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Research Article

Greater Sage-Grouse Juvenile Survival in Utah

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ABSTRACT Greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) adult hen and juvenile survival have been shown to have significant influence on population growth rates. However, assessing the sensitivity of population growth rates to variability in juvenile survival has proven difficult because of limited information concerning the potentially important demographic rate. Sage-grouse survival rates are commonly assessed using necklace-type radio transmitters. Recent technological advances have lead to increased interest in the deployment of dorsally mounted global positioning system (GPS) transmitters for studying sage-grouse ecology. However, the use of dorsally mounted transmitters has not been thoroughly evaluated for sage-grouse, leading to concern that birds fitted with these transmitters may experience differential mortality rates. We evaluated the effect of transmitter positioning (dorsal vs. necklace) on juvenile sage-grouse survival using a controlled experimental design with necklace-style and suture-backpack very high frequency (VHF) transmitters. To evaluate the effects of temporal variation, sex, and transmitter type on juvenile sage-grouse survival, we monitored 91 juveniles captured in south-central Utah from 2008 to 2010. We instrumented 19 females with backpacks, 14 males with backpacks, 39 females with necklaces, and 19 males with necklaces. We used Program MARK to analyze juvenile survival data. Although effects were only marginally significant from a statistical perspective, sex ($P = 0.103$) and transmitter type ($P = 0.09$) were deemed to have biologically meaningful impacts on survival. Dorsally mounted transmitters appeared to negatively affected daily survival ($\beta_{\text{transmitter type}} = -0.55$, SE = 0.32). Temporal variation in juvenile sage-grouse daily survival was best described by a quadratic trend in time, where daily survival was lowest in late September and was high overwinter. An interaction between the quadratic trend in time and year resulted in the low point of daily survival shifting within the season between years (27 vs. 17 Sep for 2008 and 2009, respectively). Overall (15 Aug–31 Mar) derived survival ranged 0.42–0.62 for females and 0.23–0.44 for males. For all years pooled, the probability death was due to predation was 0.73, reported harvest was 0.16, unreported harvest was 0.09, and other undetermined factors was 0.02. We observed 0% and 6.8% crippling loss (from hunting) in 2008 and 2009, respectively. We recommend the adoption of harvest management strategies that attempt to shift harvest away from juveniles and incorporate crippling rates. In addition, future survival studies on juvenile sage-grouse should use caution if implementing dorsally mounted transmitters because of the potential for experimental bias. © 2014 The Wildlife Society.

KEY WORDS *Centrocercus urophasianus*, crippling, greater sage-grouse, harvest, juvenile, radio-telemetry, survival, unreported harvest.

Wildlife managers require better information regarding the factors affecting greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) population growth to optimize the effect of management actions on species conservation. Taylor et al. (2012) argued that in the absence of quantitative data regarding population-specific mortality factors, management actions should focus ultimately on increasing hen and chick survival. However, they recognized that the lack of reliable estimates of juvenile survival may have resulted in the importance of this demographic rate being under emphasized in their analysis. Johnson and Braun (1999) previously concluded that both adult and juvenile survival were the demographic parameters most limiting to population growth for sage-grouse. Although a substantial amount of information is available concerning population dynamics of adults (Crawford et al. 2004), a gap remains range-wide regarding the dynamics of juvenile sage-grouse (e.g., survival, dispersal, predation, recruitment; Crawford et al. 2004, Beck et al. 2006, Taylor et al. 2012).

Stakeholders have expressed concern regarding the possible impacts of harvest on sage-grouse populations (Connelly et al. 2004) despite the lack of evidence to suggest that current hunting regulations pose a long-term risk to sage-grouse conservation (Reese and Connelly 2011). However, few studies have examined the effects of hunting on sage-grouse populations (Connelly et al. 2000, 2003, 2004; Reese and Connelly 2011). Reese and Connelly (2011) concluded

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appropriate harvest rates were 5–10% of the fall population. A complication in setting appropriate harvest rates is that relatively few studies have addressed the effects of crippling losses in upland gamebird populations. Those that have studied crippling losses have used varying methods and definitions making comparison and accuracy difficult to assess (see Haines et al. 2006).

Technological advances have resulted in the development and miniaturization of global positioning system (GPS) packages for use on avian species. Many GPS packages are mounted dorsally on avian species. Transmitter-type and method of attachment may constitute a potential source of experimental bias if they result in altered behavior or survival rates. Burkepile et al. (2002) demonstrated that small (<2 g) suture-on backpack transmitters were an effective means of monitoring sage-grouse chicks. Numerous authors have reported adverse effects of backpack-style transmitters on waterfowl (Pietz et al. 1993, Dzus and Clark 1996, Fleskes 2003, Robert et al. 2006) and gamebirds (Small and Rusch 1985, Marcström et al. 1989, Connelly et al. 2003). However, many authors attribute the adverse effects of backpack-style transmitters to the attachment harness, not the dorsal positioning of the transmitter. Some authors (Höfle et al. 2004, Conner et al. 2006) have incorporated acclimatization periods into their studies to mitigate potential effects of radio-marking individuals. Conversely, Holt et al. (2009) concluded the best estimates of survival are derived without the use of an acclimatization period.

The purpose of our research was to evaluate juvenile sage-grouse daily survival rates. Specifically, we assessed cause-specific mortality (e.g., predation, harvest) and tested the hypotheses that 1) overwinter survival was high, 2) mortality peaked in fall, 3) males had lower daily survival rates, and 4) dorsal orientation of transmitters reduced survival.

STUDY AREA

The study was conducted on Parker Mountain in south-central Utah. Parker Mountain lies at the southern edge of the sage-grouse range (Schroeder et al. 2004). Elevation ranges from 2,200 m to 3,000 m and rises in elevation gradually from east to west. Parker Mountain experiences 65–80 frost-free days and receives 40–50 cm of precipitation annually, most of which occurs during the dormant season as snow (60%), and the remainder as rain in the late summer (Jaynes 1982). The vegetation was primarily black sagebrush (*Artemisia nova*) on ridges and mountain big sagebrush (*A. tridentata vaseyana*) in the swales. Quaking aspen (*Populus tremuloides*) clones were present at higher elevations. Pinyon pine (*Pinus edulis*) and juniper (*Juniperus* spp.) occurred at lower elevations. Golden eagles (*Aquila chrysaetos*), weasels (*Mustela* spp.), badgers (*Taxidea taxus*), and coyotes (*Canis latrans*) are sage-grouse predators that occur on Parker Mountain. The study area consisted of lands managed by the Utah School and Institutional Trust Lands Administration, the Bureau of Land Management, and United States Forest Service. These agencies managed 46% (43,745 ha), 44% (42,643 ha), and 9% (8,327 ha) of the study area, respectively. Private lands accounted for 1% (1,363 ha) of the study area. The primary land use was cattle and sheep grazing. Big game and upland bird hunting, primarily sage-grouse, were important recreational uses. Because of the high degree of public ownership, Parker Mountain affords open public access.

The sage-grouse hunting seasons in 2008 and 2009 were 27 September–12 October and 26 September–11 October, respectively. In 2008, the Utah Division of Wildlife Resources (UDWR) issued 370, 2-bird permits on a first-come first-serve basis for the Parker Mountain unit. In 2009, the UDWR issued 265 2-bird permits on a draw basis.

METHODS

We captured juvenile birds using night spotlighting (Giesen et al. 1982, Wakkinen et al. 1992, Connelly et al. 2003) 1 August–30 September, annually. Capture effort ceased 2 days prior to the sage-grouse hunting season. Our capture effort concentrated on locations of radio-marked brood hens and areas where bird dogs detected broods. Upon capture, we distinguished adults from juveniles using characteristics of the first secondary flight feather (Beck et al. 1975). We ascertained sex in the field based on primary length and molt patterns (Beck et al. 1975 adapted from Eng 1955). For a subset of individuals ($n = 60$), we later confirmed sex through DNA analysis (Guttery et al. 2013*b*). We defined juvenile birds as young-of-the-year individuals >80 days of age through the beginning of the following breeding season. We chose 80 days because at this age sage-grouse consisted of enough body mass for instrumentation with adult-sized transmitters.

We fitted juveniles with suture-on backpack or necklace-style very high frequency (VHF) transmitters (American Wildlife Enterprises, Monticello, FL). All transmitters weighed 15 g and did not exceed 3% of the individual's body weight (Thirgood et al. 1995). The transmitters were battery powered and equipped with mortality switches (activated after 12 hours of inactivity). We randomly assigned the type of transmitter an individual received. We fitted backpack transmitters using the method described by Burkepile et al. (2002); however, we used a larger radio package and 2/0 suture thread. Suture-on backpack and necklace-style transmitters were physically identical, with the exception of mounting holes, to ensure the transmitter type comparison was between the positioning of the transmitter (i.e., necklace vs. dorsal). The study protocols were approved by the Utah State University Institutional Animal Use and Care Committee (IACUCC Number 942R).

We confirmed survival status remotely using the pulse signal emitted by the transmitters. We monitored radio frequencies from the ground daily from August–December, but did not always detect signals. During December–April, we monitored radio frequencies twice each month, largely from a fixed wing aircraft. Upon detection of mortality signals, we immediately located individuals. We classified mortalities into 4 groups: reported harvest, unreported harvest, predation, and other, using evidence from the site (e.g., marks on transmitter, feather patterns, tracks).

Reported harvests were events reported by hunters to either the UDWR or directly to investigators. We deemed a mortality to be an unreported harvest only if irrefutable evidence existed (e.g., lead shot in carcass, obvious shotgun wounds during necropsy, field dressed carcass). We defined crippled birds as a subset of unreported harvest. Cripples were sage-grouse found dead in the field with the carcass intact and with obvious shot wounds detected upon necropsy. We calculated the proportion of loss from crippling by hunters according to equation 6 in Haines et al. (2006).

To assess mortality causes and acclimatization to instrumentation period, we calculated maximum likelihood estimates and profile likelihood confidence intervals. We calculated mortality causes as conditional probabilities for each cause given death occurred. To assess the need or validity for an acclimation period, we calculated probability of mortality for the first 30 days post-capture (periods of 0–10, 11–20, and 21–30 days) for our sample of captured juveniles.

We used the nest survival model (Dinsmore et al. 2002) implemented in Program MARK (White and Burnham 1999) to estimate daily survival. We used the logit link function in all models. If an individual went missing during the study, we right-censored it on its last known survival date. We standardized time using 15 August as Day 1 and numbering sequentially through 31 March. For study Days 1–61, 1 model day equaled 1 calendar day. We compressed study Days 62–111 and 112–231 such that 1 model day equaled 10 and 15 calendar days, respectively. We compressed time in models to reflect differences in monitoring effort as a consequence of assumptions regarding survival (e.g., low winter mortality), and we explicitly accounted for the compression in Program MARK by adjusting interval lengths. We ranked models using Akaike's Information Criterion adjusted for sample size (AIC_c; Akaike 1973, Burnham and Anderson 2002), and we considered models with $\Delta\mathrm{AIC}_c \leq 2$ equally supported by the data (Burnham and Anderson 1998). We modeled variation in survival from 15 August to 31 March as a function of sex, year, transmitter type, and temporal trends. We abbreviate quadratic trends (i.e., $\mathrm{T} + \mathrm{T}^2$) in time as T^2. We used a 2-step modeling approach in which we first evaluated models with 7 different time dynamics (Table 1) and then included the competing time models ($\Delta\mathrm{AIC}_c \leq 2$) in our final analysis of covariates including sex, year, and transmitter type (Table 1). We used likelihood ratio tests to differentiate between competing models that were nested. We used the delta method (Seber 1982:7–9) to derive standard error estimates when daily survival rates were combined into longer intervals (e.g., fall, winter, total) of survival. To calculate confidence intervals for estimates derived using the delta method, we transformed estimates to the logit scale then back-transformed to the probability scale to ensure estimates were appropriately bounded at 0 and 1. For derived estimates and in our modeling framework we defined fall as the period from 15 August to 1 December, winter as 2 December to 31 March, and total as 15 August to 31 March.

Table 1. Two sets of a priori candidate models that include either time (time-structured models) or covariates (covariate models) used to evaluate daily survival of juvenile greater sage-grouse (*Centrocercus urophasianus*) on Parker Mountain, Utah, USA, 2008–2009. We used combinations of these models both additively and interactively to assess 29 candidate models of juvenile survival.

Time-structured models[a]	Covariate models
Constant	Transmitter type
Full Time Dependent	Sex
$\mathrm{Linear}_{\mathrm{fall}} + \mathrm{Constant}_{\mathrm{winter}}$	Year
$\mathrm{Constant}_{\mathrm{fall}} + \mathrm{Constant}_{\mathrm{winter}}$	Sex + transmitter type
$\mathrm{Quadratic}_{\mathrm{fall}} + \mathrm{Constant}_{\mathrm{winter}}$	Year + sex
Quadratic	Year + transmitter type
$\mathrm{Constant}_{\text{Aug–Open of Hunting Season}} + \mathrm{Constant}_{\text{Hunting Season}} + \mathrm{Constant}_{\text{14 days post Hunting Season}} + \mathrm{Constant}_{\text{Last week in Oct–30 Nov.}} + \mathrm{Constant}_{\mathrm{winter}}$	Year + sex + transmitter type

[a] fall = 15 Aug–30 Nov; winter = 1 Dec–31 Mar; models with no subscripts indicate we modeled the entire study period (15 Aug–31 Mar) similarly.

RESULTS

We captured 91 juvenile sage-grouse (8 female backpack, 7 male backpack, 10 female necklace, 5 male necklace in 2008; and 11 female backpack, 7 male backpack, 29 female necklace, 14 male necklace in 2009). Our sex assignment using Beck et al. (1975) was later confirmed 100% accurate ($n = 30$) by subsequent DNA analysis. However, in 5 instances (all females) 1 of the 2 primary length measurements (length of primary 10) for sex classification was inconclusive. Furthermore, at capture, molt had not progressed enough to implement the methods outlined by Beck et al. (1975). In these cases, we relied on DNA to classify sex. Probability of mortality was not higher during initial periods following instrumentation (Table 2). Consequently, we did not include an acclimatization period in the survival analyses.

We recorded 17 and 27 mortalities in 2008–2009 and 2009–2010, respectively. We did not record mortalities 4 January 2009–31 March 2009 (n alive = 7) or 1 December 2009–31 March 2010 (n alive = 27). The average number of model days (i.e., compressed time) from last live signal to mortality detection was 7.4 model days (SE = 1.02). The conditional probability of death was highest for predation and harvest (reported and unreported) contributed to mortality (Table 3). Harvest rate was 26.9% in 2008; 23.1% were reported as harvested and 3.9% were harvested but not reported (bird was found dressed in the field). Harvest rate was 9.3% in 2009; 2.3% were reported as harvested, and 7.0% were harvested but not reported (all were cripples).

We considered 2 time structure models to be competing (T^2 = top model and $\mathrm{T}^2_{\mathrm{fall}} + \mathrm{constant}_{\mathrm{winter}}$ $\Delta\mathrm{AIC}_c = 2.02$) from our initial model evaluation step (1 other model was $\Delta\mathrm{AIC}_c = 5.1$ and all others were $\geq \Delta\mathrm{AIC}_c = 26.73$). We then combined these 2 time structures with our covariates into our 29 a priori candidate model set (Table 4). We considered 4

Table 2. Probabilities of death and 95% confidence intervals during the initial (i.e., acclimatization) period compared to 2 later periods in juvenile greater sage-grouse (*Centrocercus urophasianus*) on Parker Mountain, Utah, USA, 2008–2009.

Days post capture	2008			2009			Both years		
	No. at risk	Probability of death	95% CI[a]	No. at risk	Probability of death	95% CI[a]	No. at risk	Probability of death	95% CI[a]
0–10	30	0.100	0.026–0.239	61	0.098	0.04–0.189	91	0.099	0.049–0.171
11–20	27	0.296	0.148–0.482	55	0.073	0.023–0.161	82	0.134	0.072–0.219
21–30	19	0.158	0.042–0.36	51	0.137	0.061–0.249	70	0.143	0.074–0.237

[a] Profile likelihood confidence interval.

Table 3. Probability death was due to specific causes for juvenile greater sage-grouse (*Centrocercus urophasianus*) on Parker Mountain, Utah, USA, 2008–2010.

Mortality causes	2008–2009		2009–2010		Combined	
	Probability of death	95% CI[a]	Probability of death	95% CI[a]	Probability of death	95% CI[a]
Reported harvest	0.353	0.158–0.589	0.037	0.002–0.153	0.159	0.072–0.285
Unreported harvest	0.059	0.004–0.234	0.111	0.029–0.263	0.091	0.029–0.199
Predation	0.588	0.354–0.797	0.815	0.643–0.929	0.727	0.585–0.844
Other	0		0.037	0.002–0.153	0.023	0.001–0.096

[a] Profile likelihood confidence interval.

survival models to be competitive ($\Delta \mathrm{AIC}_c < 2$; Table 4). Based on likelihood ratio tests, we considered sex ($\chi^2_1 = 2.654$, $P = 0.103$) and transmitter type ($\chi^2_1 = 2.873$, $P = 0.09$) to have had marginal effects on juvenile daily survival rates (Table 5). Consequently, we considered the general model biologically meaningful. The general model consisted of a quadratic relationship between time (T^2) elapsed from capture and probability of daily survival, an interaction between time and year, and an additive effect of both sex and transmitter. We did not model average parameter estimates because marginal evidence existed for an experimentally introduced source of bias in survival due

Table 4. Models evaluated in Program MARK to estimate juvenile greater sage-grouse (*Centrocercus urophasianus*) daily survival on Parker Mountain, Utah, USA, 2008–2010. AIC_c, Akaike's Information Criterion adjusted for sample size; $\Delta\mathrm{AIC}_c$, difference in AIC_c values between each model and the best model; ω_i, AIC_c weight; Model likelihood = ($\omega_i/\omega_{\text{best model}}$); *K*, number of parameters.

Model[a,b]	AIC_c	$\Delta\mathrm{AIC}_c$	ω_i	Model likelihood	*K*	Deviance
$\mathrm{T}^2 \times \text{year} + \text{sex} + \text{type}$	307.31	0.00	0.27	1.00	7	293.27
$\mathrm{T}^2 \times \text{year} + \text{type}$	307.95	0.65	0.20	0.72	6	295.92
$\mathrm{T}^2 \times \text{year} + \text{sex}$	308.17	0.86	0.18	0.65	6	296.14
$\mathrm{T}^2 \times \text{year}$	308.98	1.67	0.12	0.43	5	298.96
$\mathrm{T}^2 + \text{year} + \text{sex} + \text{type}$	311.89	4.58	0.03	0.10	6	299.86
$\mathrm{T}^2 + \text{year} + \text{type}$	312.03	4.73	0.03	0.09	5	302.01
$\mathrm{T}^2 \times \text{type}$	312.58	5.28	0.02	0.07	5	302.56
$\mathrm{T}^2 + \text{sex} + \text{type}$	312.61	5.31	0.02	0.07	5	302.59
$\mathrm{T}^2 + \text{year} + \text{sex}$	312.85	5.54	0.02	0.06	5	302.83
$\mathrm{T}^2_{\text{fall}} + \text{sex} + \text{type} + \text{constant}_{\text{winter}}$	312.94	5.63	0.02	0.06	5	302.92
$\mathrm{T}^2 + \text{year}$	313.04	5.73	0.02	0.06	4	305.02

[a] T^2 = quadratic trend in time (i.e., $\mathrm{T} + \mathrm{T}^2$); type = transmitter type; fall = 15 Aug–30 Nov; winter = 1 Dec–31 Mar; models with no time subscripts indicate we modeled the entire study period (15 Aug–31 Mar) similarly.

[b] Models with $\omega_i \leq 0.01$ not shown: $\mathrm{T}^2 + \text{type}$; $\mathrm{T}^2_{\text{fall}} + \text{year} + \text{sex} + \text{type} + \text{constant}_{\text{winter}}$; $\mathrm{T}^2_{\text{fall}} + \text{year} + \text{type} + \text{constant}_{\text{winter}}$; $\mathrm{T}^2 \times \text{sex} + \text{type}$; $\mathrm{T}^2_{\text{fall}} + \text{year} + \text{sex} + \text{constant}_{\text{winter}}$; $\mathrm{T}^2_{\text{fall}} + \text{year} + \text{constant}_{\text{winter}}$; $\mathrm{T}^2 + \text{sex}$; $\mathrm{T}^2_{\text{fall}} + \text{type} + \text{constant}_{\text{winter}}$; $\mathrm{T}^2_{\text{fall}} + \text{sex} + \text{constant}_{\text{winter}}$; T^2; $\mathrm{T}^2_{\text{fall}} \times \text{year} + \text{sex} + \text{type} + \text{constant}_{\text{winter}}$; $\mathrm{T}^2_{\text{fall}} \times \text{year} + \text{type} + \text{constant}_{\text{winter}}$; $\mathrm{T}^2_{\text{fall}} \times \text{year} + \text{sex} + \text{constant}_{\text{winter}}$; $\mathrm{T}^2 \times \text{sex}$; $\mathrm{T}^2_{\text{fall}} \times \text{type} + \text{constant}_{\text{winter}}$; $\mathrm{T}^2_{\text{fall}} \times \text{year} + \text{constant}_{\text{winter}}$; $\mathrm{T}^2_{\text{fall}} \times \text{sex} + \text{constant}_{\text{winter}}$; $\mathrm{T}^2_{\text{fall}} + \text{constant}_{\text{winter}}$.

Table 5. Likelihood ratio test of top 4 models evaluated for juvenile survival (*S*) of greater sage-grouse (*Centrocercus urophasianus*) on Parker Mountain, Utah, USA, 2008–2010.

General model[a]	Reduced model[a]	χ^2	df	*P*	Hypothesis tested
$S(\mathrm{T}^2 \times \text{year} + \text{sex} + \text{type})$	$S(\mathrm{T}^2 \times \text{year} + \text{type})$	2.65	1	0.103	Sex-specific survival
$S(\mathrm{T}^2 \times \text{year} + \text{sex} + \text{type})$	$S(\mathrm{T}^2 \times \text{year} + \text{sex})$	2.87	1	0.090	Transmitter-specific survival
$S(\mathrm{T}^2 \times \text{year} + \text{sex} + \text{type})$	$S(\mathrm{T}^2 \times \text{year})$	5.69	2	0.058	Sex- and transmitter-specific survival

[a] T^2 = quadratic trend in time, type = transmitter type.

to transmitter type. Because transmitter type negatively influenced survival, we consider this approach to produce conservative survival estimates.

Female survival rates appeared to be higher (odds ratio = 1.7, 90% CI = 1.0–2.88) than males, and backpack radios appeared to negatively (odds ratio = 0.58, 90% CI = 0.34–0.98) affect survival (Tables 5 and 6). Survival was lower in 2008 than in 2009. In 2009, daily survival was lowest around 17 September, whereas in 2008 daily survival was lowest around 27 September (Figs. 1 and 2). Derived survival estimates varied 0.23–0.61, 0.33–0.62, and 0.69–0.98 by sex and year for total, fall, and winter, respectively (Table 7). We did not detect an acute transmitter-specific effect on mortality (i.e., mortality rates by transmitter type during all post-capture periods overlapped; Table 8).

DISCUSSION

The debate over radio handicapping of birds (see Guthery and Lusk 2004, Terhune et al. 2007) has led some researchers to question the use of radio transmitters for assessing survival. Using a controlled experimental design, we provide new evidence of differential survival rates by transmitter attachment type (dorsal vs. necklace) for juvenile sage-grouse. Although both necklace-style (Connelly et al. 1993, 2000; Schroeder and Robb 2003; Beck et al. 2006; Doherty et al. 2008) and harness-style backpack (Eng and Schladweiler 1972, Connelly et al. 1988) transmitters have been used to study sage-grouse, our results indicate that dorsal positioning of transmitters reduces survival. Our findings support additional studies that demonstrated other dorsal attachment methods (i.e., harness-style backpack transmitters) affect survival of gamebirds (Small and Rusch 1985, Marcström et al. 1989) and waterfowl (Pietz et al. 1993, Rotella et al. 1993, Ward and Flint 1995, Dzus and Clark 1996, Robert et al. 2006). However, some researchers have attributed the negative effect to the harness rather than the dorsal positioning of the transmitter. Several authors concluded radio-tags can cause adverse effects to individuals (Marks and Marks 1987, Caizergues and Ellison 1998, Bro et al. 1999), and conversely others have demonstrated appropriate (e.g., weight, size, color, etc.) radio packages have no measurable effects on survival of gamebirds (Boag et al. 1973, Hines and Zwickel 1985, Thirgood et al. 1995, Hagen et al. 2006, Terhune et al. 2007). Our results outline differential effects by attachment method and the need to consider appropriate positioning of transmitters on study subjects. We did not document any juvenile mortalities during winter of either year regardless of transmitter type, and consequently the negative effect of backpack-type transmitters relative to necklace-style transmitters appears to have resulted in increased mortality during the fall. Caution should be exercised when extending our results to other dorsal attachment methods (e.g., leg loop harness) for which reduced survival has not been explicitly tested.

Table 6. Parameter estimates for the model of juvenile greater sage-grouse (*Centrocercus urophasianus*) daily survival on Parker Mountain, Utah, USA, 2008–2010.

Parameter	β	SE	90% CI Lower	90% CI Upper
Intercept	7.77	1.15	5.88	9.66
Year	1.21	0.85	−0.19	2.61
Sex	0.53	0.32	0.00	1.06
Transmitter type	−0.55	0.32	−1.08	−0.02
Time	−2.41	0.61	−3.41	−1.41
Time^2	0.35	0.08	0.22	0.48
Year × time^2	−0.08	0.03	−0.13	−0.03

Conflicting reports in the literature regarding the effect of marking method on gamebirds may be a consequence of capture myopathy, which can affect gamebird survival (Spraker et al. 1987, Nicholson et al. 2000, Höfle et al. 2004, Abbott et al. 2005, Conner et al. 2006). We did not control for the effect of handling time on backpack versus necklace birds, which could have influenced capture myopathy (Nicholson et al. 2000). Fitting a backpack transmitter required a longer handling time, but we did not document the actual difference in time. Despite our inability to formally evaluate the effect of handling time on survival, we contend any adverse effects of prolonged handling would have likely caused an acute effect on survival. However, our evaluation did not detect an acute transmitter-specific effect on survival (Table 8). Although capture method can affect capture myopathy in mallards (*Anas platyrhynchos*; Bollinger et al. 1989, Dabbert and Powell 1993) our method did not appear to cause acute mortality (Tables 2 and 8).

Survival estimates for juvenile sage-grouse are largely lacking (Taylor et al. 2012). On Parker Mountain, juvenile sage-grouse exhibited lower survival rates than reported by Beck et al. (2006), but similar juvenile female survival rates in fall, winter, and overall to those reported by Wik (2002). We found marginal evidence to support differential survival by sex similar to Swenson (1985) but in contrast to Beck et al. (2006). Our model indicated that in 2008–2009, the lowest survival was later in the season when compared to 2009–2010. The higher harvest rates in 2008–2009 in conjunction with later movements (Caudill 2011) to wintering areas, could have contributed to the lower overall survival rate. During our study, the majority of sage-grouse mortalities occurred during fall (15 Aug–1 Dec), which is a trend similar to the seasonal patterns reported by others (Wik 2002, Beck et al. 2006, Anthony and Willis 2009). Juvenile birds on Parker Mountain exhibited high overwinter survival, and severe winter weather did not appear to affect survival based on the 2 winters in this study. In 2009–2010, survival was high (0.98 and 0.97 for necklace-only females and males, respectively) even though winter snow depth was above average (Caudill et al. 2013), whereas in 2008–2009, winter survival was relatively low (0.8 and 0.69 for necklace-only females and males, respectively), and snow depth was below average (Caudill et al. 2013). Our findings agree with Zablan et al. (2003) but not Moynahan et al. (2006) who reported 1 severe winter, particularly a single storm, during the course of their 3-year study had a large negative impact on survival. Reported differences for the impact of winter weather may

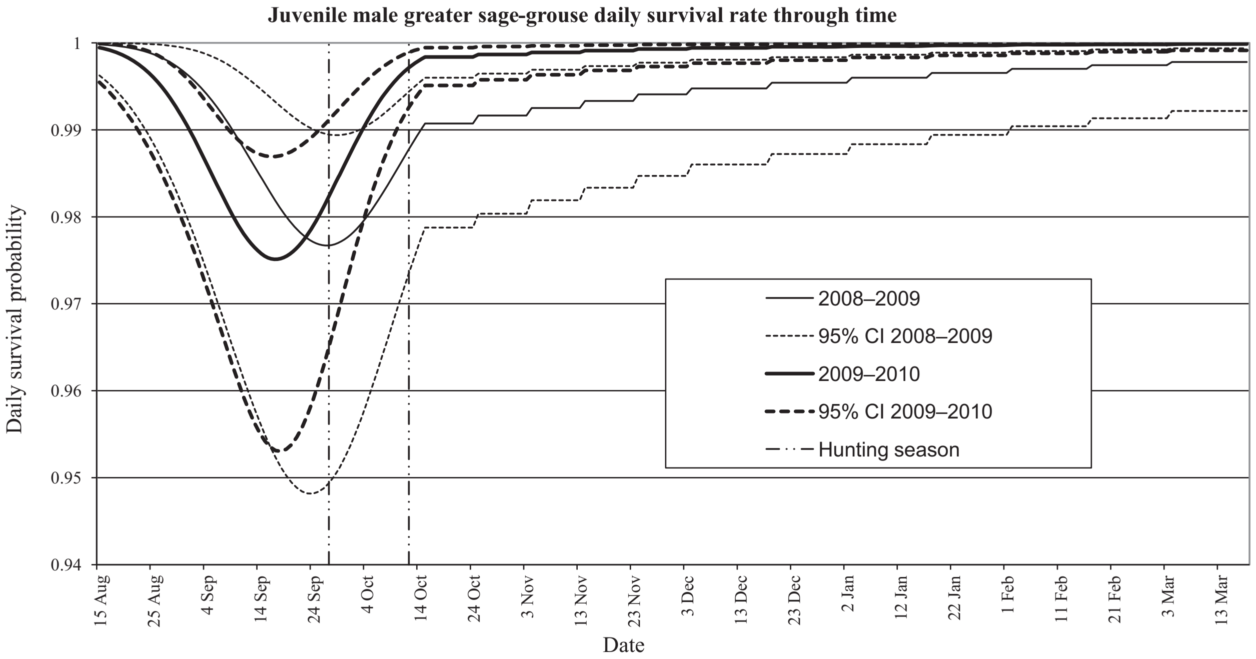

Figure 1. Juvenile male greater sage-grouse (*Centrocercus urophasianus*), fitted with necklace style radios, daily survival rate by day of study on Parker Mountain, Utah, USA, 2008–2010.

reflect differences in availability and quality of wintering habitats. The availability of lower elevation winter habitat sites in our study could have mitigated the effect of heavy snowfall (Caudill et al. 2013).

Sage-grouse may have evolved winter survival strategies such that high survival rates are positively correlated with snowpack, particularly in higher elevation habitats with substantial elevation gradients (i.e., migratory populations). As such, timing of transition from fall (i.e., high mortality) to winter survival (i.e., low mortality) strategies has major implications for population dynamics. Food is typically not a limiting factor for most grouse species during winter (Bergerud and Gratson 1988), as evidenced for sage-grouse based on substantial weight gain during winter (Beck and

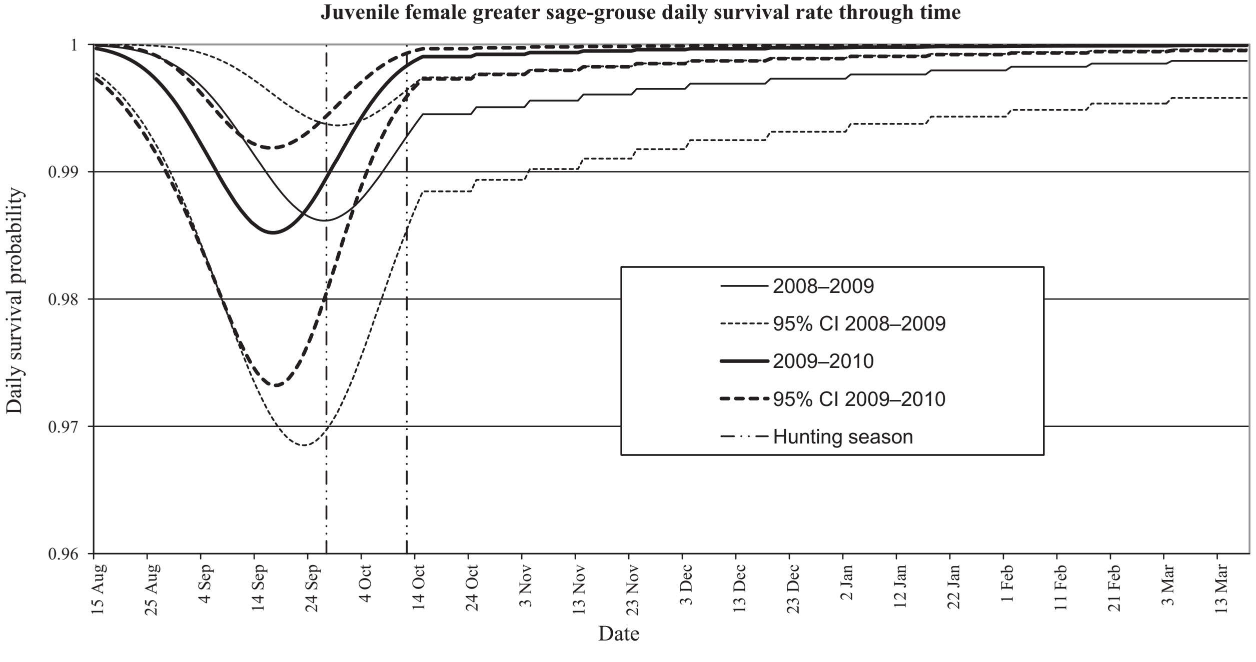

Figure 2. Juvenile female greater sage-grouse (*Centrocercus urophasianus*), fitted with necklace style radios, daily survival rate by day of study on Parker Mountain, Utah, USA, 2008–2010.

Table 7. Estimates of survival (S) for juvenile greater sage-grouse (*Centrocercus urophasianus*) using the model $S(\mathrm{T}^2 \times \text{year} + \text{sex} + \text{transmitter type})$ and only individuals fitted with necklace-type transmitters on Parker Mountain, Utah, USA, 2008–2010. Survival rates are derived estimates using daily survival rates and the delta method.

			Necklace only	
Year	**Sex**	**Season**[a]	***S***	**95% CI**
2008	Female	Total	0.418	0.207–0.665
2008	Female	Fall	0.522	0.299–0.736
2008	Female	Winter	0.802	0.570–0.925
2008	Male	Total	0.228	0.067–0.548
2008	Male	Fall	0.332	0.131–0.621
2008	Male	Winter	0.687	0.371–0.891
2009	Female	Total	0.612	0.448–0.755
2009	Female	Fall	0.623	0.461–0.763
2009	Female	Winter	0.982	0.919–0.966
2009	Male	Total	0.435	0.245–0.647
2009	Male	Fall	0.449	0.258–0.656
2009	Male	Winter	0.969	0.861–0.994

[a] Total = 15 Aug–31 Mar; Fall = 15 Aug–30 Nov; Winter = 1 Dec–31 Mar.

Braun 1978) and high winter survival (see Connelly et al. 2004, this study). Consequently, avoidance of predation is likely the driver of winter population dynamics for most grouse species (i.e., Bergerud and Gratson 1988).

Previous research has shown that snowfall and snowpack influence the timing of migration from summer to wintering habitats (Dunn and Braun 1986), even before snow depth limits food availability in late summer habitats (Bergerud and Gratson 1988), as well as flock size for sage-grouse (Bergerud and Gratson 1988 adapted from Beck 1975, 1977). As such, climatic factors in late fall and winter may influence sage-grouse movement and flocking behaviors such that earlier and deeper snowpack may be conducive to high survival, as observed in our study. One possible explanation for high overwinter survival of sage-grouse could be that snow events result in dispersal and reduce mobility of avian and mammalian predators and alleviate predation pressure on grouse (Murray and Boutin 1991). Furthermore, sage-grouse use snow burrows (Back et al. 1987). Grouse species use snow burrows for both thermoregulation (Korhonen 1980, Marjakangas et al. 1984) and predator avoidance (Bergerud and Gratson 1988). Delayed onset and reduced depth of snow pack as a result of climate change (Mote et al. 2005, Knowles et al. 2006) may pose a threat to sage-grouse conservation by altering seasonal dynamics of sage-grouse such that juvenile survival diminishes (i.e., juveniles persist in fall survival strategy for longer periods of time). Similarly, Guttery et al. (2013*a*) suggest that reductions in snowpack may be a major threat to sage-grouse chick survival.

Although predation was the primary cause of juvenile sage-grouse mortality, non-native or human-subsidized predators are not common on Parker Mountain. Given the largely endemic predator community and contiguity of habitat, predation rates should be within historical levels (Hagen 2011). Consequently, harvest is the remaining mortality metric within the purview of managers. Reported and unreported harvest of sage-grouse varied annually in our study. The estimated crippling rates were 0% in 2008 and 6.8% in 2009, and were similar to those reported for other gamebirds (Braun and Beck 1985, Hoffman 1985, Small et al. 1991, Haines et al. 2006). However, our estimates are minimum values as monitoring effort was intense during the hunting season, but cripples could have been scavenged prior to investigator discovery and misclassified as predation. Dunn and Braun (1986) reported movement of juvenile sage-grouse was tied to snowfall. Earlier movements to the wintering areas in 2009–2010 versus 2008–2009 could have been a result of earlier snowfall events in 2009–2010 (Caudill 2011). Similar to the factors affecting blue grouse (*Dendragapus* spp.) harvest rates reported by Mussehl (1960), variable harvest rates on Parker Mountain could have been influenced by differing stages of the altitudinal migration between years during the hunting seasons. Our results support the need for incorporating crippling and other

Table 8. Mortality rates of juvenile greater sage-grouse (*Centrocercus urophasianus*) by transmitter type for 3 different periods post-capture on Parker Mountain, Utah, USA, 2008–2009.

		2008			2009		
Transmitter type	**Days post capture**	**No. at risk**	**Probability of death**	**95% CI**[a]	**No. at risk**	**Probability of death**	**95% CI**[a]
Backpack	0–10	15	0.067	0.004–0.262	18	0.111	0.019–0.305
Backpack	11–20	13	0.231	0.060–0.495	16	0.063	0.004–0.247
Backpack	21–30	9	0.333	0.096–0.655	15	0.267	0.092–0.515
Necklace	0–10	15	0.133	0.024–0.358	43	0.093	0.030–0.203
Necklace	11–20	12	0.250	0.069–0.528	39	0.154	0.064–0.287
Necklace	21–30	10	0.200	0.036–0.499	33	0.333	0.189–0.502

[a] Profile likelihood confidence interval.

unreported harvest loss when establishing sage-grouse harvest regulations. Further research into the effects of crippling on sage-grouse populations is needed.

Hunters and predators may key on clumped groups of juvenile and successful hen sage-grouse in late fall, and our harvest mortality results support other observations for sage-grouse (Connelly et al. 2000, Wik 2002) and blue grouse (Bendell and Elliot 1967, Redfield 1975). Habitat (Autenrieth 1981, Brøseth and Pedersen 2010), proximity to human access points (Fischer and Keith 1974, Brøseth and Pedersen 2000), and landownership (Small et al. 1991) have been shown to influence Tetraonidae harvest rates. The higher elevation swales of Parker Mountain provide the best brood habitat (Dahlgren et al. 2006), and as a result could lead to the relatively high-observed harvest rates on Parker Mountain due to clumped distributions (Bendell and Elliot 1967, Redfield 1975, Connelly et al. 2000, Wik 2002). Additionally, a majority of high elevation mesic habitats on Parker Mountain are proximal to roads, allowing access by hunters (Caudill 2011) to juveniles in clumped distributions. High accessibility, public ownership, and habitat characteristics pose unique challenges in harvest management, and mitigating actions could be necessary where these conditions cause a propensity towards higher harvest rates.

MANAGEMENT IMPLICATIONS

Our estimates of juvenile sage-grouse survival and factors affecting survival fill a knowledge gap in sage-grouse biology that has been identified as a significant driver of population growth rates. As a result, we provide managers with information to weigh decisions and trade-offs for promoting sage-grouse conservation. Additionally, we present evidence on differential survival by transmitter type that can guide researchers when designing future studies and managers with interpretation of research findings. Further, our results indicated juvenile survival may be more influenced by and susceptible to harvest than originally thought. Consequently, conservative harvest management is likely prudent. Shifting the hunting season to later in the year could allow for juveniles to intersperse with the larger population. Additionally, unreported harvest (mainly crippling) may have a larger impact on sage-grouse than was previously recognized. Our evidence in conjunction with previously published findings suggests managers should take into account an approximately 5% crippling and unreported harvest loss when determining sage-grouse harvest recommendations.

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