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EFFECTS OF RADIO COLLARS ON SURVIVAL AND LEKKING BEHAVIOR OF MALE GREATER SAGE-GROUSE

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Abstract. Monitoring of birds often requires the use of very-high-frequency radios or satellite telemetry to enhance detectability of individuals. An assumption implicit in such studies is that radio-marked individuals are representative of the population at whole, which requires that radios do not influence an individual's behavior or demographics. We present results from a capture–mark–recapture study of male Greater Sage-Grouse (*Centrocercus urophasianus*), some radio collared, others only banded, in an experimental framework to assess whether radio collars influenced the birds' behavior or survival. We generated encounter histories of 906 male Greater Sage-Grouse and used a robust-design framework in program Mark to estimate probabilities of annual survival, detection, and temporary emigration from the lek for the radio-collared and banded segments of the sample population. Results of models suggested that seasonal detection rates at leks the year after capture were 3–5 times higher for males only banded than for males equipped with radio collars. These results also suggested a possible negative influence of radio collars on males' annual survival and annual lek attendance. We suggest researchers should exercise caution when designing studies or analyzing data that rely on radio-collared male Greater Sage-Grouse.

Key words: *Capture–mark–recapture*, *radio telemetry, lek dynamics, detection.*

Efectos de los Radio Collares en la Supervivencia y el Comportamiento en la Asamblea de Cortejo de los Machos de *Centrocercus urophasianus*

Resumen. El monitoreo de aves usualmente requiere el uso de radios de muy alta frecuencia (VHF) o de telemetría satelital para mejorar la detectabilidad de los individuos. Una suposición implícita en estos estudios es que los individuos marcados con radios son representativos de la población en su conjunto, lo que requiere que las radios no influencien el comportamiento o la demografía del individuo. Presentamos resultados de un estudio de captura-marcado-recaptura de machos de *Centrocercus urophasianus*, algunos marcados con radios y otros solo con anillos, en un diseño experimental para evaluar si los radio collares influenciaron el comportamiento o la supervivencia de las aves. Generamos historias de encuentro de 906 machos de *C. urophasianus* y usamos un marco de diseño robusto en el programa Mark para estimar las probabilidades de supervivencia anual, detección y emigración temporal de la asamblea de cortejo para los segmentos con radio collares y anillados de la población de muestra. Los resultados de los modelos sugieren que las tasas de detección estacional en las asambleas de cortejo en el año luego de la captura fueron 3–5 veces más altas para los machos solo anillados que para los machos con radio collares. Estos resultados también sugieren una posible influencia negativa de los radio collares en la supervivencia anual de los machos y en la asistencia anual a la asamblea de cortejo. Sugerimos que los investigadores deberían tener cuidado cuando diseñan estudios o analizan datos que se basan en machos de *C. urophasianus* marcados con radio collares.

INTRODUCTION

The use of marked individuals in ecological studies allows for robust estimation of various vital rates that are often of interest. The fundamental assumptions made with data from a marked sample of individuals are that (1) the marked sample was selected at random and (2) the attached mark does not influence the behavior or demographic rates of the individual (White and Garrott 1990). These assumptions are critical to the validity of the results from demographic analyses because researchers interpret patterns in the marked sample as representative of the entire population (Murray and Fuller

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2000). The first assumption is usually ignored or attempts are made to meet it through marking a larger proportion of the population (White and Garrott 1990). The second assumption is also widely ignored (Murray and Fuller 2000), though numerous studies have attempted to document or quantify behavioral or demographic responses to various marking techniques across a wide variety of species (summarized by Barron et al. 2010). Many of these studies have been limited by small sample sizes or lack of control groups (White and Garrott 1990), were unable to separate effects of capture from those of the marker (Guyn and Clark 1999), or could not investigate long-term effects of the mark (Caizergues and Ellison 1998, Gauthier-Clerc et al. 2004).

Over the last four decades, radio telemetry has become a common tool for collection of data on wild animals (Mech 1983, White and Garrott 1990, Barron et al. 2010). Use of a radio-transmitting device on an individual requires the same assumptions as other methods of marking, but the weight and size of transmitters being greater than those of other marks such as bands or tags increases the potential for negative effects. Assessing transmitter effects requires data from a control group that can be monitored without the use of a radio mark (White and Garrott 1990). Male Greater Sage-Grouse (*Centrocercus urophasianus*) meet this criterion: they are visible and available for detection in consistent locations (leks) for approximately 3 months during the breeding season each year (Gibson and Bradbury 1987, Connelly et al. 2003); therefore, an experiment comparing radio-marked and non-radio-marked individuals is possible.

The sage-grouse is endemic to the sagebrush-steppe ecosystem of western North America (Schroeder et al. 2004) and is of conservation concern because both the species' range and population size have decreased by approximately half since the 1950s (Connelly et al. 2004, Schroeder et al. 2004). Population declines have often been attributed to habitat degradation or loss (Connelly et al. 2000) due to a variety of causes, such as alterations of wildfire regimes (Baker 2011), grazing (Pyke 2011), urbanization (Brown et al. 2005), and energy development (Naugle et al. 2011), which has led to the current designation as a candidate species under the Endangered Species Act (Stiver 2011). Concerns over the species' health and potential for listing have resulted in its being widely studied (Knick and Connelly 2011). Radio telemetry has been extensively used to investigate the sage-grouse's demographics and patterns in habitat use (Connelly et al. 2003). Despite the widespread use of radio telemetry on sage-grouse, few studies have investigated the effects of transmitters on sage-grouse behavior or demography (e.g., Gregg et al. 2007, Fedy et al. 2012). Caizergues and Ellison (1998) suggested the necklace-style radio collars were the most benign for female grouse. Radio collars are used in most contemporary efforts to monitor sage-grouse (Connelly et al. 2003) despite early concerns that attachments to the neck might be problematic for male grouse (Pyrah 1970).

Male sage-grouse may be affected adversely by radio collars because of morphological and behavioral characteristics related to their breeding display. Breeding males produce a complex visual and acoustic display ("strut"), and both the quantity (rate) and quality (acoustic features) of this display are related to a male's mating success (Gibson and Bradbury 1985, Gibson 1996, Patricelli and Krakauer 2010). Struts involve mechanically produced sounds (a "swish" of the wings across breast feathers) as well as vocal elements. A conspicuous component of the strut is the extreme inflation and manipulation of an esophageal air sac behind a pair of pliable apterygia on the breast (i.e., the vocal sacs) (Clarke et al. 1942, Honess and Allred 1942, Dantzker and Bradbury 2006, Krakauer et al. 2009). The inflation and movement of this complex vocal apparatus may be impaired if a bird is wearing a device around its neck (Amstrup 1980). Struts and other lekking behaviors, such as territorial defense, are energetically costly. Males displaying on leks expend 2–4 times more energy than their basal rate (Vehrencamp et al. 1989), and male sage-grouse lose approximately 23% of their body mass during the breeding season, with much of this loss related to depletion of lipid reserves (Beck and Braun 1978, Hupp and Braun 1989). If wearing a radio collar causes additional stress or energy expenditure, or if it decreases the attractiveness of the vocalizations produced, then these effects could depress the mating success or probability of survival of individuals so equipped.

We monitored male sage-grouse in a capture–mark–recapture framework over the course of a 10-year study (2003–2012) at 13 leks in Eureka County, Nevada. During the study, we investigated whether survival or behavior of male sage-grouse was influenced by wearing radio collars. We used a robust-design model framework to estimate annual survival (ϕ), detection probability (p), and the probability of not attending a lek during the breeding season (γ) of male sage-grouse equipped with very-high-frequency radio collars ("radioed") as well as of males banded only on the tarsus ("control"). We hypothesized that lek attendance, detectability, and survival of males equipped with a radio collar would be lower than for the control group.

METHODS

FIELD METHODS

We captured and banded male sage-grouse at each lek at least once weekly during each breeding season (March–May) by spotlighting at night (Connelly et al. 2003). We systematically searched within ~1 km of leks during each attempt at capture. We classified as captured males as juveniles (<1 year old) or adults (>1 year old) by wear of the primaries (Crunden 1963). Each individual was marked with a size 16 National Band and

Tag metal band (Newport, KY), and colored plastic tarsal band engraved with a three-character alphanumeric code (Spinner Plastics, Springfield, IL). Additionally, a subset of males were equipped with a black 22-g radio collar with a whip antenna (Advanced Telemetry Systems, model number A4060, Asanti, MN; dimensions: 16 × 36 × 22 mm). The attachment mechanism comprised a steel cable with a clear plastic sheath covered with black plastic tubing, which wrapped around the individual's neck. Radio collars were fit to allow for at least two fingers to be easily slid between the sage-grouse's neck and cable, a finger's width greater than recommended guidelines (Connelly et al. 2003). This method of attachment did not allow the radio collar to slip over the sage-grouse's head or between its mandibles but was less restrictive during breeding display or foraging. The 22-g radio collar weight approximately 1% of the lightest male's body weight (1.75 kg), and the ratio of transmitter to body mass for all radioed individuals fell within the current guidelines for both sage-grouse and birds in general (Samuel and Fuller 1994, Connelly et al. 2003). A bird's assignment to the radio-collar treatment was haphazard. We attempted to distribute radio collars evenly across all leks, we radio collared both adults and juveniles, and we targeted both previously unbanded and banded individuals. Capture and handling of sage-grouse was approved by the Institutional Animal Care and Use Committee of the University of Nevada, Reno (protocol numbers A02/03-22, A05/06-22, A07/08-22, A09/10-22).

We redetected previously marked individuals either by physical recapture or by re-sighting of plastic tarsal bands during morning observations at a lek, and we made observations at each lek approximately once a week for approximately 10 weeks. Observers arrived at the leks 0.5 hr before first light and remained until birds dispersed (Walsh 2002). Observers monitored leks from mobile blinds with high-powered spotting scopes, and attempted to resight banded males. During 2011 and 2012, we placed trail cameras on leks to produce additional records of marked individuals. To account for misreading of bands due to the poor quality of images from the cameras, three observers had to read the same number in an image independently. We constructed capture histories on the basis of physical captures and resighting of bands. Inclusion in the capture history was contingent on first detection at a lek. That is, we included only males that were initially radio-collared at one of the leks we studied, and we recorded the capture histories of males captured outside the breeding season as part of other studies only if they were subsequently encountered at one of the 13 leks. We monitored radio signals of radioed males opportunistically during the breeding season; however, to facilitate direct comparison between the radio-collared and control groups, we did not use this telemetry data for our capture–mark–recapture analysis. Estimates generated from telemetry data on birds of known fate and estimates generated from capture–mark–recapture data are not comparable because of differences in detection rates, which bias comparisons of survival estimates by each method (Alisauskas and Lindberg 2002). However, we evaluated locations of radioed males to quantify their proximity (km) to the nearest lek. We recorded these coordinates with hand-held GPS units (±5 m), and included locations of both live and dead birds. Because we could not similarly monitor the proximity of control males to leks, we present these data as a qualitative assessment of the distribution of radioed males during the breeding season rather than for direct comparison between the two groups.

STATISTICAL ANALYSES

We used the robust design function in program MARK (White and Burnham 1999), which allowed us to estimate apparent survival (ϕ), temporary emigration from the sample area (γ), and the probability of encountering (p) and re-encountering (c) an individual, conditioned on its presence within the sample area (Kendall et al. 1997). We arbitrarily divided each primary interval of sampling (breeding season) into three 21-day secondary intervals (e.g., Kendall and Nichols 2002). Temporary emigration was equivalent to never attending a study lek during a given breeding season, while re-encounter probability represented the probability of a marked individual being encountered during April or May, given that it had been encountered during an earlier secondary interval.

Our objective was to assess differences in either survival (ϕ), or behavior (γ or p) between radioed and control males. We reasoned that behavioral differences should be manifested in either reduced lek attendance (γ) or in our ability to detect males (p) based on the number of days they visited leks or their activities while present on leks. For example, carrying a radio could influence the amount of time a male spent on a lek or the amount of time it spent displaying while on a lek, thus reducing our ability to detect radioed males through capture or resighting.

We modeled presence of a radio collar as a time-varying binary covariate (radio), which allowed males to enter or leave the radioed group when applicable. That is, males received a one in years they carried a radio collar and a zero in years when they did not. The radio covariate was considered for φ, γ, or p in candidate models. To account for additional sources of variation in φ, γ, and p, on the basis of our previous research we included additional constraints on these parameters (Blomberg et al. 2012). Survival was constrained to vary temporally as a function of average maximum summer temperature (May–August) for each year of the study. Temporary emigration was modeled as random temporary emigration (i.e., no Markovian structure, Kendall et al. 1997), with annual variation in temporary emigration influenced by an index to the density of males during the year prior. We constrained p and c to differ from each other by a constant amount within a year but allowed them to covary among primary intervals (years) and secondary intervals (months) to account for variability in observer effort, method, or sage-grouse behavior, both within and among years. The probability of an individual being detected at least once during a primary interval (p^*) was estimated as $1 - (1 - p_1)(1 - p_2)(1 - p_3)$, where each p_i corresponds to the conditional detection probability for a given secondary interval (Kendall and Nichols 1995). Finally, we considered an effect of age at first capture on φ, γ, and *p*.

All covariates were *z*-standardized ($\bar{x}$ = 0.0, SD = 1.0) (White and Burnham 1999). We used program RDSURVIVE (Hines 1996) and the most global model that converged [$\varphi(t)\gamma(.)p(t)c(t)$] to assess goodness of fit and to estimate an overdispersion parameter $\hat{c}$. We accounted for potential overdispersion in the data by adjusting AIC_c to $QAIC_c$ (Burnham and Anderson 2002). We note that this typically produces an overly conservative estimate of $\hat{c}$, because meaningful sources of variation (i.e., explanatory covariates) cannot easily be incorporated with RDSURVIVE (Sedinger et al. 2006). We used an information-theoretic approach to evaluate support for competitive models, considering models with $\Delta QAIC_c < 2.0$ competitive and deriving the relative likelihood of a model from its Akaike weight (Burnham and Anderson 2002). We created models with an iterative approach, developing the most competitive model lacking radio effects (base model), then using to assess potential radio effects. We rejected our null hypothesis of no effect if inclusion of the radio covariate improved the model's fit over that of the base model and if 85% confidence intervals of β coefficients describing the radio effect did not overlap 0.0 (Arnold 2010). We estimated model-averaged parameters with β coefficients from competitive models (Buckland et al. 1997) and report variance as 85% confidence intervals unless otherwise noted.

RESULTS

We captured 906 individual male sage-grouse, of which we classified 506 as adults, 323 as juveniles, and 77 as of unknown age. Additionally, 307 sage-grouse were recaptured and 642 bands were read during the study. Sixty-five sage-grouse were equipped with radio collars; of these 47 were collared as adults, 17 as juveniles, and 1 of unknown age. Radioed individuals constituted 7% of the total sample; radioed adults accounted for 9% of the sample of adults, while radioed juveniles accounted for 5% of that of juveniles. Radio-telemetry locations (n = 23) and recoveries of dead birds (n = 11) suggested radioed males were consistently near a study lek; 70% of locations of live males and 45% of recoveries of dead ones were within 1 km of a study lek (Fig. 1).

Goodness-of-fit tests suggested the presence of extra-binomial variation within the data ($\hat{c}$ = 2.36), so we adjusted AIC_c to $QAIC_c$. Modeled parameter estimates supported the temporal constraints on φ and γ from previous analyses (Blomberg et al. 2012). Model-averaged results suggested a negative effect of summer temperature (Temp) on φ (β = –0.36, 85% C.I.: –0.59 to –0.12) and positive effect of estimates of densities of males the year prior (*N*) on γ (β = 0.51, 85% C.I.: 0.26–0.76). Model-averaged probabilities of true detection (p^*) increased through the study, ranging from a low of 0.60 (±0.06 SE) in 2003 to a high of 0.88 (±0.06 SE) in 2011. The structure of competitive models also included an effect of age (Age) on *p* (β = 0.17, 85% C.I. 0.06–0.27), which indicated adult males had a higher probability of being detected on a lek than did juvenile males. We assessed the effect of radio collars on the following model, using it as the base model: φ(Temp) γ(*N*) *p*~*c*(Year + Month + Age).

Inclusion of an effect of the radio improved a model's fit over the base model for φ, γ, and $p_{(t+1)}$ (2.63, 4.08, and 8.86 $\Delta QAIC_c$ units, respectively) (Table 1). The greatest support (w_i = 0.47) was for the $p_{(t+1)}$-radio model, indicating a strong negative carry-over effect from wearing a radio collar in year *t* on detection at a lek in year *t* + 1 (β = -0.57, 85% C.I.: –0.84 to –0.31). Models that contained an effect of the radio on $p_{(t+1)}$ as well as on φ or γ were competitive but did not perform better than models that attributed the radio's effect to detection only. The average probability of a control male being detected at least once (p^*) during the breeding season was 0.72 (±0.07 SE), whereas that of a radioed male being detected was 0.17 (±0.02 SE) (Fig. 2). Although inclusion of a radio effect on either φ or γ in models that also contained the radio effect on detection were competitive, confidence intervals for the model-averaged β coefficients for both φ and γ overlapped zero widely ($\beta_{\phi\text{-radio}}$ = –0.02, 85% C.I.: –0.16–0.13; $\beta_{\gamma\text{-radio}}$ = –0.07, 85% C.I.: –0.57–0.42) (Figs. 3 and 4). However, inclusion of a radio effect on either φ and γ in models that did not contain the radio effect on detection improved

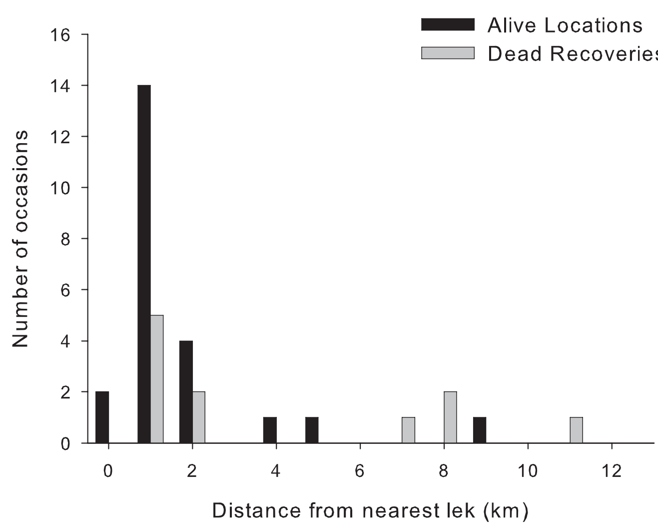

FIGURE 1. Frequency distribution of distances from radio-telemetry locations or locations of recoveries of dead radioed male Greater Sage-Grouse to the nearest monitored lek during the breeding seaon, Eureka County, Nevada, 2003–2012.

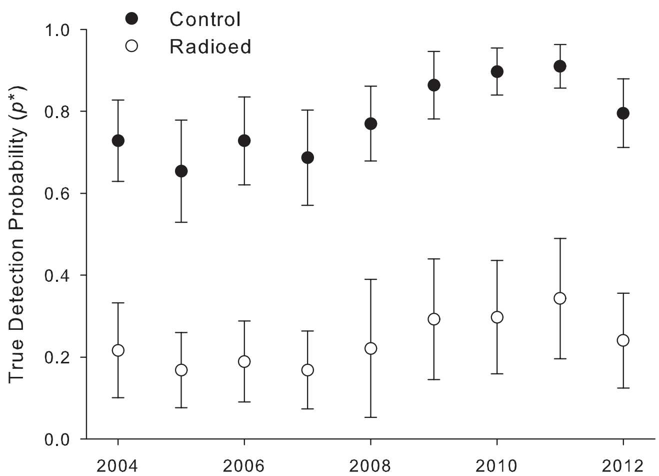

FIGURE 2. Probabilities of a male Greater Sage-Grouse being detected at least once during the breeding season for individuals equipped with a radio collar the breeding season prior (radioed) and those not so collared (control) in Eureka County, Nevada, 2003–2012. Detection was conditioned on survival during the sampling period and availability for detection. Error bars represent standard errors (SE) of model averaged estimates of "true" detection (p^*).

a model's fit over the base model, and confidence intervals for parameters linking radio effects to φ and γ did not overlap zero ($\beta_{\phi\text{-radio}} = -0.30$, 85% C.I.: –0.50 to –0.10; $\beta_{\gamma\text{-radio}} = 0.45$, 85% C.I.: 0.18−0.72), but these models were not as well supported as those applying radio effects to $p_{(t+1)}$. The discrepancies between the effect size and significance of the radio effect on φ and γ when those paramters were included in models that contained the radio effect on detection or not indicates that sampling covariance precludes a clear assessment of the radio effect on all three parameters simultaneously. Finally, inclusion of a radio effect in year *t* on detection in year *t* did not improve a model's fit over the null model, and the confidence interval widely overlapped zero (β = 0.001, 85% C.I.: –0.004–0.006).

DISCUSSION

We found clear evidence that radio collars influenced the behavior of male sage-grouse; the detectability of the control group on leks was 3–5 times higher than that of radioed males (Fig. 2). In our study, detections were based on observations of males displaying on leks and captures of males in the vicinity of leks, and we suggest that radio collars affected either the time males spent on or near leks, their behavior while actually on a lek, or both. Our models suggest modest support (Table 1) for the hypothesis that fitting male sage-grouse with radio collars reduced the probability that they attended a lek at all during a breeding season or reduced their apparent annual survival, but we cannot clearly infer a radio effect on φ (Fig. 3) and γ (Fig. 4) because of sampling covariance that arose when the φ, γ, and detection parameters were modeled with radio effects simultaneously.

In robust design analyses, detection is conditioned on both survival and presence within the sampling area (Kendall and Nichols 1995). Under these conditions, radioed males that survived the year and were available for recapture or resighting at a lek the following year had a lower probability of being detected than did control males. Our telemetry data for a subset of radioed males provides additional support that radioed males were often within 1 km of leks and were available for detection (Fig. 1). We did not find evidence, either through model selection or β coefficients, of an influence of being equipped with a collar in year *t* on detection probability during the same year (Table 1). The effect of radio collars on *p* in year *t* + 1 being greater than in year *t* indicates carry-over effects of radio collars.

At least four mechanisms could account for lower probabilities of detection of radioed males: (1) individuals attended a lek on fewer occasions during a given breeding season; (2) individuals attended leks for a shorter period on days they attended leks; (3) individuals were located nearer the periphery, or least territorial portions, of leks (Gibson and Bradbury 1987); or (4) individuals roosted farther from leks and so were less available for nighttime recapture. These mechanisms, while not mutually exclusive, suggest that attachment of radios to sage-grouse lowered their quality, competitive ability, energetic status, or other attributes that influence success in obtaining and maintaining a territory on the lek and displaying. Regardless of the mechanism, reduction in detectability for a subset of the population of males creates additional bias in lek-focused studies. For example, studies in which the effects of anthropogenic disturbances on lek dynamics are inferred from male sage-grouse (e.g., Walker et al. 2007, Blickley et al. 2012) would be biased if radioed males were included.

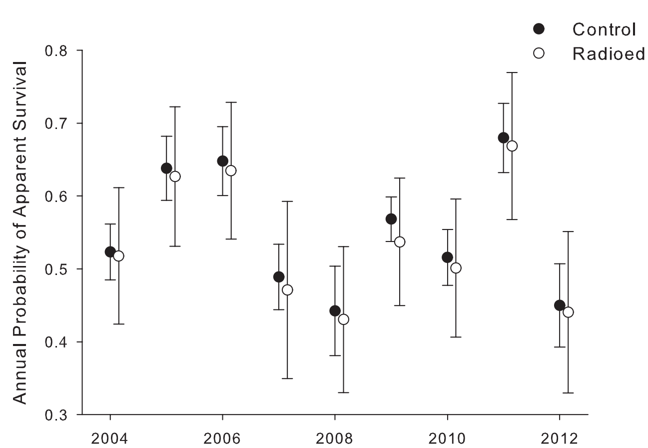

FIGURE 3. Probabilities of apparent annual survival (φ) of Greater Sage-Grouse equipped with a radio collar (radioed) and not so equipped (control) in Eureka County, Nevada, 2003–2012. Error bars represent standard errors (SE) of model-averaged estimates of φ.

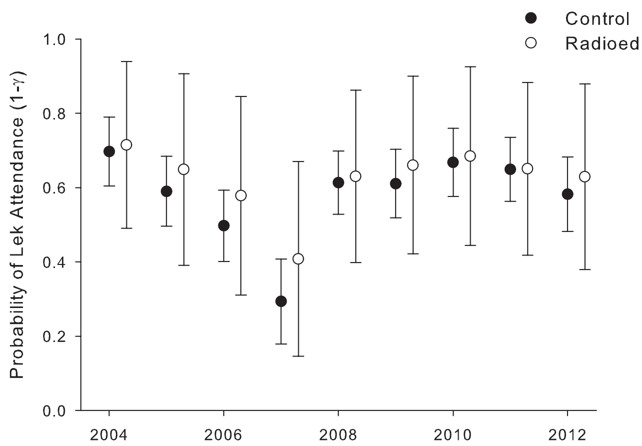

FIGURE 4. Probabilities of annual lek attendance ($1-\gamma$) for Greater Sage-Grouse equipped with a radio collar (radioed) and not so equipped (control) in Eureka County, Nevada, 2003–2012. Error bars represent standard errors (SE) of model averaged estimates of γ.

Short-term observational studies are not able to differentiate between a perceived source of environmental variation and the radio-collar bias on detection at a lek.

Pyrah (1970) reported that poncho-markers, which also attach around a bird's neck, interfere with a male's ability to inflate and deflate its specialized esophageal air sacs, a critical component of its courtship display (Clarke et al. 1942, Honess and Allred 1942, Wiley 1973, Krakauer et al. 2009). This difficulty may increase the costs of an already costly behavior (Vehrencamp et al. 1989) or decrease the attractiveness of the male's vocalizations to females and the effectiveness of these vocalizations in competition among males for breeding territories. Further studies are needed to determine whether other species of grouse with esophageal air sacs (i.e., *Tympanuchus* and *Dendragapus* spp.) respond similarly to radio collars.

To our knowledge this is the first published report of a negative effect of radio collars on sage-grouse behavior, but it adds to the growing literature of adverse effects of radio transmitters on birds (Barron et al. 2010, White et al. 2013). Other studies have detected effects of radio collars on survival or reproductive success of gallinaceous birds. Rothenmaier (1979) reported lower survival of radio-marked female sage-grouse, but that work used an orange radio transmitter with reflective solar panels, which likely increased the birds' visibility to predators. Additionally, radio collars have been associated with lower survival in the Sharp-tailed Grouse (*Tympanuchus phasianellus*; Marks and Marks 1987), lower breeding success in the Black Grouse (*Tetrao tetrix;* Caizergues and Ellison 1998), lower survival and breeding success in female Ring-necked Pheasants (*Phasianus colchicus*; Venturato et al. 2009), lower survival in female Gray Partridges (*Perdix perdix*; Bro et al. 1999), and lower survival of male Rock Ptarmigans (*Lagopus muta*; Cotter and Gratto 1995).

TABLE 1. Performance of robust-design capture–mark–recapture models of survival (φ), temporary emigration from the breeding area (γ), capture (p), and probability of recapture (c) of male Greater Sage-Grouse in Eureka County, Nevada, 2003–2012. Models including "Radio" effects differentiated males fitted with radio collars from control males without them.

Model[a]	K	$\Delta QAIC_c$[b]	w_i	Deviance
ϕ(Temp), $\gamma(N)$, $p{\sim}c$(Base + Radio($t+1$) + Age)	19[c]	0.00	0.45	2537.33
ϕ(Temp), $\gamma(N$ + Radio), $p{\sim}c$(Base + Radio($t+1$) + Age)	20	1.74	0.19	2537.02
ϕ(Temp + Radio), $\gamma(N)$, $p{\sim}c$(Base + Radio($t+1$) + Age)	20	1.94	0.17	2537.22
ϕ(Temp), $\gamma(N$ + Radio), $p{\sim}c$(Base + Age)	19	4.61	0.04	2541.91
ϕ(Temp + Radio), $\gamma(N)$, $p{\sim}c$(Base + Age)	19	6.03	0.02	2543.34
ϕ(Temp), $\gamma(N)$, $p{\sim}c$(Base + Age)	18	8.67	0.01	2548.02
ϕ(Temp), $\gamma(N)$, $p{\sim}c$(Base + Radio(t) + Age)	19	10.48	0.00	2547.79
ϕ(Temp), $\gamma(N)$, $p{\sim}c$(Base)	17	10.90	0.00	2552.11
ϕ(Temp + Age), $\gamma(N)$, $p{\sim}c$(Base)	18	12.50	0.00	2551.67
ϕ(Temp), $\gamma(.)$, $p{\sim}c$(Base)	16	12.84	0.00	2556.10
$\phi(.)$, $\gamma(N)$, $p{\sim}c$(Base)	16	12.92	0.00	2556.18
ϕ(Temp), $\gamma(N$ + Age), $p{\sim}c$(Base)	18	12.93	0.00	2552.10
$\phi(.)$, $\gamma(.)$, $p{\sim}c$(Base)	15	13.79	0.00	2559.09
$\phi(.)$, $\gamma(.)$, p, $c(.)$	4	87.97	0.00	2655.55

[a]Annual variation in φ was constrained by an index of average maximum summer temperature (Temp); γ was modeled under the assumption that temporary emigration was random ($\gamma'' = \gamma'$) and constrained with an estimate of males' lek attendance from the year prior (N). Our base model of detection parameters constrained p and c to a common intercept with additive variation between the parameters, which allowed for p and c to vary among primary (year) and secondary (month) intervals by a constant amount. Age denotes the age of an individual upon original capture, Radio denotes an effect of radio collar, and (.) denotes constancy over time.
[b]$QAIC_c$ values are reported to account for extrabinomial dispersion in the data.
[c]Minimum value of $QAIC_c = 2575.83$

Other studies have reported no effects of radio collars on survival of Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*; Hagen et al. 2006), of female Ring-necked Pheasants (Marcstrom et al. 1989) or breeding success and survival of females in the Red Grouse (*Lagopus lagopus scotica*; Thirgood et al. 1995).

We suggest that researchers should exercise caution when designing studies or analyzing data on radio-collared male sage-grouse. Researchers interested in estimating demographic rates or behavior patterns of male grouse can use a capture–mark–recapture framework without having to attach radios (e.g., Hagen et al. 2005, Nooker and Sandercock 2008, Blomberg et al. 2012). Because our analysis was able to investigate the effects of radio collars on the breeding behavior and survival of male sage-grouse only, we cannot make inferences about general patterns of habitat use or demographics of females, both of which currently require radio or satellite telemetry to be monitored effectively. Although the potential of these techniques has yet to be realized, advances in telemetry with smaller next-generation passive integrated transponder tags, as well as spatial data generated from microphone arrays, may offer new methods for collection of various types of data on the demography, behavior, and movement of terrestrial wildlife (Boatman et al. 1998, Mennill et al. 2012a, b, Walter et al. 2012).

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