

**From:** [Terry Messmer](#)  
**To:** [noreen\\_walsh@fws.gov](mailto:noreen_walsh@fws.gov); [larry\\_crist@fws.gov](mailto:larry_crist@fws.gov)  
**Subject:** FW: Vital Rates and Lek paper  
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**Attachments:** [PM\\_Dy\\_JAE\\_RevisedNov2014.docx](#)  
[Caudilljuvenilesurvival.pdf](#)

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opps

Here you go

Terry

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**From:** Terry Messmer  
**Sent:** Friday, January 09, 2015 12:45 PM  
**To:** [noreen\\_walsh@fws.org](mailto:noreen_walsh@fws.org)  
**Cc:** [michael\\_bean@ios.doi.gov](mailto:michael_bean@ios.doi.gov); [michael\\_anderson@ios.doi.gov](mailto:michael_anderson@ios.doi.gov); Kathleen Clarke; John Harja; [jpalma@blm.gov](mailto:jpalma@blm.gov); [qfbahr@blm.gov](mailto:qfbahr@blm.gov); [larry\\_crist@fws.org](mailto:larry_crist@fws.org); [nkornze@blm.gov](mailto:nkornze@blm.gov); [amatheson@utah.gov](mailto:amatheson@utah.gov)  
**Subject:** Vital Rates and Lek paper

Noreen

Attached please find an advance copy of the vital rate and lek count paper which i attempted to summarize yesterday.

This is at the Journal of Applied Ecology editorial office for the final decision. We are very optimistic it will be published. However, it may have some additional editorial changes, but we do not anticipate these will affect our conclusions.

As soon as we are notified it has been accepted, I will provide the final paper. Thus at this point, I would discourage wide spread distribution. We also believe this work has important implications to the pre-decision range wide modeling efforts regarding the effects of conservation actions on sage-grouse production and abundance. Once published we will follow up with the USFWS and USGS team leads. We have presented this work at the recent WAFWA technical committee meeting held in Elko.

The key point of the paper, it that if we make assumptions or decisions about the factors affecting sage-grouse vital rates based on relatively short term studies, we may overlook more important metrics. Even a meta-analysis based on short term studies can exploit this sampling bias. I used the example of grass height and the effects on nest success. Grass height and nest success are subject to annual sampling bias. Meaning depending on environmental conditions, in a short term study, you can experience wide variation in this parameter.

When we modeled all of the Parker MT vital rate data collected over our long term study, we found that juvenile survival exhibited the greatest potential (elasticity) to affect population growth.

Thus conservation strategies and plans must consider all of the habitats important to the life cycle of sage-grouse. There is no one "smoking gun." The Utah Plan does this.

I included another paper on juvenile survival which provides additional insights.

Please let me know if you have specific questions.

Best

Terry Messmer

1 12 November 2014  
2 David K. Dahlgren  
3 Department of Wildland Resources  
4 College of Natural Resources  
5 Utah State University  
6 5230 Old Main Hill  
7 Logan, UT 84322-5230  
8 [dave.dahlgren@usu.edu](mailto:dave.dahlgren@usu.edu)  
9

10 **Warranted but Precluded: Evaluating Vital-Rate Contributions to Greater Sage-Grouse**

11 **Population Dynamics to Inform Conservation**

12 David K. Dahlgren, Jack H. Berryman Institute, Department of Wildland Resources, Utah State  
13 University, Logan, UT 84322-5230, USA

14 Michael R. Guttery, Department of Forest and Wildlife Ecology, University of Wisconsin,  
15 Madison, WI 53706, USA

16 Terry A. Messmer, Jack H. Berryman Institute, Department of Wildland Resources, Utah State  
17 University, Logan, UT 84322-5230, USA

18 Danny Caudill, Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation  
19 Commission, Gainesville, FL 32601-9044, USA

20 R. Dwayne Elmore, Department of Natural Resource Ecology and Management, Oklahoma State  
21 University, Stillwater, OK 74078-6013, USA

22 Renee Chi, U.S. Department of Interior, Bureau of Land Management, Utah State Office, Salt  
23 Lake City, UT 84101-1345, USA

24 David N. Koons, Department of Wildland Resources and the Ecology Center, Utah State  
25 University, Logan, UT 84322-5230, USA

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## Summary

1. Population life cycle models that identify key demographic vital rates can optimize species conservation efforts. We used a long-term data set of radio-marked greater sage-grouse *Centrocercus urophasianus*, an umbrella species in the sagebrush biome, to determine population dynamics that most influence population change for a species of conservation concern. Thus, policy makers and land managers may proceed with more certainty in management actions that improve populations and this ecosystem.

2. We used data from 180 females constituting 276 annual survival histories (after second year [ASY] females = 136; second year [SY] females = 140), to estimate temporal process (co)variation in vital rates and performed both prospective and retrospective perturbation analysis of a life cycle model. We also compared estimates of the finite population growth rate ( $\lambda$ ) from annual female-based matrices to estimates of  $\lambda$  from male-based lek counts.

3. Our population demonstrated stability during the study period, with a mean  $\lambda$  of 1.0. Post-fledging (ASY, SY, and juvenile) survival contributed most to observed past variation in  $\lambda$  and had the greatest potential to change  $\lambda$  in the future, indicating these vital rates were important determinants of sage-grouse population dynamics. When sampling variation was removed, nest initiation and success variance was much reduced through time, suggesting these vital rates were buffered against environmental stochasticity despite their lower sensitivity and elasticity values, contradicting the theory of demographic buffering.

4. *Synthesis and applications.* Long-term demographic studies can provide increased certainty of the role of conservation actions in ameliorating species conservation threats. Our results suggest that current sage-grouse conservation efforts may need reevaluation prior to an ESA listing decision. There exists a pattern of short-term studies focusing primarily on drivers of

nesting success. Only by considering the species' entire life-cycle can scientists determine critical vital rates for management. For sage-grouse, we recommend conservation approaches that provide adequate large-scale extents of habitat to maintain post-fledging (i.e., ASY, SY, and juvenile) survival, while promoting reproduction and recruitment factors at smaller scales. When we compared annual  $\lambda$ 's from female-based and male-based data we found similar values and fluctuations, therefore providing evidence that spring lek counts of males were a valid index to population change and vital rate estimates from radio-marked individuals can be unbiased and used for assessing population responses to conservation actions.

**Key-words:** *Centrocercus urophasianus*, elasticity, life table response experiment, radio-telemetry, population model, population stability, sensitivity, Utah

## Introduction

Identification of key demographic parameters that most influence population dynamics can optimize conservation returns for declining species (Nichols & Hines 2002). Retrospective perturbation analyses, such as life-table response experiments (LTRE), allow scientists to evaluate how variation in specific vital rates contributed to past population dynamics (Caswell 2000, Oli & Armitage 2004). Prospective perturbation analyses, such as sensitivity and elasticity analyses, quantify how equivalent changes in vital rates would affect future population growth. Collectively, these demographic tools can provide new information about the ecology and life history of a species, prioritize research and conservation actions, and develop species recovery plans (Crowder *et al.* 1994, Doak *et al.* 1994, Caswell 2001).

In western North America, the degradation and loss of sagebrush *Artemisia* spp. plant communities has led to a decline in associated species populations, e.g., sage-grouse

75 *Centrocercus urophasianus* (hereafter sage-grouse; Schroeder *et al.* 2004, Garton *et al.* 2011).  
76 Sage-grouse were listed as an endangered species in Canada in 1998 (Harris *et al.* 2001), and in  
77 2010, the United States Fish and Wildlife Service (USFWS) designated sage-grouse as  
78 'warranted but precluded' from listing under the Endangered Species Act (ESA) (USFWS 2010,  
79 Stiver 2011).

80         Currently, sage-grouse are assumed to be long-lived with lower reproductive rates than  
81 other galliformes (Schroeder *et al.* 1999). However, it is thought that like other ground-nesting  
82 birds (Johnson *et al.* 1992, Hoekman *et al.* 2002, Hagen *et al.* 2009), nesting success plays an  
83 influential role in population dynamics (Taylor *et al.* 2012). As such, conservation  
84 recommendations have often been focused on improving nesting habitat conditions (Johnson &  
85 Braun 1999, Connelly *et al.* 2000, Taylor *et al.* 2012). However, the contribution of a vital rate to  
86 population dynamics, such as nest success, has yet to be studied over the long-term in any sage-  
87 grouse population.

88         Projection and perturbation of life-cycle models may help managers formalize their  
89 understanding of how vital rates (e.g., nest survival, chick survival, female survival) affect  
90 population dynamics (Taylor *et al.* 2012), allowing for more informed conservation strategies  
91 (Akçakaya & Raphael 1998, Cooch *et al.* 2001, Clutton-Brock & Coulson 2002). A combination  
92 of retrospective and prospective perturbation analyses can help identify whether a species  
93 exhibits demographic buffering responses to environmental variability, whereby vital rates with  
94 the greatest potential to affect population growth (i.e., greatest elasticity) exhibit the least amount  
95 of temporal variability; a pattern thought to arise from natural selection against the potentially  
96 deleterious impacts of temporal variation in vital rates on fitness (Pfister 1998). Alternatively, a  
97 species may exhibit demographically lability to fluctuating environmental conditions if the

benefits of booms in demographic performance outweigh the busts (Koons et al. 2009). Long-lived animals tend to exhibit demographic buffering (Gaillard et al. 2000, Gaillard & Yoccoz 2003, Schmutz 2009), but little is known about species, such as sage-grouse, that are intermediate on the slow-fast life history continuum (Koons et al. 2014).

Although sage-grouse are of eminent conservation concern, there remains a paucity of information on the effects vital rates have on population dynamics (Johnson & Braun 1999, Taylor *et al.* 2012). Population models based on meta-analyses are useful learning tools, but they confound spatial and temporal variation, which limit guidance for management of specific populations (Morris & Doak 2002, Koons *et al.* 2006, Taylor *et al.* 2012). Using data from one of the longest continuous studies of sage-grouse demography, we evaluated both retrospective and prospective vital-rate contributions to the dynamics of a population that is generally considered to be stable to provide a benchmark conservation target for less robust populations (Caswell 2000, Dobson & Oli 2001). We also examine whether sage-grouse have a life history that buffers against, or is labile to, environmental variation. Because lek counts are used for monitoring sage-grouse populations and initiating management actions, we also compared estimates of  $\lambda$  from male-based lek counts to those from our female-based population model. To our knowledge, this is the first formal assessment of how representative sage-grouse lek counts are of radio-marked female-based population dynamics.

## **Materials and methods**

### **STUDY AREA**

Field data were collected on Parker Mountain (PM) in south-central Utah, USA. The PM sage-grouse population occupied habitat at the southern extreme of the species' range (Schroeder *et al.* 2004). PM is a high elevation (~ 2000-3000 meters) sagebrush semi-desert located on the

Colorado Plateau (West 1983). PM is largely dominated by black sagebrush *A. nova*; however, there are also large areas of mountain big *A. tridentata vaseyana* and silver *A. cana* sagebrush with some Wyoming big sagebrush *A.t. wyomingensis*. PM largely consists of state and federal land. Livestock grazing was the dominant land use.

## FIELD METHODS

Second-year (SY) and after second-year (ASY) females were captured during the springs of 1998-2009 (Geisen *et al.* 1982). Each captured bird was fitted with a 19 or 21-gram necklace-style VHF radio-transmitter with at least 2-years of battery life (Advanced Telemetry Systems™, Isanti, MN, USA and Holohil™, Carp, Ontario, Canada). Age and sex were determined by wing and body size differences (Ammann 1944). Following capture, radio-marked females were monitored for nesting activities. Nests were not flushed due to increased abandonment for this species, but visually monitored every other day to determine fate and nests that hatched  $\geq 1$  egg were considered successful (Connelly *et al.* 2011). We were unable to monitor partial depredation, though partial depredation is a rare occurrence for sage-grouse (Coates 2007). We only used clutch sizes of successful nests during our study, although there is potential for bias if clutch size differed for unsuccessful nests (Schroeder 1997). Effective clutch size (ECS) refers to the number of hatched eggs within a clutch that survived incubation, and excluded unhatched eggs in successful nests.

Radio-marked females with broods were monitored using telemetry every 3 and 2 days in 1998-2004 and 2005-2009, respectively. During 2005-2009 we radio-marked chicks from broods of marked females within ~ 48 hours of hatch (Dahlgren *et al.* 2010a, Guttery *et al.* 2013a). Throughout the study period brood success was estimated as the proportion of broods where  $\geq 1$

chick was observed alive  $\geq 42$  days post-hatch. If at 42 days no radio-marked chicks remained in broods, pointing dogs were used to detect if unmarked chicks were present (Dahlgren *et al.* 2010b, Dahlgren *et al.* 2012). Survival of juveniles (hatch-year from August to March) was monitored from 2008-2010 (Caudill *et al.* 2014).

## VITAL-RATE ESTIMATION

We fit generalized linear mixed models (GLMM) to vital-rates with fixed age effects and random year effects. The mixed-effect structure allowed for direct decomposition of temporal variance in each response variable into sampling and process components. Consequently, we obtained annual ‘shrinkage’ estimates of each vital-rate attributable to process variance and not confounded by sampling variance (Royle & Link 2002). We then estimated ‘process correlation’ among vital rates; a statistic that has been difficult to isolate from empirical studies of demography (Morris & Doak 2002). Analyses were performed in program R using the ‘RMark’ package or directly in Program MARK unless otherwise specified (R Development Core Team 2012, Laake & Rexstad 2012).

For marked females, we modeled the probability of nest initiation in R using a logit-link GLMM, with the model structure described above. Variation in ECS was modeled similarly using GLMM in R, but with log-normal errors. We estimated daily survival rates (DSR) of nests using the nest survival model (Cooch & White 2014). Due to convergence issues with maximum likelihood optimization of the temporal random effect, nest survival was modeled using the MCMC routine in MARK. The nest survival probability was estimated as  $DSR^{34}$  (Schroeder 1997), and corresponding estimates of standard errors were attained using the delta method (Seber 1982).



We modeled radio-marked chick survival from hatch to 42-days using a mixed-effect Cox proportional hazard model and ‘coxme’ package in R (Therneau *et al.* 2003). Brood survival was modeled from 1998-2009 using a GLMM with a logit-link and binomial distribution in R. We then determined brood survival estimates from 2005-2009 to be highly correlated with chick survival estimates ( $p>0.7$ ). Hence, we used a simple linear model to predict chick survival rates for 1998-2004 based on estimated brood survival.

Variation in monthly survival rate (MSR) between age classes (SY and ASY) and years was modeled using the logit-link and nest survival model because monitoring was ‘ragged’ in nature (White & Burnham 1999). Females that went “missing” were right-censored ( $n = 125$  of 401; 62 of 125 were monitored  $\geq 4$  months post-capture) at their last known survival period. We defined the survival year as April 1 of calendar year  $t$  to March 31 in year  $t+1$ , and subsequently estimated annual survival for each year and age class as  $MSR^{12}$ . As above, we used the delta method to estimate standard errors for annual survival. Juvenile survival 2008-2009 was estimated by Caudill *et al.* (2014). Although they did not use mixed-effects models to estimate juvenile survival, we used their reported survival estimates as they represent the best available data for juvenile survival on our study site. For the remaining years (1998-2007) we used the monthly survival probability for SY females (i.e.,  $MSR_{SY}^8$ ) as a surrogate for juvenile survival.

## LIFE-CYCLE MODELING

We constructed a female-based table from estimated vital rates (Table 1). Then a 2-stage projection matrix (**A**) was computed for each year using a pre-breeding census and birth-pulse reproduction format (Caswell 2001). Each matrix consisted of SY and ASY fertility ( $F$ ) and hen survival ( $HS$ ):

$$\mathbf{A} = \begin{pmatrix} F_{SY} & F_{ASY} \\ HS_{SY} & HS_{ASY} \end{pmatrix} \text{ eqn 1}$$

Age-specific fertility was computed for each age-class  $x$  using the following equation:

$$F_x = NI_x * ECS_x * 0.50 * NS_x * CS_x * JS \text{ eqn 2}$$

where

$NI_x$  = age-specific probability of nest initiation

$ECS_x$  = age-specific effective clutch size adjusted for hatch failure

$NS_x$  = age-specific nest survival

$CS_x$  = age-specific chick survival

$JS$  = juvenile survival

The 0.50 in the fertility equation accounts for the fraction of offspring that are female (Guttry *et al.* 2013b). Equation 2 calculates the number of females recruited to breeding age in year  $t + 1$  per breeding female of age  $x$  in year  $t$ . We additionally constructed a matrix with mean vital rates across all years. We used a basic eigen-analysis of the mean matrix to calculate the asymptotic finite population growth rate ( $\lambda$ ), stable stage distribution, reproductive values, expected lifetime number of replacements for each age class ( $R_0$ ), and generation time ( $\mu_1$ , the mean age of parents for a cohort of newborn offspring; Caswell 2001). We calculated statistical error for the mean and annual  $\lambda$  estimates using 10,000 Monte Carlo simulations of uncorrelated annual vital rates and their associated standard errors (Taylor *et al.* 2012).

Prospective and retrospective analyses were performed in R. We calculated sensitivity of  $\lambda$  to each lower-level vital rate  $x$  according to:

$$s_x = \sum_{i,j} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x}, \text{ eqn 3}$$

where  $a_{ij}$  is the  $i,j$ th entry of  $\mathbf{A}$  (Caswell 1978). We calculated elasticity of  $\lambda$  to proportional changes in vital rates as (de Kroon *et al.* 2000):

$$e_x = \frac{x}{\lambda} \sum_{i,j} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x} \text{. eqn 4}$$

To retrospectively decompose vital-rate contributions to historic changes in  $\lambda$ , we used annual vital-rate estimates and associated matrix models in a random-effects LTRE design. Specifically, we decomposed the process variance in  $\lambda$  among annual matrices  $V(\lambda)$  as:

$$V(\lambda) \approx \sum_x \sum_y \text{cov}(x, y) s_x s_y \text{, eqn 5}$$

where  $\text{cov}(x, y)$  is the process covariance of lower-level vital rates  $x$  and  $y$ , and  $s_x$  and  $s_y$  are the vital rate sensitivities evaluated at a reference matrix (average matrix across years; Caswell 2001). We set the process correlation, and thus covariance, to 0 for pairs of vital rates that were not directly related (Table 3). Contributions of a single vital rate to process variance in  $\lambda$  ( $\chi_x$ ) were calculated as (Horvitz *et al.* 1997):

$$\chi_x \approx \sum_y \text{cov}(x, y) s_x s_y \text{. eqn 6}$$

Hence, vital-rate contributions to variation in  $\lambda$  are a function of  $\lambda$ 's sensitivity to changes in a vital rate, vital rate variation over time, and its correlation with other vital rates. LTRE contributions can also be estimated with elasticities and a mean-standardized covariance matrix containing coefficients of variation ( $\text{CV}_{\text{matrix}}$ , for which the diagonal contains respective values of  $\text{CV}^2$ ; Gaillard *et al.* 2000):

$$\chi_x \approx \sum_y \text{cov}(x, y) s_x s_y \approx \sum_y \text{CV}_{\text{matrix}}(x, y) e_x e_y \text{ eqn 7}$$

LEK COUNT

Male sage-grouse attending each lek were counted  $\geq 3$  different mornings each spring (Bernalles *et al.* 2012). We used the maximum male lek-count for each lek to estimate  $\lambda_{\text{lek}, t}$  from year  $t$  to  $t+1$  as:

$$\lambda(\text{lek}, t) = \frac{\sum_{i=1}^n M_i(t+1)}{\sum_{i=1}^n M_i(t)} \quad \text{eqn 8}$$

Where  $M_i(t)$  = maximum number of males counted at lek  $i$  in year  $t$ , and then we summed across  $n$  leks surveyed in both years  $t$  and  $t+1$ . Variance and standard error were estimated using a standard ratio estimator (Scheafer *et al.* 1996):

$$\text{Var}(\lambda_t) = \frac{fpc}{n\overline{M}(t)^2} \frac{\sum_{i=1}^n [M_i(t+1) - \lambda(t)M(t)]^2}{n-1}, \quad (\text{eqn 9}) \text{ where } fpc \text{ is assumed to be } 1.0.$$

Annual model- and lek-derived  $\lambda$  estimates were then plotted against each other for visual comparison.

## Results

We captured, radio-marked, and monitored 180 females, totaling 276 annual life histories accounting for females that graduated age-classes (ASY  $n = 136$ , SY  $n = 140$ ). NS and ECS was monitored for 153 nests. We captured and radio-marked 335 chicks in 76 broods. From 2008-2009, 91 juvenile sage-grouse were captured in late summer and monitored until the following spring. Estimated vital rates are reported in Table 1.

## 248 LIFE CYCLE MODELING

249           Given the mean matrix, the estimated long-term  $\lambda$  indicated the PM sage-grouse  
250 population was generally stable during our study ( $\lambda = 0.998$ ,  $SE = 0.025$ ). The stable age  
251 distribution for SY and ASY females was 0.391 ( $SE = 0.015$ ) and 0.609 ( $SE = 0.015$ ),  
252 respectively, and corresponding reproductive values were 0.433 ( $SE = 0.011$ ) and 0.567 ( $SE =$   
253 0.011). Expected lifetime reproductive output was 0.994 ( $SE = 0.077$ ), and the generation time  
254 was 3.029 years ( $SE = 0.164$ ).

255           According to our LTRE analysis, process variation in JS made the largest contribution to  
256  $\lambda$ , followed by variation in ASY female survival, ASY ECS, SY female survival, ASY chick  
257 survival, SY clutch size, SY chick survival and then the remaining vital rates associated with  
258 nesting (Table 2). Thus, past changes in  $\lambda$  were influenced most by post-fledging (i.e., ASY, SY,  
259 and juvenile) transitions in survival for each age class (i.e., SY and ASY), the next greatest  
260 contributions came from variation in ECS and CS (Table 2). In total, past variation in the post-  
261 fledging survival rates made a greater contribution (0.008) to past fluctuations in  $\lambda$  than summed  
262 contributions of pre-fledging vital rates (0.003).

263           In the prospective perturbation analyses,  $\lambda$  was most sensitive to per unit (sensitivity) and  
264 proportional (elasticity) changes in the annual survival of ASY females. Given the multiplicative  
265 fashion of our fertility equation (eqn 2), elasticities for several pre-fledging vital rates were  
266 constrained to be equal (Table 2). Given comparable numeric scaling of vital rates, however, we  
267 found the unconstrained sensitivities to be useful in comparing prospective impacts of some  
268 vital-rate perturbations on  $\lambda$ . As such, JS and ASY nest survival had the next highest sensitivity  
269 and elasticity values, respectively, followed closely by SY HS and CS of ASY brood hens, then  
270 the remaining components of fertility (Table 2).

## LEK COUNT

The estimated mean  $\lambda$  from lek counts ( $\lambda_{\text{male lek}} = 1.07$ ,  $\text{SE} = 0.10$ ) did not differ from  $\lambda$  estimated from our female-based population model. Moreover, estimated annual fluctuations in  $\lambda$  based on lek counts generally agreed with those estimated from the female-based population model (Fig. 1).

## Discussion

We evaluated prospective and retrospective vital-rate contributions to  $\lambda$  for an imperiled tetraonid under consideration for ESA protection. We demonstrated long-term population stability, and thus our results provide a benchmark for conserving other sage-grouse populations. Our demographic modeling approach can be applied to other species of conservation concern, and we encourage the study of remaining stable populations (Caughley 1994). Perturbation analyses based on long-term demographic studies provide enhanced scientific rigor for guiding the most effective conservation and management, which can lead to a prioritized expenditure of limited funds (Akçakaya & Raphael 1998, Cooch *et al.* 2001, Clutton-Brock & Coulson 2002, Baxter *et al.* 2006).

During our study, survival of post-fledging females had greater prospective and retrospective impact on  $\lambda$  relative to equivalent changes in pre-fledging vital rates related to reproductive output. According to the theory of demographic buffering, the vital rates with the greatest ‘potential’ to affect population growth (i.e., highest elasticity) should exhibit the least amount of temporal variance because of the negative impact such variability can have on long-term fitness and population dynamics (Pfister 1998, Gaillard *et al.* 2000). Contrary to this theory, we found that although post-fledging survival rates exhibited high sensitivity and elasticity

values; they also exhibited high process variation and thus contributed the most to past changes in  $\lambda$ . Moreover, the overall estimate of  $\lambda$  was  $\sim 1.0$ ; indicating population stability during our study period and that departure from the demographic buffering life history strategy is not due to a case of maladaptation to the contemporary environment (Schmutz 2009). Rather, sage-grouse may exhibit a unique type of life history where survival is important and lability in related traits allows them to exploit opportune environments (Koons *et al.* 2009), and survive at rates that, on average, are higher than most other galliformes (Johnsgard 1983, Madge *et al.* 2002).

Our results differ from other studies of population dynamics for other tetraonid species, which have generally concluded that reproductive success, especially nest survival, has greater potential to influence  $\lambda$  compared to female survival (Sandercock *et al.* 2005, Tirpak *et al.* 2006, Hagen *et al.* 2009). Sage-grouse are characterized by greater longevity and lower reproductive investment than other tetraonids and most galliformes (Schroeder *et al.* 1999, Sæther & Bakke 2000, Taylor *et al.* 2012).

Our results suggest that current sage-grouse research and conservation efforts may need to be reevaluated prior to finalizing an ESA listing decision. There exists a pattern of short-term studies focusing primarily on drivers of nesting success (Connelly *et al.* 1991, Gregg *et al.* 1994, Connelly *et al.* 2000, Holloran *et al.* 2005, Moynahan *et al.* 2007). In a range-wide perturbation meta-analysis of vital rates, Taylor *et al.* (2012) found that nest success explained the most variation in  $\lambda$ . Because of the emphasis on nesting for ground-nesting birds in general and tetraonids specifically, we expected nest survival to be a major driver of past population change in our study population. However, nest survival and nest initiation rates contributed relatively little to past changes in  $\lambda$  (Table 2), primarily because of low process variation exhibited by these vital rates (Fig. 2). This low annual variability could be characteristic of our study population

that inhabits a relatively large, intact sagebrush landscape with only minor disturbances (e.g., livestock grazing, low traffic roads). We suggest the lack of variability in annual nesting rates and success of our stable population has broad conservation implication. For example, nesting success did have a relatively high sensitivity value in our study (Table 2) and others (Taylor *et al.* 2012), indicating a potential to contribute to population dynamics. Large changes in nesting success resulting from, e.g., habitat degradation and fragmentation, could have thus easily contributed to population declines elsewhere (eqn. 6; Schroeder 1997, Aldridge & Boyce 2007, Taylor *et al.* 2012).

Concomitantly, annual fixed-effect estimates of nest initiation and survival demonstrated relatively high annual variation (Fig. 2). When estimating nest initiation and survival using mixed models that yield shrinkage estimates, however, much of the temporal variance diminished (Fig. 2). Given these results, we suggest caution when considering short-term avian nesting studies, especially those with ample sampling variation. Ironically, the importance of nesting success in any wildlife population can only be determined by long-term research that is able to compare the relative effects of vital rates on population dynamics using perturbation analyses. Going forward, long-term sage-grouse demographic studies replicated across space will be important to understand regional differences in population dynamics (Williams *et al.* 2003).

Avian studies have generally reported low contributions of clutch size to population dynamics (e.g., Newton 1998, Cooch *et al.* 2001). Our population's clutch sizes were low compared to other sage-grouse studies (Blomberg *et al.* 2014). Variation in ECS during our study was due to increased hatch failure rates in certain years (Appendix A). Though ECS exhibited the lowest sensitivity in our study, we found the variation in annual ECS to be an important contributor to past changes in  $\lambda$ . We suggest hatch failure could have been impacted by extreme



cold temperatures at our high elevation study area during the 7-10 day laying phase, or possibly pre-laying conditions of reproductive females (Hassan *et al.* 2004, Stoleson & Beissinger 1999). Female pre-laying nutrition can also influence overall clutch size (Barnett & Crawford 1994). We recommend future research consider factors which may influence hatch failure and clutch size in this, and other populations.

Survival of chicks made moderate contributions to past population dynamics. Chicks raised by ASY females contributed more to  $\lambda$  than those reared by SY females (Table 2). ASY females had higher nest initiation and nest success, as well as being a larger proportion of the population; thus, ASY females contributed significantly more chicks to the population. Of note, estimates of chick survival at PM are among the highest reported for sage-grouse (Aldridge & Boyce 2007, Gregg *et al.* 2007, Dahlgren *et al.* 2010a, Guttery *et al.* 2013a, Blomberg *et al.* 2013b).

Ecology and conservation of a species can be conceptualized and implemented at various spatial scales (Tilman & Kareiva 1997). Using sage-grouse as an example where large investments have and may soon occur, we relate our demographic results to the current knowledge-base of this umbrella species, and suggest a prioritized three-tiered spatial scale approach to sage-grouse and sagebrush landscape conservation (Knick & Connelly 2011).

**First tier:** Sage-grouse populations have been most stable in areas with large, high percentage sagebrush cover landscapes and in areas with limited fragmentation (Aldridge *et al.* 2008, Knick *et al.* 2013). Post-fledging survival rates were the most influential vital rates in our study. Therefore, we suggest conservation of sagebrush habitat at large landscape scales provided the highest priority setting to support post-fledging survival. In contrast, habitat fragmentation (e.g., energy development) and the associated large movements needed to meet

seasonal habitat requirements have shown negative impact on juvenile, SY, and ASY female survival (Holloran 2005, Beck *et al.* 2006, Holloran *et al.* 2010, Naugle *et al.* 2011). Currently, the minimum acreage to support a stable population is unknown, but our study area consisted of over 107,000 ha of nearly contiguous sagebrush habitat. Others have found that at least 25%, 30%, and 40% of landscapes in sagebrush cover at 18-, 30-, and 5 km scales, respectively, is required for population persistence while higher percentages (e.g., > 65%) provide more certainty (Aldridge *et al.* 2008, Wisdom *et al.* 2011, Knick *et al.* 2013). Conservation of large landscapes can be accomplished through land management agency policy; voluntary incentives for private lands; wildfire prevention and restoration; and conifer encroachment control (Pellant 1990, Knick *et al.* 2003, Pocewicz *et al.* 2011, Pyke 2011, Baruch-Mordo *et al.* 2013). These large landscapes require adequate extents of breeding, summer, and winter habitats (Connelly *et al.* 2000, Fedy *et al.* 2012).

**Second tier:** We determined ‘nesting-related’ vital rates (NI, ECS, NS) had the next most important influence on population dynamics. Thus, after the large landscape has been considered, conservation measures can scale down to nesting habitat; areas of relatively high sagebrush canopy in close proximity to leks (Connelly *et al.* 2011). Nesting habitat can be conserved by maintaining sagebrush canopy cover and residual grass cover in large areas of intact sagebrush (Connelly *et al.* 2000). Connelly *et al.* (2000) suggests managing for 80% or more sagebrush cover with 15-25% canopy and leaving adequate residual grass height and cover.

**Third tier:** After considering the first two tiers, brood-rearing habitat at the smaller scale can be managed to improve conditions for CS. To survive, chicks require arthropods and forbs for food (Johnson & Boyce 1990). Early brood-rearing (<6 weeks old) habitat is closely associated with nesting habitat, and sagebrush removal to improve forb and insect abundance is

generally considered counterproductive to nesting habitat (Connelly *et al.* 2000, Hagen *et al.* 2007). Late brood-rearing (>6 weeks old) areas are generally associated with lower sagebrush canopy mesic sites or higher elevations with higher forb cover (Connelly *et al.* 2000, Hagen *et al.* 2007, Connelly *et al.* 2011). In areas where sagebrush canopy may be limiting herbaceous understory in late summer habitat, shrub reduction at small scales can improve conditions for chicks (Connelly *et al.* 2000, Dahlgren *et al.* 2006).

We used sage-grouse as an example to demonstrate how population dynamics can be used to prioritize conservation actions at various scales for an umbrella species of conservation concern that requires large, intact landscapes. This approach creates greater confidence in management actions when large conservation investments will be implemented; and greater efficiency in achieving conservation objectives (Baxter *et al.* 2006). This approach may be applicable to other species of concern, especially those requiring large landscapes to persist.

Count indices are often used to monitor and assess wildlife population status (Bibby *et al.* 1992, Pollock *et al.* 2002), and scientists continually assess the validity of population indices (Sandercock & Beissinger 2002, Skalski *et al.* 2010). Lek counts have been widely used as an index for sage-grouse population change and to guide management decisions (Connelly *et al.* 2004, Garton *et al.* 2011). Although the validity of lek counts has been questioned for monitoring changes in population numbers (Beck & Braun 1980, Walsh *et al.* 2004), none have evaluated their utility. Lek count protocols during our study generally followed range-wide guidelines (Emmons & Braun 1984, Connelly *et al.* 2003a). Lek-based and vital-rate data were male- and female-based, respectively, thus providing independent sources for  $\lambda_{\text{female model}}$  and  $\lambda_{\text{male lek}}$ . We found that  $\lambda_{\text{female model}}$  and  $\lambda_{\text{male lek}}$  generally tracked each other over time, and for the majority of years, both estimates of  $\lambda$  were within one standard error (Fig. 1). We suggest that our results

provide evidence that: 1) male-based leks counts of sage-grouse can be an effective index to overall population change, and 2) telemetry-based studies can provide unbiased demographic information for analysis and monitoring. The integration of both types of data could provide insight into population dynamics at sites where the entire life cycle has not been studied (Davis *et al.* 2014), and be used to examine population dynamics at greater spatio-temporal scales.

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Table 1. A summary of female-based vital rates for the greater sage-grouse population at Parker Mountain, UT, 1998-2009. SY = second year female (first breeding season); ASY = after second year female (second or more breeding seasons); NI = nest initiation probability where a female must have been documented on a nest using telemetry and binoculars; ECS = effective clutch size excluding hatch failures, NS = nest survival based on a 7-day laying and 27-day incubation period; CS = chick survival probability based on a 42-day brooding period; JS = juvenile survival for young of the year from August 1 to March 31; HS = annual female (hen) survival based on monthly survival rates (MSR<sup>12</sup>). All vital-rate values represent shrinkage estimates (see Methods) that are based solely on process variance and exclude sampling variance.

Year	Sample Size		NI		ECS		NS		CS <sup>a</sup>		JS <sup>b</sup>	HS	
	SY	ASY	SY	ASY	SY	ASY	SY	ASY	SY	ASY		SY	ASY
1998	19	10	0.59	0.79	5.63	6.05	0.44	0.54	0.67	0.57	0.66	0.54	0.68
1999	17	26	0.59	0.79	5.54	5.96	0.41	0.52	0.67	0.57	0.66	0.53	0.68
2000	8	19	0.62	0.81	5.64	6.07	0.44	0.55	0.64	0.55	0.68	0.56	0.68
2001	15	10	0.63	0.81	5.63	6.05	0.42	0.52	0.66	0.56	0.66	0.54	0.68
2002	14	15	0.62	0.81	5.52	5.94	0.42	0.52	0.64	0.55	0.67	0.54	0.68
2003	13	13	0.62	0.81	5.47	5.88	0.42	0.52	0.66	0.57	0.61	0.48	0.68
2004 <sup>c</sup>	0	9	0.59	0.79	5.56	5.98	0.43	0.54	0.65	0.56	0.66	0.54	0.68
2005	38	17	0.61	0.80	5.31	5.71	0.44	0.54	0.70	0.61	0.82	0.74	0.68
2006	13	46	0.61	0.80	5.37	5.78	0.44	0.54	0.66	0.56	0.64	0.51	0.68
2007	22	21	0.56	0.77	5.34	5.74	0.42	0.52	0.60	0.49	0.58	0.44	0.68
2008	12	32	0.56	0.77	5.61	6.04	0.44	0.55	0.69	0.60	0.42	0.50	0.68
2009	8	31	0.60	0.79	5.47	5.89	0.39	0.50	0.68	0.59	0.61	0.48	0.68
mean			0.60	0.80	5.51	5.92	0.43	0.53	0.66	0.56	0.64	0.53	0.68
process variance			0.0005	0.0003	0.0140	0.0158	0.0002	0.0002	0.0007	0.0008	0.0082	0.0055	0.0046

a: Available radio-marked chick survival estimates for 2005-2009 were correlated with brood survival ( $\geq 1$  chick surviving to 42 days) estimates (unpublished data). Chick survival estimates for 1998-2004 were calculated by using the linear model to interpolate chick survival as a function of available brood survival.

b: Estimates for 1998-2007 were calculated using the corresponding monthly survival rate for SY females (MSR<sup>8</sup>), whereas survival estimates for 2008 and 2009 were directly estimated from radio-marked juveniles (Caudill 2011).

c: SY females were not available in 2004. However, the use of additive age + year models for all vital rates allowed us to attain 'predicted' estimates of all vital rates for SY females in 2004 given the constraint of the statistical models.

Table 2. A calculation of Life Table Response Experiment (LTRE) contributions to annual process variation in population growth rate, and estimates of the sensitivity ( $s_x$ ) and elasticity ( $e_x$ ) of the finite population growth rate to changes in the underlying vital rates ( $x$ ) evaluated at temporal mean values for the greater sage-grouse population at Parker Mountain, Utah, 1998-2009. SY = second year female (first breeding season); ASY = after second year female (second or more breeding seasons); NI = nest initiation probability where a female must have been documented on a nest using telemetry and binoculars; ECS = effective clutch size excluding hatch failures; NS = nest survival based on a 7-day laying and 27-day incubation period; CS = chick survival probability based on a 42-day brooding period; JS = juvenile survival for young of the year from August 1 to March 31; HS = annual female (hen) survival based on monthly survival rates (MSR<sup>12</sup>).

$x$	LTRE	LTRE Rank	$e_x$	$e_x$ Rank	$s_x$	$s_x$ Rank
JS	0.00532	1	0.3290	2	0.5131	2
ASY HS	0.00163	2	0.4402	1	0.6710	1
ASY ECS	0.00116	3	0.0981	5	0.0778	10
SY HS	0.00099	4	0.2308	3	0.4310	4
ASY CS	0.00058	5	0.2308	3	0.4082	5
SY ECS	0.00054	6	0.0981	5	0.0356	11
SY CS	0.00048	7	0.0981	5	0.1484	9
ASY NS	0.00014	8	0.2308	3	0.4360	3
SY NS	0.00004	9	0.2307	4	0.2295	7
ASY NI	7.03e-6	10	0.2308	3	0.2895	6
SY NI	2.96e-6	11	0.0981	5	0.1633	8

Table 3. The greater sage-grouse vital rate covariance matrix for Parker Mountain, Utah, 1998-2009. Covariance values without direct biological relationships were set to zero (see text). SY = second year female (first breeding season); ASY = after second year female (second or more breeding seasons); NI = nest initiation probability where a female must have been documented on a nest using telemetry and binoculars; ECS = effective clutch size excluding hatch failures, NS = nest survival based on a 7-day laying and 27-day incubation period; CS = chick survival probability based on a 42-day brooding period; JS = juvenile survival for young of the year from August 1 to March 31; HS = annual female (hen) survival based on monthly survival rates (MSR<sup>12</sup>).

Vital Rate	SY HS	ASY HS	SY NI	ASY NI	SY ECS	ASY ECS	SY NS	ASY NS	SY CS	ASY CS	JS
SY HS	0.00550	0.00495	0.00000	0.00000	-0.00082	0.00000	0.00042	0.00000	0.00094	0.00000	0.00507
ASY HS	0.00495	0.00458	0.00000	0.00000	0.00000	-0.00048	0.00000	0.00033	0.00000	0.00100	0.00469
SY NI	0.00000	0.00000	0.00054	0.00037	0.00013	0.00000	-0.00003	0.00000	0.00002	0.00000	0.00000
ASY NI	0.00000	0.00000	0.00037	0.00026	0.00000	0.00010	0.00000	-0.00003	0.00000	0.00006	0.00000
SY ECS	-0.00082	0.00000	0.00013	0.00000	0.00349	0.00372	0.00025	0.00000	0.00008	0.00000	0.00000
ASY ECS	0.00000	-0.00048	0.00000	0.00010	0.00372	0.00396	0.00000	0.00025	0.00000	0.00025	0.00000
SY NS	0.00042	0.00000	-0.00003	0.00000	0.00025	0.00000	0.00025	0.00024	0.00003	0.00000	0.00000
ASY NS	0.00000	0.00033	0.00000	-0.00003	0.00000	0.00025	0.00024	0.00023	0.00000	0.00005	0.00000
SY CS	0.00094	0.00000	0.00002	0.00000	0.00008	0.00000	0.00003	0.00000	0.00067	0.00073	0.00016
ASY CS	0.00000	0.00100	0.00000	0.00006	0.00000	0.00025	0.00000	0.00005	0.00073	0.00081	0.00030
JS	0.00507	0.00469	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00016	0.00030	0.00824

Values in grey represent process variance within each vital rate and correspond to Table 1; however, values for ECS are different because they were calculated from ECS\*0.50 to represent the female portion of the population in this table (see text).

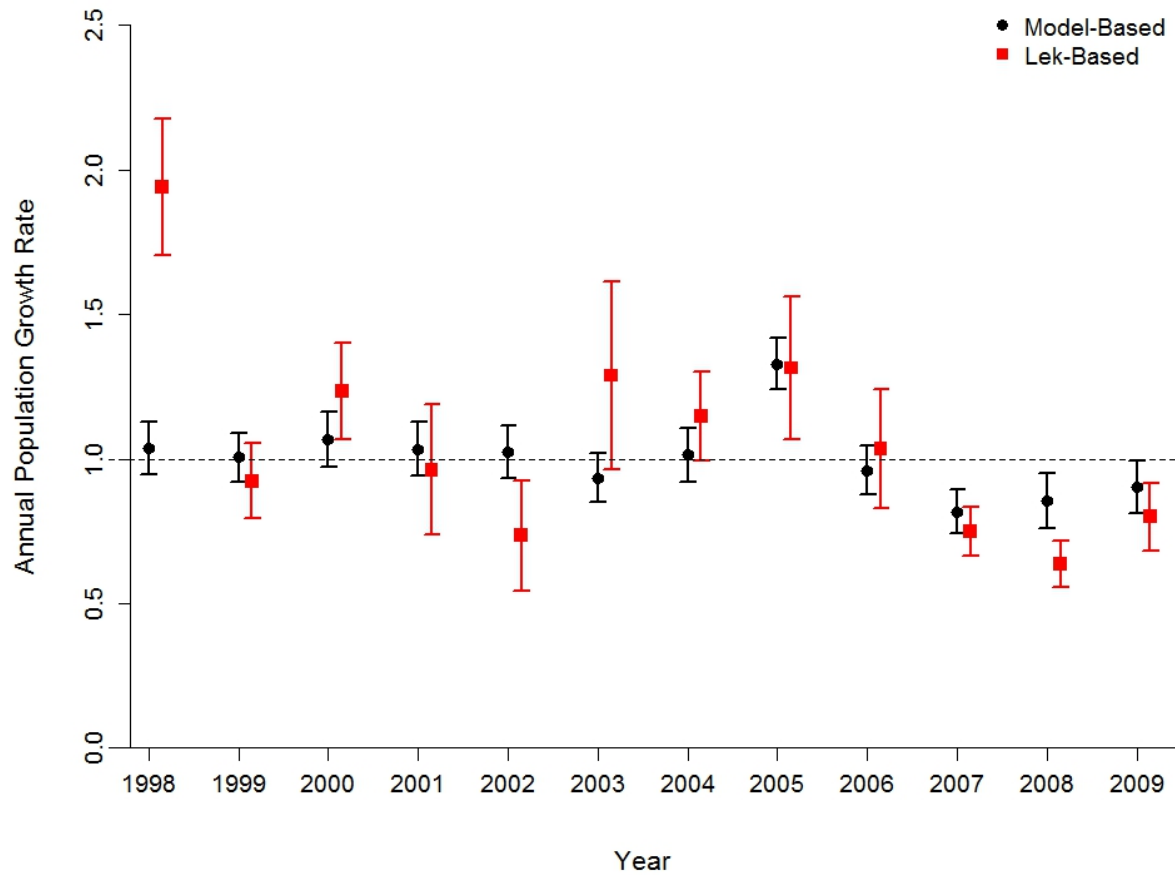


Figure 1. Greater sage-grouse *Centrocercus urophasianus* annual estimates of radio-marked female-based matrix model and male-based lek count estimates of finite growth rate ( $\lambda$ ), 1998-2009, Parker Mountain, Utah, USA.

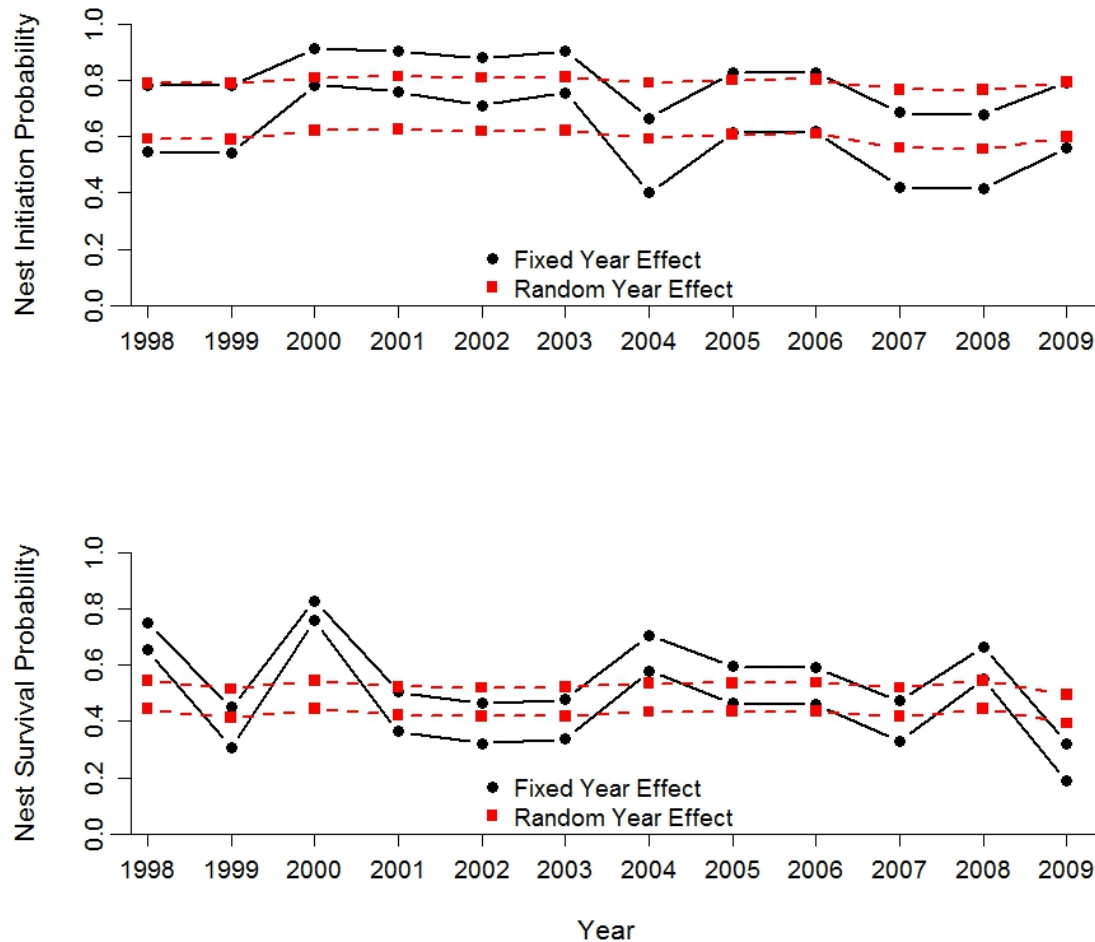


Figure 2. Greater sage-grouse *Centrocercus urophasianus* annual estimates of nest initiation and nest success of after second year (higher probability values) and second year (lower probability values) for fixed-year effects and random-year effects models where sampling error was removed for random-year effects results, 1998-2009, Parker Mountain, Utah, USA.



Research Article

# Greater Sage-Grouse Juvenile Survival in Utah

DANNY CAUDILL,<sup>1,2</sup> Jack H. Berryman Institute, Department of Wildland Resources, Utah State University, Logan, UT 84322-5230, USA  
 TERRY A. MESSMER, Jack H. Berryman Institute, Department of Wildland Resources, Utah State University, Logan, UT 84322-5230, USA  
 BRENT BIBLES, Center for Natural Resources Management and Protection, Unity College, Unity, ME 04988, USA  
 MICHAEL R. GUTTERY, Department of Forest and Wildlife Ecology, University of Wisconsin, Madison, WI 53706, USA

**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 led 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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<sup>1</sup>E-mail: charles.caudill@myfwc.com

<sup>2</sup>Present address: Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, 1105 S.W. Williston Road, Gainesville, FL 32601, USA

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. Burkepille 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 (Gutierrez et al. 2013b). 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 Burkepille 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  $\Delta AIC_c \leq 2$  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.,  $T + T^2$ ) 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 ( $\Delta AIC_c \leq 2$ ) 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 <sup>a</sup>	Covariate models
Constant	Transmitter type
Full Time Dependent	Sex
Linear <sub>fall</sub> + Constant <sub>winter</sub>	Year
Constant <sub>fall</sub> + Constant <sub>winter</sub>	Sex + transmitter type
Quadratic <sub>fall</sub> + Constant <sub>winter</sub>	Year + sex
Quadratic	Year + transmitter type
Constant Aug–Open of Hunting Season + Constant <sub>Hunting Season</sub> + Constant <sub>14 days post Hunting Season</sub> + Constant <sub>Last week in Oct–30 Nov.</sub> + Constant <sub>winter</sub>	Year + sex + transmitter type

<sup>a</sup> 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 ( $T^2 = \text{top model}$  and  $T^2_{\text{fall}} + \text{constant}_{\text{winter}}$   $\Delta AIC_c = 2.02$ ) from our initial model evaluation step (1 other model was  $\Delta AIC_c = 5.1$  and all others were  $\geq \Delta AIC_c = 26.73$ ). 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 <sup>a</sup>	No. at risk	Probability of death	95% CI <sup>a</sup>	No. at risk	Probability of death	95% CI <sup>a</sup>
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

<sup>a</sup> 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 <sup>a</sup>	Probability of death	95% CI <sup>a</sup>	Probability of death	95% CI <sup>a</sup>
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

<sup>a</sup> Profile likelihood confidence interval.

survival models to be competitive ( $\Delta AIC_c < 2$ ; 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<sub>c</sub>, Akaike's Information Criterion adjusted for sample size;  $\Delta AIC_c$ , difference in AIC<sub>c</sub> values between each model and the best model;  $\omega_i$ , AIC<sub>c</sub> weight; Model likelihood = ( $\omega_i/\omega_{\text{best model}}$ );  $K$ , number of parameters.

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

<sup>a</sup>  $T^2$  = quadratic trend in time (i.e.,  $T + T^2$ ); 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.

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

**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 <sup>a</sup>	Reduced model <sup>a</sup>	$\chi^2$	df	$P$	Hypothesis tested
$S(T^2 \times \text{year} + \text{sex} + \text{type})$	$S(T^2 \times \text{year} + \text{type})$	2.65	1	0.103	Sex-specific survival
$S(T^2 \times \text{year} + \text{sex} + \text{type})$	$S(T^2 \times \text{year} + \text{sex})$	2.87	1	0.090	Transmitter-specific survival
$S(T^2 \times \text{year} + \text{sex} + \text{type})$	$S(T^2 \times \text{year})$	5.69	2	0.058	Sex- and transmitter-specific survival

<sup>a</sup>  $T^2$  = 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

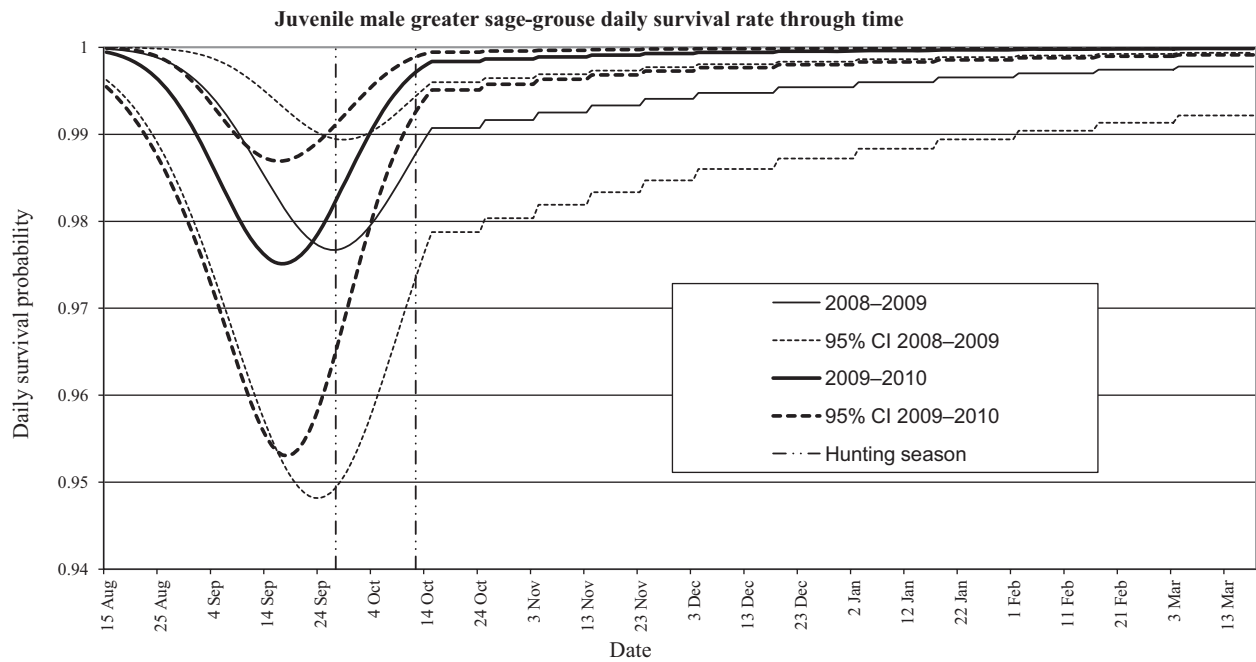
et al. 2007). Our results outline differential effects by attachment method and the need to consider appropriate positioning of transmitters on study subjects. We did not document any juvenile mortalities during winter of either year regardless of transmitter type, and consequently the negative effect 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.

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

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

Parameter	$\beta$	SE	90% CI	
			Lower	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 <sup>2</sup>	0.35	0.08	0.22	0.48
Year × time <sup>2</sup>	−0.08	0.03	−0.13	−0.03

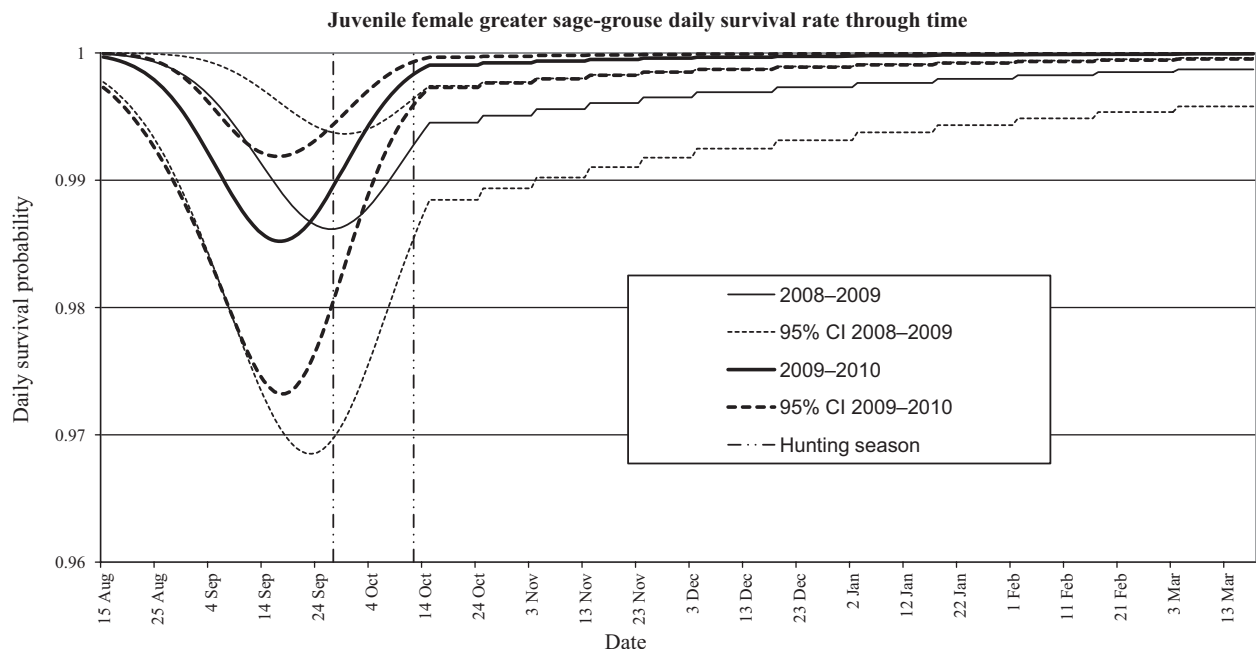


**Figure 1.** Juvenile male greater sage-grouse (*Centrocercus urophasianus*), fitted with necklace style radios, daily survival rate by day of study on Parker Mountain, Utah, USA, 2008–2010.

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  $S(T^2 \times \text{year} + \text{sex} + \text{transmitter type})$  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.

Year	Sex	Season <sup>a</sup>	Necklace only	
			$S$	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

<sup>a</sup> 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.

(2013a) 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.

Transmitter type	Days post capture	2008			2009		
		No. at risk	Probability of death	95% CI <sup>a</sup>	No. at risk	Probability of death	95% CI <sup>a</sup>
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

<sup>a</sup> 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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