compared these factors between groups to ensure representative samples. The mean body mass at capture of radiomarked birds ($\bar{x}_{\text{radio}} = 790$, SE = 5.1 g, $n =$

Table 2. Model-averaged parameter estimates (± SE) from joint-models of survival for radiomarked and banded male lesser prairie-chickens in Finney County, Kansas, USA, 1998–2000.

Parameter estimate[a]	**Marker type**	
	Banded	**Radio**
S_{spring}	0.671 ± 0.075	0.670 ± 0.061
S_{autumn}	0.615 ± 0.085	0.650 ± 0.065
p_{spring}	0.571 ± 0.138	0.845 ± 0.071
p_{autumn}	0.166 ± 0.055	0.457 ± 0.092
r_{spring}	0.104 ± 0.050	0.482 ± 0.092
r_{autumn}	0.092 ± 0.038	0.485 ± 0.094

[a] Parameter estimates include survival (S), detection rate (p), and reporting rate (r). Site fidelity (F) was fixed at 0.993.

68) and leg-banded birds ($\bar{x}_{\text{band}} = 802$, SE = 3.6 g, $n = 126$; $t = 1.97$, df = 192, $P = 0.068$) was not significantly different ($\bar{x}_{\text{difference}} = -11.4$ g, CI: −23.7, 0.8 g). Additionally, the proportion of yearlings in each sample was similar between radiomarked 0.59 (SE = 0.06, $n = 72$) and leg-banded birds 0.62 (SE = 0.04, $n = 144$), respectively (Fisher's exact test, $P = 0.657$). Seven radiomarked birds died within 2 weeks of capture. Autumn trapping resulted in fewer birds captured per unit effort than spring trapping (Salter and Robel 2000), and this was evident in the additive parameter structures (marker + season) in the model selection below.

The fit of the global model ($S_{\text{marker}\times t}$, $p_{\text{marker}\times t}$, $r_{\text{marker}\times t}$, $F_{\text{marker}\times t}$) was reasonable ($\chi^2_6 = 9.156$, $P < 0.165$) but was adjusted for over-dispersion $\hat{c} = 1.526$. Model selection and inference were made from QAIC$_c$ (Anderson et al. 1994) and standard errors were adjusted by $\hat{c}$. Some of the over-dispersion may have been due to a lack of independence, as some individuals transitioned between banded and radiomarked groups.

There was some model uncertainty (ΔQAIC$_c$ <2) for the top 3 models, but model S_c, $p_{\text{marker+season}}$, r_{marker}, F_x was 2.22 times (w_1/w_2) more likely to be supported by the data than the next best model and indicated that 6-month survival was best modeled as a single parameter ($\hat{S}_c = 0.656$, SE = 0.048) for both radiomarked and banded birds (Table 1). Another parsimonious model (ΔQAIC$_c$ <2), S_{marker}, $p_{\text{marker+season}}$, r_{marker}, F_x, had a marker effect in S, but survival was greater among radiomarked birds ($\hat{S}_{\text{radio}} = 0.671$, SE = 0.056; $\hat{S}_{\text{band}} = 0.625$, SE = 0.074) contrary to our prediction. Both competing models only added 1 parameter and did not affect deviance; thus, the effects of these parameters on model selection were minimal. Survival estimates from model averaging indicated that radiomarked individuals had similar or slightly greater survival than banded birds in summer ($\hat{S}_{\text{radio}} = 0.670$, SE = 0.061; $\hat{S}_{\text{band}} = 0.671$, SE = 0.075) and winter, respectively ($\hat{S}_{\text{radio}} = 0.650$, SE = 0.065; $\hat{S}_{\text{band}} = 0.615$, SE = 0.085). Reporting rates as estimated from the most parsimonious model were greater for radiomarked birds ($\hat{r} = 0.481$, SE = 0.090) than banded birds ($\hat{r} = 0.093$, SE = 0.037). Recapture probabilities varied additively over time for both groups (Table 2), and, overall, radiomarked birds had greater recapture rates ($\hat{p}_{\text{radio}} = 0.621$, SE = 0.075; $\hat{p}_{\text{band}} = 0.268$, SE = 0.057; S_c, p_{marker}, r_{marker}, F_x).

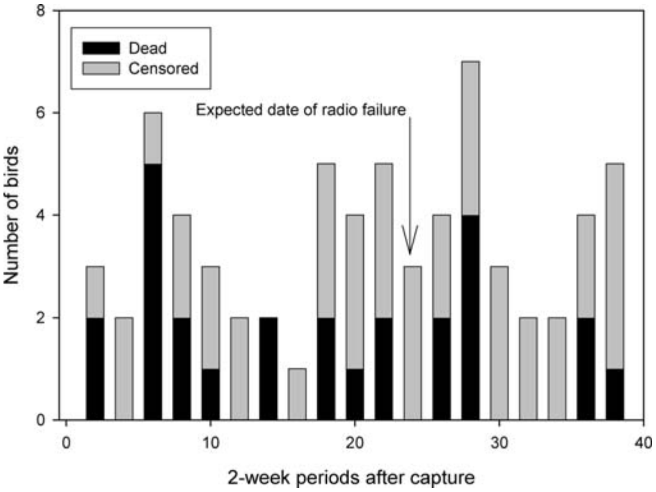

Figure 1. The distribution of dates of mortality (black) and right-censoring (gray) of radiomarked and expected radio-failure date of male lesser prairie-chickens in southwestern Kansas, USA, 1998–2000.

Effects of Right-Censoring

We permanently lost radio signals for 16 birds during the 6-month sampling intervals and right-censored them. An additional 24 radio signals were lost after the 6-month battery life expired, and were detected as alive at last encounter occasion (this accounts for part of known-fate percentages). Signal loss occurred throughout the monitoring period and appeared to be independent of periods of high mortality (Fig. 1). We subsequently recaptured 50% (SE = 12.5%, $n = 16$) of right-censored birds, which was not measurably different from the return rates for known-fate birds (39.0%, SE = 6.3%, $n = 59$; $G^2_1 = 0.163$, $P = 0.685$, $\bar{d} = -11.0\%$; CI: −38.5, 16.5%), suggesting that right-censored birds had similar survival to that of known-fate individuals.

Discussion

We tested 2 fundamental assumptions of capture–recapture analyses of known-fate data. Our major conclusions were 2-fold: 1) we found no evidence that radiomarking male lesser prairie-chickens negatively impacted their survival, and 2) right-censoring did not bias estimates of survival. Contrary to our predicted outcome, radiomarked individuals had a slightly greater survival than banded birds. Right-censored birds had similar return rates when compared to those with known fates. Inference about survival in this group was based on relatively small sample sizes, but return rates were similar enough to provide support for a comparable mortality rate between them. Our study improves on past work by use of joint-models and multiple data types. However, our analyses were retrospective and an experimental design would have had greater statistical power. Nonetheless, given the greater survival among radiomarked than banded birds, our study suggests that radios had little impact on summer or winter survival of male prairie-chickens. Our inference was limited to the male cohort of the population. Female lesser prairie-chickens (730 g) are smaller than males (800 g; Hagen et al. 2004), but transmitters are still <3% of female body mass. The same transmitters (<12 g) are unlikely to impact female survival unless radio antennas impact a female's flight response and ability to evade predators, particularly from nesting sites (Marks and Marks 1987).

To our knowledge this study is the first to demonstrate that radios had no measurable effect on prairie grouse (*Tympanuchus* spp.) survival. Thirgood et al. (1995) found no measurable effect of radiomarking (necklace-style transmitters) on red grouse (*Lagopus lagopus scotica*) when compared to patagium-tagged birds. Together, our results indicate that miniaturization of necklace-style transmitters has alleviated some of the lethal effects reported previously for other grouse species with early transmitters and attachment techniques (Marks and Marks 1987, Pekins 1988). Previous work on both sharp-tailed grouse (*T. phasianellus*) and greater prairie-chickens (*T. cupido*) detected negative effects of radios on return rates and daily survival, respectively (Marks and Marks 1987, Burger et al. 1991). However, Marks and Marks (1987) and Burger et al. (1991) measured effects of larger (13.5–22 g) poncho-style solar-powered transmitters with a large reflective surface, in contrast to the 12-g lithium-battery–powered necklace-style attachment used in our study. Marks and Marks (1987) used banded birds as a control group, but sample sizes ($n = 9$) may have hampered comparisons of return rates to that of radiomarked birds ($n = 35$). However, 23 of 35 radiomarked birds in the Marks and Marks (1987) study succumbed to predation, of which 65% occurred during the breeding season. Burger et al. (1991) documented birds marked with larger 2-stage transmitters (18–22 g) with reflective surfaces had twice the probability of being depredated than those fitted with 1-stage radios (14 g). Similar patterns of mortality were documented for ruffed grouse (*Bonasa umbellus*) and ring-necked pheasant (*Phasianus colchicus*) when birds were marked with heavier backpack-style transmitters (Warner and Etter 1983, Small and Rusch 1985). The cause of marker-specific survival may not be easily understood, if yearly variation in environmental conditions impacts the outcome of these studies (Cotter and Gratto 1995, Bro et al. 1999). The negative effect of radiomarking may be greater during years when birds are stressed or in poor body condition. Because of the limited duration of our study, yearly variation in survival could not be examined. Radiomarking also may have more pronounced impacts on juvenile or yearling age-classes. Although we did not examine age as a covariate in this study, we did not anticipate lower survival in yearling birds (Hagen et al. 2005), and any potential biases for yearlings and adults were equally represented in each marked group.

Random censoring is a critical assumption of telemetry studies, and violation of the assumption can result in significant bias in $\hat{S}$ (Tsai et al. 1999, Winterstein et al. 2001) but has been difficult to evaluate in the field (Esler et al. 2000). Return rates were similar between known-fate and right-censored individuals despite small sample sizes. Because return rates are comprised of 4 parameters, true survival, site fidelity, site propensity, and detection probability, return rates can be difficult to interpret. However, few males (2%) permanently left our study area, no males were known to temporarily emigrate (site propensity), and detection probabilities were relatively large 82% (Hagen et al. 2005); therefore, we assert that return rates were a reasonable index of true survival. Thus, our estimates of survival were not likely biased by right-censored birds. To our knowledge our study is only the second to test this assumption. Esler et al. (2000) documented a similar pattern in radiomarked harlequin ducks (*Histrionicus histrionicus*), but also acknowledged the low power of their study design.

In conclusion, miniaturization and method of attaching transmitters appear to have reduced the impact of radios on survival of prairie grouse. Annual survival of radiomarked birds in our study ($\hat{S}_{\text{spring}} \times \hat{S}_{\text{autumn}} = 44\%$, $n = 72$) was greater than rates previously reported for radiomarked populations of sharp-tailed grouse (16%, $n = 35$; Marks and Marks 1987) and greater prairie-chicken (32%, $n = 54$; Burger et al. 1991). Our inference was limited to the male cohort of this population, and future work should include a rigorous experimental study to examine effects of transmitters on free-living birds of both sexes under field conditions. The results from our study are encouraging because they demonstrate that 2 critical assumptions underlying analyses of known-fate data can be met with radios currently used in field studies of wild populations of game birds.

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