



Population Ecology

Survival of Resident and Translocated Greater Sage-Grouse in Strawberry Valley, Utah: A 13-Year Study

RICK J. BAXTER,¹ *Plant and Wildlife Sciences Department, Brigham Young University, 275 WIDB, BYU, Provo, UT 84602, USA*

RANDY T. LARSEN, *Plant and Wildlife Sciences Department and the Monte L. Bean Life Sciences Museum, Brigham Young University, 407 WIDB, BYU, Provo, UT 84602, USA*

JERRAN T. FLINDERS, *Emeritus Professor, Brigham Young University, 17082 Snake River Rd., Asotin, WA 99402, USA*

ABSTRACT Survival of greater sage-grouse (*Centrocercus urophasianus*) has been well described in large populations across the species range. Very little published information exists, however, on survival rates of translocated sage-grouse or grouse from a long-term (>10 yr) study. Our objectives were to estimate seasonal and annual survival rates; assess differences in survival between resident and translocated, adult and yearling, and male and female sage-grouse; identify environmental and behavioral factors associated with survival; and assess the influence of mammalian predator control on survival rates of radio-marked sage-grouse in Strawberry Valley, Utah from 1998 to 2010. We used a 2-stage model selection approach using Akaike's Information Criterion corrected for sample size (AIC_c) with known-fate models in Program MARK to evaluate the influences of seasonal, annual, demographic, and behavioral effects on survival rates of sage-grouse. We captured and fitted 535 individual sage-grouse (male and female, resident and translocated) with radio transmitters over a 13-year period and monitored them weekly. The top model of survival, which accounted for 22% of the AIC_c weight, included 3 seasons that varied by year where rates were influenced by residency, sex, and whether a female initiated a nest. A group-level covariate for the number of canids killed each year received some support as this variable improved model fit compared to identical models without it, although confidence intervals around β estimates overlapped zero slightly. All other demographic or environmental variables showed little or no support. Annual estimates of survival for females ranged between 28% and 84% depending on year and translocation source. Survival was consistently highest during the fall–winter months with a mean monthly survival rate of 0.97 (95% CI = 0.96–0.98). The lack of a control site and other potential confounding factors limit the extent of our inference with respect to predator control. Nonetheless, we suggest managers consider enhancing nesting habitat, translocating sage-grouse, and possibly controlling predators to improve survival rates of sage-grouse. © 2013 The Wildlife Society.

KEY WORDS *Centrocercus urophasianus*, lag-effect, mortality, predator control, sage-grouse, seasonal, survival, telemetry.

Understanding survival and cause-specific mortality are important aspects of wildlife management (Gehrt 2005). Seasonal and annual survival estimates can help managers understand population fluctuations, which may allow for responsive changes in management (White and Garrott 1990). Nonetheless, managers must often make decisions with limited or incomplete information. Although much is known about seasonal and annual survival (Zablan et al. 2003, Moynahan et al. 2006, Anthony and Willis 2009, Sedinger et al. 2011) of greater sage-grouse (*Centrocercus urophasianus*; hereafter referred to as sage-grouse or grouse), the relative contribution or role of influences linked to site-

specific survival vary widely (Beck et al. 2006, Moynahan et al. 2006, Aldridge and Boyce 2008, Baxter et al. 2008). Moreover, reported annual survival estimates for adult, yearling, male, and female sage-grouse have varied widely ranging from 25% to 96% depending on location and method of assessment (June 1963, Connelly et al. 1994, Zablan et al. 2003, Anthony and Willis 2009, Sedinger et al. 2011). Management prescriptions based on range-wide factors affecting survival may not be applicable to all locales, underscoring the need for site-specific information.

Currently, sage-grouse are a candidate species for listing under the 1973 Endangered Species Act (ESA) and are considered endangered in Canada. In this recent listing decision, the United States Fish and Wildlife Service (USFWS) found that listing greater sage-grouse as threatened or endangered was warranted, but precluded due to

Received: 26 October 2011; Accepted: 15 November 2012
Published: 19 February 2013

¹E-mail: rjb47rjb47@gmail.com

higher priority listing actions (50 CFR Part 17—FWS-R2-ES-2010-0018). Declines in our study population in Strawberry Valley, Utah have been more drastic and severe than the commonly cited 17–47% (Connelly and Braun 1997) range-wide decline. In the 1930s Griner (1939) estimated Strawberry Valley's sage-grouse population at 3,500 individuals. He observed and documented individual flocks with more than 1,000 grouse concentrated on winter habitats. By 1998, when we initiated this study, Bunnell (2000) estimated a population of only 150.

This observed decline precipitated a sage-grouse recovery effort in 1998, wherein the long-term objectives were to identify factors limiting population growth, remove or mitigate those factors, and recover the population to a size no longer threatened with extirpation. Despite summer habitat (Bunnell et al. 2004) that met or exceeded published guidelines (Connelly et al. 2000), numbers of sage-grouse counted each spring on leks continued to decline. In response to this decline, we translocated sage-grouse from 4 different populations during 6 years (2003–2008) with the objective of increasing population size and genetic diversity. As part of this work, more than 530 sage-grouse (resident and translocated) were radio-marked and monitored weekly over a 13-year period (1 Apr 1998–31 Mar 2011).

The length of time and sample size represented by these data allowed us to evaluate seasonal and environmental influences on survival rates of sage-grouse in Strawberry Valley, Utah over more than a decade. Our specific objectives were to 1) estimate seasonal and annual survival rates, 2) assess differences in survival between resident and translocated, adult and yearling, and male and female sage-grouse, 3) identify environmental and behavioral factors associated with survival, and 4) assess the influence of predator control on survival rates in our study area.

STUDY AREA

The core study area was centered in the Strawberry Valley of north central Utah, USA (NAD 83 Zone 12T; UTM 0492078/4445216; Fig. 1). This area was characterized as montane sagebrush steppe with mountain big sagebrush (*Artemisia tridentata vaseyana*) as the dominant shrub and silver sagebrush (*A. cana*) occurring at lower abundance in wet meadows and riparian areas. The valley was approximately 24 km long and 9 km wide. Strawberry Reservoir was the central and dominant feature in the area, covering more than 6,900 surface hectares. Land uses in the core area included livestock grazing, summer home development, and recreation in the form of fishing, boating, camping, and hunting. To the east of the core area were the migratory areas known locally as Wildcat, Fruitland, and Lower Red Creek. They were distinguished by differing precipitation regimes, successively lower elevations, and different habitat types (Table 1). During our study years, no energy development activities occurred in the area. Much of the sagebrush habitat in this area was fragmented by natural changes in vegetation (i.e., aspen stands, pinyon-juniper woodlands), the reservoir, summer homes, roads, power lines, camp sites, and other features.

Translocation source sites were 122–275 km from release sites in Strawberry Valley and varied by elevation, terrain, sagebrush type, and precipitation regime (Table 1). The principal land use in all of these areas was grazing; however, recreational activities did occur. In addition, on Diamond Mountain a very small amount of energy development (natural gas) occurred during our study years. Additional details concerning source areas are available in Baxter et al. (2008).

METHODS

Capture and Monitoring

Beginning in March 1998, we trapped resident male and female sage-grouse on, near, and around leks during the breeding season (1 Mar–31 May) at night using the original and a modified spotlight method (Giesen et al. 1982, Wakkinen et al. 1992). We captured grouse in every year from 1998 to 2010. In addition, opportunistic trapping events occurred sporadically during the fall using the same methods. After capture, we assigned each sage-grouse an age class (yearling = 11–23 months, adult ≥ 24 months) as described by Crunden (1963) and Connelly et al. (2004), and fitted them with a 22-g necklace-style radio transmitter (Advanced Telemetry Systems, Inc.[®] Isanti, MI; 19 hr duty cycle, 45 ppm, with mortality after 8 hr and max. battery life of 30 months). We used a 22-g necklace-style transmitter because it was consistently $< 2.5\%$ of body mass and because necklace-style transmitters are commonly used in sage-grouse research. Following capture and radio-marking, we released sage-grouse at the point of capture.

In addition to resident sage-grouse captured throughout the study period, we trapped female sage-grouse (2003–2008) from up to 4 source populations in Utah deemed stable by the Utah Division of Wildlife Resources (Baxter et al. 2008). Source populations were chosen because of their robust size, distance from release site, and their behavioral (Barber 1991) and genetic compatibility (Oyler-McCance et al. 2005) with Strawberry Valley sage-grouse. We translocated sage-grouse from multiple locations to maximize genetic diversity and minimize individual impacts to each population. We followed the suggestion of Oyler-McCance et al. (2005) to translocate between neighboring rather than distant populations given the isolation by distance population genetic structure of sage-grouse. Trapping and handling of sage-grouse was approved by the Utah Division of Wildlife Resources and Brigham Young University's Institutional Animal Care and Use Committee (IACUC approval #08-0402).

We monitored sage-grouse weekly, throughout each year, using a 4-element Yagi antenna and a TR-2 receiver (Telonics Incorporated[®], Mesa, AZ) or an R-1000 digital radio receiver (Communication Specialists Incorporated[®], Orange, CA). We also used periodic flights in fixed-wing aircraft to locate radio-marked birds ($\bar{x} = 6$ flights/yr). We listened for signals from radio-marked sage-grouse within an 80-km radius of the lek or release site to detect movement of any grouse with active radios out of Strawberry Valley and the eastern migratory areas. We recorded locations of radio-

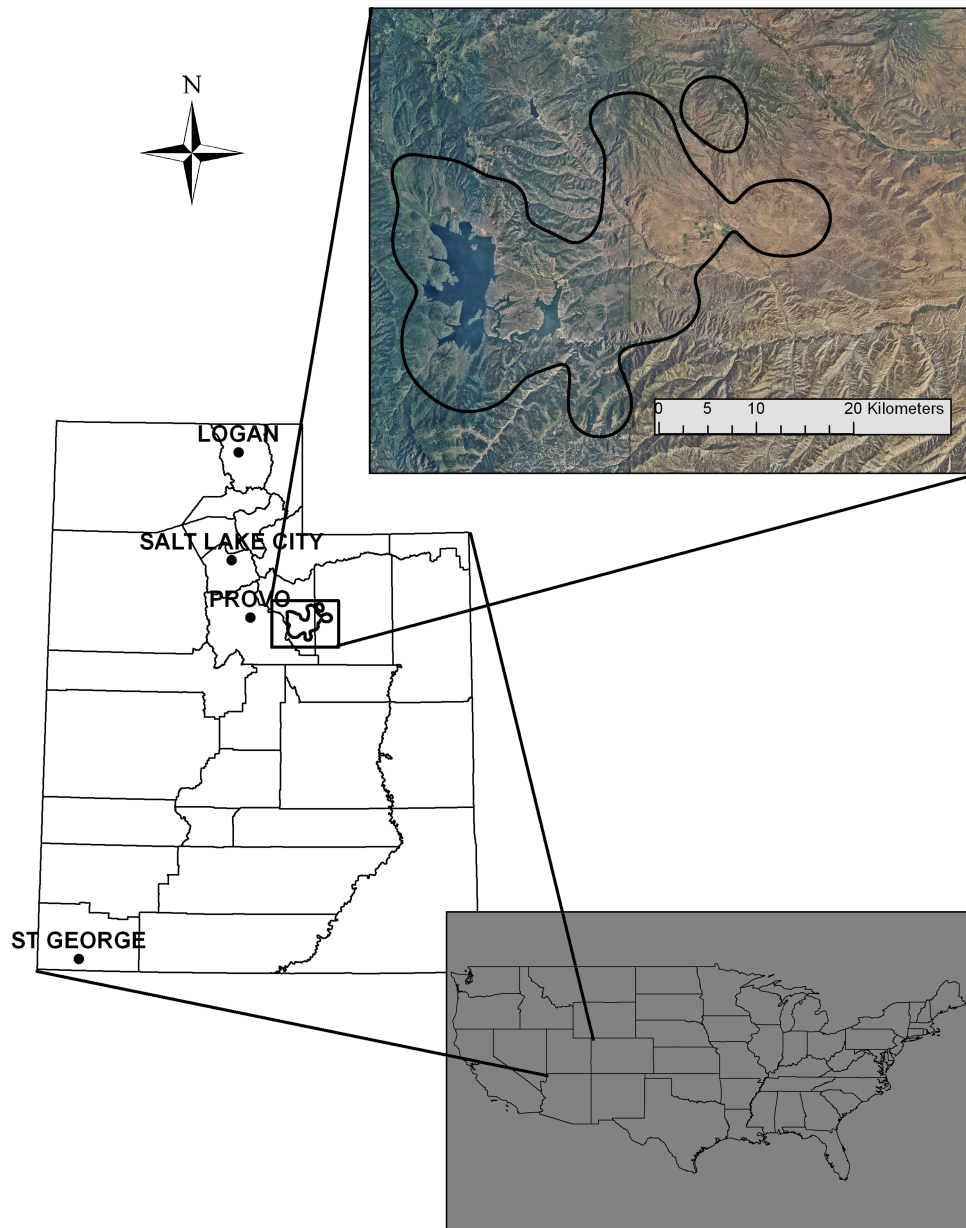


Figure 1. Strawberry Valley study area in north central Utah, USA where we monitored sage-grouse survival from 1 April 1998 to 31 March 2011.

marked grouse with a global positioning system (GPS) receiver. Upon discovery of a mortality signal, we attempted to recover transmitters within 24 hours. When we did not hear a radio for several weeks, we used fixed-wing aircraft to assist with relocation. Once relocated, we resumed monitoring from the ground and located birds visually to confirm survival or mortality.

Initial research during the first 2 years suggested that predation by canids (red fox [*Vulpes vulpes*] and coyotes [*Canis latrans*]) was a potential limiting factor for this population (Bunnell 2000). Consequently, a predator control program, administered by the United States Department of Agriculture Wildlife Services, began in 2000 as part of the overall recovery objectives. Annual control efforts occurred from January to the end of the early brood-rearing season (end of Jun) beginning in 2000. The goal of the predator control program was to reduce numbers of red

fox and coyotes in the study area in an attempt to increase sage-grouse survival and promote population growth. We report predators killed by Wildlife Services during the study (Table 2).

Survival Analysis and Modeling

We estimated seasonal and annual survival rates (s) using known-fate models in Program MARK 5.1 (White and Burnham 1999) and used model selection (Burnham and Anderson 2002) to evaluate hypotheses about survival across the 13-year study period. We formatted an encounter history into months beginning 1 April 1998 and ending 31 March 2011. We coded each encounter (month) for each bird as live, dead, or censored. We used months as opposed to seasons for 2 reasons. First, it allowed us to model seasonal variation by grouping months (e.g., comparison of 3 vs. 4 season models) without recoding encounters. Second, because the mean

Table 1. Dominant vegetation type, elevation, precipitation (precip) regime, and distance (km) to Strawberry Valley (SV), Utah for resident and translocated source populations where we captured greater sage-grouse from 1 April 1998 to 31 March 2011.

Population	Dominant vegetation	Elevation (m)	Precipitation regime	Mean precip (cm)	Distance to SV release site (km)
Strawberry Valley core area Strawberry Valley ^a	Mountain and Wyoming big sagebrush	2,250–2,720	Cool dry summers Cold wet winters	58	0
Migratory areas Wildcat ^a	Mountain and Wyoming big sagebrush	2,310–2,580	Cool dry summers Cold wet winters	58	10
Fruitland ^b	Wyoming big sagebrush and greasewood	2,070–2,200	Warm dry summers Cold wet winters	40	21
Lower Red Creek ^c	Wyoming big sagebrush and greasewood	2,040–1,950	Warm dry summers Cold wet winters	32	32
Translocation source sites Parker Mountain ^d	Black sagebrush	2,140–3,000	Hot dry summers Cold wet winters	45	204
Diamond Mountain ^c	Mountain and Wyoming big sagebrush	2,130–2,550	Warm dry summers Cold wet winters	61	147
Box Elder County ^f	Black and Wyoming big sagebrush	1,500–2,100	Warm dry summers Cold wet winters	29	275
Deseret Land and Livestock ^{g,h}	Wyoming big sagebrush	1,920–2,130	Warm dry summers Cold wet winters	25	122

^a Baxter et al. (2008).

^b Goodrich et al. (1999).

^c Bambrough (2002).

^d Jarvis (1973).

^e Ralphs and Busby (1979) and Laycock and Conrad (1981).

^f Knerl and Messmer (2005).

^g Bromley and Gese (2001).

^h R. Danvir, Deseret Land, and Livestock (unpublished data).

annual initiation of the breeding season, nest initiation, and mean hatch occurred within a few days of monthly breaks for our study population, it permitted accurate seasonal groupings.

We formatted our input file with year as a group. This structure allowed us to graduate individuals from yearlings to adults and translocated to resident when they survived the year as well as facilitating staggered entry of individuals. We then estimated annual survival rates as derived parameters (complete with appropriate SEs and CIs estimated using the delta method) within Program MARK 5.1 (White and Burnham 1999). This format allowed us to compare annual survival rates to other published estimates throughout the range of greater sage-grouse. We included capture location (Strawberry Valley, Parker Mountain, Box Elder County, Deseret Land and Livestock, and Diamond Mountain), age, sex, residency (resident or translocated), nest initiation status, and nest success as individual covariates potentially influencing survival rates. We included nest initiation status and nest success in our model list to test the hypothesis that females that started and completed incubation would have a lower probability of survival than females that did not because incubating females may be more susceptible to predation. We followed standard model selection protocol and built a list of a priori candidate models (Burnham and

Anderson 2002). To limit the number of potential models, we used a 2-stage approach where we first identified the best model for time (month, seasonal, year, and interactions) and then assessed the influence of individual covariates assuming the time structure identified in stage 1 (Miller and Conner 2005; Table 3). This 2-stage approach was an attempted balance between under and over-fitting our data given the large number of conceivable models and unknown problems

Table 2. Canids killed by United States Department of Agriculture Wildlife Services in Strawberry Valley, Utah from 1 April 1998 to 31 March 2011.

Year	Red fox	Coyotes	Total
1998	0	0	0
1999	5	2	7
2000	9	6	15
2001	9	2	11
2002	13	6	19
2003	28	10	38
2004	22	23	45
2005	35	11	46
2006	12	14	26
2007	15	7	22
2008	10	10	20
2009	11	11	22
2010	2	2	4
2011	0	0	0

Table 3. A priori models used to determine the influence of group and individual covariates on survival of sage-grouse in Strawberry Valley, Utah from 1 April 1998 to 31 March 2011.

Model structure	Hypothesis description
$\delta(3 \text{ season} \times \text{translocation})$	Survival varied by 3 seasons and the number of birds translocated annually multiplicatively
$\delta(3 \text{ season} \times \text{year} + \# \text{ canids killed influenced rates from January to August})$	Survival varied by 3 seasons and year multiplicatively with the number of canids killed in a given year influencing rates from January through August of each year
$\delta(3 \text{ season} \times \text{year} + \# \text{ canids killed influenced rates from January to December})$	Survival varied by 3 seasons and year multiplicatively with the number of canids killed in a given year influencing rates from January through December of each year
$\delta(3 \text{ season} \times \text{year} + \text{age})$	Survival varied by 3 seasons and year multiplicatively, individual covariate grouse age
$\delta(3 \text{ season} \times \text{year} + \text{all individual covariates})$	Survival varied by 3 seasons and year multiplicatively, all individual covariates (sex, age, residency, source population, nest initiation, and nest success)
$\delta(3 \text{ season} \times \text{year} + \text{sex})$	Survival varied by 3 seasons and year multiplicatively, individual covariate sex
$\delta(3 \text{ season} \times \text{year} + \text{sex} + \text{age})$	Survival varied by 3 seasons and year multiplicatively, individual covariates sex and age
$\delta(3 \text{ season} \times \text{year} + \text{sex} + \text{age} + \text{nest initiation} + \text{nest success})$	Survival varied by 3 seasons and year multiplicatively, individual covariates sex, age, nest initiation, and nest success (successfully hatching 1 egg)
$\delta(3 \text{ season} \times \text{year} + \text{nest initiation})$	Survival varied by 3 seasons and year multiplicatively, individual covariate nest initiation
$\delta(3 \text{ season} \times \text{year} + \text{nest success})$	Survival varied by 3 seasons and year multiplicatively, individual covariate nest success (successfully hatching at least 1 egg)
$\delta(3 \text{ season} \times \text{year} + \text{residency})$	Survival varied by 3 seasons and year multiplicatively, individual covariate residency
$\delta(3 \text{ season} \times \text{year} + \text{residency} + \text{sex} + \text{age} + \text{nest initiation} + \text{nest success})$	Survival varied by 3 seasons and year multiplicatively, individual covariates residency, sex, age, nest initiation, and nest success (successfully hatching at least 1 egg)
$\delta(3 \text{ season} \times \# \text{ translocated} + \text{residency} + \text{sex} + \text{nest initiation})$	Survival varied by 3 seasons and the number of birds translocated annually multiplicatively, individual covariates residency, sex, and nest initiation
$\delta(3 \text{ season} \times \text{year} + \text{residency} + \text{sex} + \text{nest initiation})$	Survival varied by 3 seasons and year multiplicatively, individual covariates residency, sex, and nest initiation
$\delta(3 \text{ season} \times \text{year} + \text{residency} + \text{sex} + \text{nest initiation} + \# \text{ canids killed influenced rates from January to August})$	Survival varied by 3 seasons and year multiplicatively with the number of canids killed in a given year influencing rates from January through August of each year, individual covariates residency, sex, nest initiation
$\delta(3 \text{ season} \times \text{year} + \text{residency} + \text{sex} + \text{nest initiation} + \# \text{ canids killed influenced rates from January to December})$	Survival varied by 3 seasons and year multiplicatively with the number of canids killed in a given year influencing rates from January to December of each year, individual covariates residency, sex, nest initiation
$\delta(3 \text{ season} \times \text{year} + \text{residency} + \text{sex} + \text{nest initiation} + \# \text{ canids killed influenced rates from January to June})$	Survival varied by 3 seasons and year multiplicatively with the number of canids killed influencing rates from January through June of each year, individual covariates residency, sex, and nest initiation
$\delta(3 \text{ season} \times \text{year} + \text{residency} + \text{sex} + \text{nest initiation} + \# \text{ foxes killed influenced rates from January to August})$	Survival varied by 3 seasons and year multiplicatively with the number of red foxes killed influencing rates from January through August of each year, individual covariates residency, sex, and nest initiation
$\delta(3 \text{ season} \times \text{year} + \text{residency} + \text{sex} + \text{nest initiation} + \# \text{ canids killed influenced rates annually} + \text{dens gassed annually})$	Survival varied by 3 seasons and year multiplicatively with the number of canids killed and possible canid dens treated influencing rates from January through December of each year, individual covariates residency, sex, and nest initiation
$\delta(3 \text{ season} \times \text{year} + \text{residency} + \text{sex} + \text{nest initiation} + 1 \text{ year lag in the influence of the } \# \text{ of canids killed on rates from January to December})$	Survival varied by 3 seasons and year multiplicatively with the number of canids killed in the previous year influencing rates from January to December of the current year, individual covariates residency, sex, and nest initiation
$\delta(3 \text{ season} \times \text{year} + \text{residency} + \text{sex} + \text{nest initiation} + 3\text{-month lag in the influence of the } \# \text{ of canids killed on rates from January to December})$	Survival varied by 3 seasons and year multiplicatively with a 3-month lag for the number of canids killed influencing rates from January to December of each year, individual covariates residency, sex, and nest initiation
$\delta(3 \text{ season} \times \text{year} + \text{source})$	Survival varied by 3 seasons and year multiplicatively with grouse source location

of an all-possible-models approach (Burnham and Anderson 2002).

Our candidate models for stage 2 (Table 3) included those with hypothesized differences in survival between resident and translocated sage-grouse, where we expected translocated sage-grouse to demonstrate lower survival compared to resident birds. We also evaluated the support of models accounting for differences in survival related to the timing, implementation, and intensity of predator control plans by using the number of coyotes and red fox killed by Wildlife Services as a group-level covariate. Additional models accounted for the possible influence of increased numbers of birds from the translocations on survival rates. For this model, we used the number of released sage-grouse as a group-level covariate and called it translocation effect to investigate its effect on a given year's estimates.

We based model selection on the minimization of Akaike's Information Criterion (Akaike 1973) corrected for small

sample size (AIC_c; Lebreton et al. 1992), and AIC_c weights (w_i ; Buckland et al. 1997, Burnham and Anderson 2002). In the face of model uncertainty, we obtained model-averaged estimates (Burnham and Anderson 2002) of survival for the various time periods and influences. To evaluate effect sizes, we looked at overlap in confidence intervals associated with survival estimates and whether or not confidence intervals around β estimates (individual covariates) included zero.

RESULTS

We captured and fitted 535 sage-grouse with radio transmitters during the 13 year study. This sample included 383 females and 152 males (Table 4). We captured most of these individuals in the spring at or near leks; we captured <5% of individuals in the fall. Our sample included 336 translocated female sage-grouse that were moved over a 6-year period from 2003 to 2008 and 199 resident male and female sage-grouse captured from 1998 to 2010.

Table 4. Sex, age, and residency of all 535 radio-marked greater sage-grouse in Strawberry Valley, Utah from 1 April 1998 to 31 March 2011.

Group	Category	No.
Sex	Male	152
	Female	383
Age	Adult	296
	Yearling	222
	Unknown ^a	17
Residency	Resident	199
	Translocated	336

^a These grouse were either not assigned an age or we could not determine an age at time of capture given anatomical characteristics.

The first stage of our modeling approach identified a top model for time that split each year into the breeding-nesting (Apr and May), summer (Jun–Aug), and fall–winter (Sep–Mar) seasons (Table 5). This model received 98% of the AIC_c weight, with the next best model (4 seasons each year) only receiving 2%. Survival was consistently greatest during the fall–winter months (Fig. 2) with a mean monthly survival rate of 0.96 (95% CI = 0.96–0.97).

In the next stage of survival analysis, we added the group-level and individual covariates to our best time model. We only report those models from our a priori list that received $\geq 1\%$ of AIC_c weight (Table 5). The top model from this stage of analysis included 3 seasons that varied by year where rates were influenced by residency, sex, and whether a female initiated a nest. This model accounted for 22% of overall AIC_c weight. Residency, sex, and nest initiation were consistent influences in 7 of the top 8 models, which accounted for a combined total of almost 92% of overall AIC_c weight (Table 5).

The β estimate for the individual covariate of residency (residents = 1) in these top models had a positive influence on survival (model-averaged estimates for residency

$\beta = 0.41$, 95% CI = 0.07–0.74). Converting these values to odds ratios showed that resident sage-grouse were 1.51 times (95% CI = 1.07–2.10) more likely to survive than translocated sage-grouse. Similarly, the β estimate for nest initiation (initiated = 1) was positive (model-averaged $\beta = 0.58$, 95% CI = 0.21–1.00). Females that initiated nests were 1.79 times more likely to survive than those that did not (95% CI = 1.23–2.72). The β estimate for sex (male = 1), however, was negative (model-averaged $\beta = -0.34$, 95% CI = -0.74–0.02) suggesting that males had lower survival than females (odds ratio 0.71, 95% CI = 0.48–1.02); however, the confidence interval for sex slightly overlapped zero. Resident adult females survived better than any other group at a mean annual rate of 0.66 (95% CI = 0.49–0.79) across the study period, but significant overlap in confidence intervals occurred across categories (Table 6). Mean annual translocated yearling female sage-grouse survival was the lowest group survival rate recorded at 0.47 (95% CI = 0.35–0.61). In addition, survival rates for birds from each translocated source population were similar with significant overlap in confidence intervals (Table 7).

Models with group-level covariates associated with the number of canids killed received modest support as they improved model fit (deviance), but not enough to reduce AIC_c values compared to the top model (Table 5). For each of these models, the β estimates associated with predators killed was positive (range: 0.011–0.057), but in each case, the confidence intervals around these estimates slightly overlapped zero. For each model's β estimate associated with the influence of predators killed, zero was closest to the lower confidence bound. In some cases, such as the second-ranked model (19% of AIC_c weight), the overlap was very slight ($\beta = 0.011$, 95% CI = -0.006–0.029). Overlap in confidence

Table 5. Akaike's Information Criterion (adjusted for small sample sizes AIC_c) selected models predicting survival (\hat{s}) for resident and translocated sage-grouse in Strawberry Valley, Utah, USA, between 1 April 1998 and 31 March 2011. We report AIC_c , change in AIC_c (ΔAIC_c), AIC_c weight (w_i), number of parameters (K), and deviance (Dev, defined as $-2 \times \log$ likelihood) for all time models (stage 1, top half of table) and time plus group and individual covariate models (stage 2, bottom half of table) with $w_i \geq 0.01$.

Model	AIC_c	ΔAIC_c	w_i	K	Dev
Time models					
$\hat{s}(3 \text{ season} \times \text{year})$	2178.94	0.00	0.98	39	2,100.38
$\hat{s}(4 \text{ season} \times \text{year})$	2186.48	7.54	0.02	52	2,081.48
$\hat{s}(\text{breeding} \times \text{year})$	2225.27	46.33	0.00	26	2,173.01
$\hat{s}(\text{year})$	2240.85	61.91	0.00	13	2,214.78
$\hat{s}(4 \text{ season})$	2242.78	63.83	0.00	4	2,234.77
$\hat{s}(3 \text{ season})$	2247.96	69.02	0.00	3	2,241.95
$\hat{s}(\text{predator control year})$	2258.24	79.30	0.00	2	2,254.24
$\hat{s}(\text{breeding})$	2271.61	92.67	0.00	2	2,267.61
$\hat{s}(\cdot)$	2280.58	101.64	0.00	1	2,278.58
$\hat{s}(g \times t)$	2289.55	110.61	0.00	156	1,968.50
Time models with covariates					
$\hat{s}(3 \text{ season} \times \text{year} + \text{residency} + \text{sex} + \text{nest initiation})$	2168.89	0.00	0.22	42	2084.23
$\hat{s}(3 \text{ season} \times \text{year} + \text{residency} + \text{sex} + \text{nest initiation} + \# \text{ canids killed influenced rates January to August})$	2169.21	0.33	0.19	43	2082.53
$\hat{s}(3 \text{ season} \times \text{year} + \text{residency} + \text{sex} + \text{nest initiation} + \# \text{ foxes killed influenced rates January to August})$	2169.54	0.66	0.16	43	2082.86
$\hat{s}(3 \text{ season} \times \text{year} + \text{residency} + \text{sex} + \text{nest initiation} + \# \text{ canids killed influenced rates January to December})$	2170.04	1.15	0.13	43	2083.35
$\hat{s}(3 \text{ season} \times \text{year} + \text{residency} + \text{sex} + \text{nest initiation} + 3\text{-month lag on influence of canids killed})$	2170.59	1.70	0.10	43	2083.90
$\hat{s}(3 \text{ season} \times \text{year} + \text{residency} + \text{sex} + \text{nest initiation} + \# \text{ canids killed influenced rates January to June})$	2170.91	2.03	0.08	43	2084.23
$\hat{s}(3 \text{ season} \times \text{year} + \text{nest initiation})$	2171.58	2.70	0.06	40	2090.99
$\hat{s}(3 \text{ season} \times \text{year} + \text{residency} + \text{sex} + \text{age} + \text{nest initiation} + \text{nest success})$	2172.26	3.37	0.04	44	2083.54
$\hat{s}(3 \text{ season} \times \text{year} + \text{sex} + \text{age} + \text{nest initiation} + \text{nest success})$	2174.80	5.91	0.01	43	2088.11

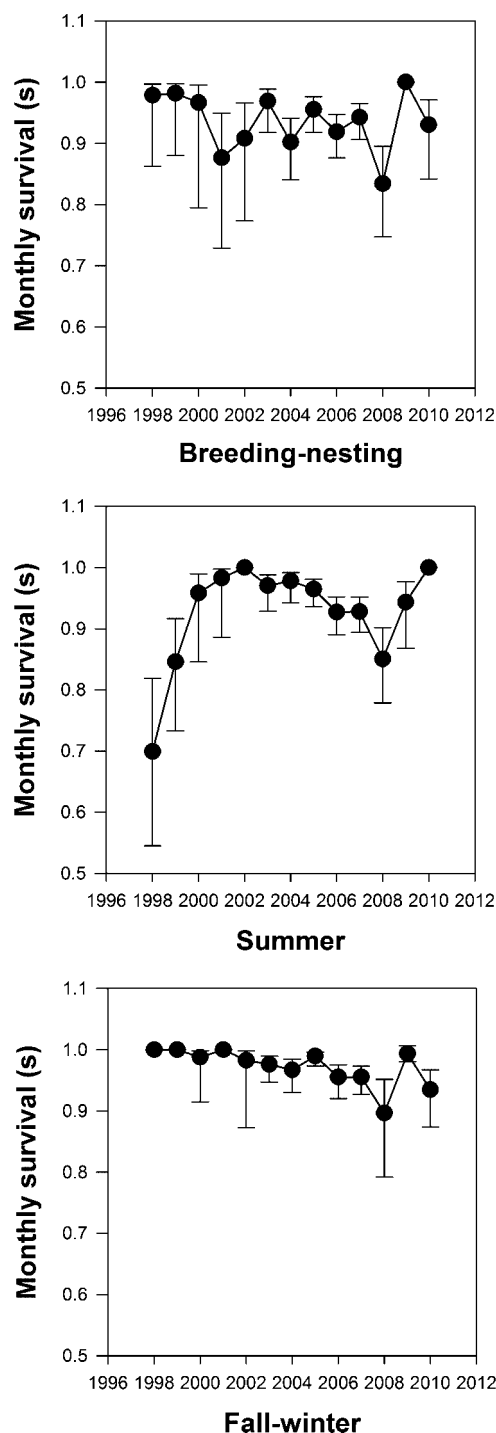


Figure 2. Mean monthly survival estimates of all radio-marked sage-grouse by season in Strawberry Valley Utah, USA from 1 April 1998 to 31 March 2011. Confidence intervals (95%) are denoted by bars above and below each mean value. Breeding-nesting = April–May, summer = June–August, and fall-winter = September–March.

intervals was driven largely by high survival rates observed in 2009 where annual survival estimates were >0.80 . Without this high rate, the confidence intervals around the β estimates associated with the influence of number of canids killed did not overlap zero. We found little support for any model containing the group-level covariate of source or a translocation effect because of the number of grouse released each year.

DISCUSSION

Survival of sage-grouse in our study area was influenced by seasonal year effects, status of grouse as resident or translocated, sex, and whether females initiated nesting. These findings are similar to those of Moynahan et al. (2006), who found that demographics (nesting), seasonal effects, and management (hunting), played a role in survival of grouse in Montana. Anthony and Willis (2009) were unable to detect within-year variation in survival based on environmental variables; however, they did find evidence for a strong lag effect of prolonged winter weather on survival rates. Our top model included an additive offset for residency suggesting that environmental conditions acted similarly upon sage-grouse regardless of their status as translocated or resident. A difference between male and female survival was expected (Bunnell 2000) and has been observed in other areas (June 1963, Connelly et al. 1994, Wik 2002). However, support for models containing the covariate of nest initiation was not expected. In our study, females that attempted to nest were more likely to survive than those that did not initiate a nest. Although this finding may seem counter intuitive, nesting females, which are able to expend large quantities of energy to initiate a nest and incubate the clutch, may have greater fitness, thus making them more likely to survive than a less fit female that is not able to initiate a nest.

Based on our experience with this population and given the high rate of observed mortality during the early years, we hypothesized that models accounting for the number of canids killed would receive support. For these models (Table 5), the β estimates associated with the number of canids killed were positive suggesting some influence of predator control on sage-grouse survival rates in Strawberry Valley. This observed influence, however, was rather modest as the improvement in model fit (deviance) for models with the number of canids killed did not result in a smaller AIC_c value (Table 5). Moreover, number of removed canids was only a coarse metric and may have been a poor surrogate for overall predator population numbers. In addition, we did not possess data on the number of canids killed by other predators or recreational hunters every year. Therefore, actual canid populations and their potential influence on survival rates could have varied from numbers reported by Wildlife Services. Moreover, we did not include the context of predator community structure or habitat variables in our analysis, further limiting our inference (Hagen 2011). All of these factors are likely associated with survival rates of sage-grouse in our study area and suggest caution be used when interpreting these results. Nonetheless, investigation of seasonal habitats (winter, nesting, brood-rearing, non-reproductive, occupied, and unoccupied summer habitat) used by sage-grouse in our study area have shown these habitats to be similar if not more complete (Bunnell 2000, Bambrough 2002, Baxter 2003, Bunnell et al. 2004) than those of many other populations throughout the species' range (Schroeder et al. 1999; Connelly et al. 2000, 2004).

Because seasonal effects influenced survival rates in our study, we cannot rule out the cyclic nature of sage-grouse populations as evidenced by research in Wyoming (Fedy and Aldridge 2011). Although Fedy and Aldridge (2011) could

Table 6. Mean annual survival estimates (s) grouped by age class, sex, and residency, with associated standard errors (SE) and lower and upper confidence intervals (LCI and UCI) for greater sage-grouse in Strawberry Valley, Utah, 1 April 1998 to 31 March 2011.

Group	s	SE	LCI	UCI
Translocated adult females	0.49	0.07	0.37	0.63
Translocated yearling females	0.47	0.07	0.35	0.61
Resident adult females	0.66	0.08	0.49	0.79
Resident yearling females	0.64	0.09	0.45	0.79
Resident adult males	0.57	0.09	0.39	0.73
Resident yearling males	0.55	0.10	0.36	0.73

not determine whether sage-grouse cycles occurred because of endogenous or exogenous factors, evidence suggested that exogenous factors played a role because cottontail rabbits (*Sylvilagus* spp.) experienced similar cycles, but with a 1-year lag. Nonetheless, we did not detect evidence of cyclic changes in the survival rates we observed in Strawberry Valley, possibly because we used radio-marked animals instead of lek counts and hunter harvest surveys as denoted in the Wyoming study (Fedy and Aldridge 2011). Moreover, yearling and adult survival rates are likely less responsive to cyclic change than lek attendance rates or production.

Annual survival rates of resident and translocated sage-grouse in our study were comparable to those reported in resident sage-grouse populations from Wyoming (35–67%; June 1963), Idaho (46–85%; Connelly et al. 1994), Colorado (37–78%; Zablán et al. 2003), and Montana (25–96%; Moynahan et al. 2006). In Idaho, Musil et al. (1993), reported survival of translocated grouse, using radio-telemetry and patagial tags, at 24% and 41% from March–April to August (6 months) in 1986 and 1987, respectively. In contrast, annual survival of translocated female sage-grouse for our study area ranged between 28% and 75% depending on source location with most estimates >45% (Table 7). This difference may have been due to translocated birds flocking with a remnant population of grouse in the valley, predator control during the translocation years, site-specific differences in habitat quality, or other unknown reasons.

The degree to which our results are applicable to other populations remains unclear because Strawberry Valley is a relatively isolated high-mountain mesic valley with frag-

mented, but productive habitat. This scenario is somewhat different from the fragmented and typically degraded habitats thought to be responsible for range-wide population declines (Connelly and Braun 1997). Additional work is warranted in light of predator community structure, the cyclic nature of sage-grouse populations, and habitat availability, fragmentation, and suitability. Understanding the complex nature of these systems will allow managers to maintain, enhance, and preserve other populations of sage-grouse.

MANAGEMENT IMPLICATIONS

Managers cannot eliminate the inter- and intra-annual variation that may affect sage-grouse survival rates. However, in our study, 3 features found in our top models can be manipulated by wildlife and land managers including translocation, habitat quality and quantity with special emphasis on nesting habitats, and predator control. Survival rates of translocated sage-grouse were consistently lower than residents, yet well within the observed range for resident sage-grouse and much greater than previous results for other translocations (e.g., Musil et al. 1993). Additional translocations are needed to quantify survival without concomitant predator control or to better understand survival when translocated birds are moved during the breeding season into recently extirpated areas. We suggest managers assess our results (Baxter et al. 2008, 2009) and the questions posed by Reese and Connelly (1997) prior to attempting a translocation. Additionally, improvement of seasonal year-round habitat will likely improve fitness and potentially increase nest initiation rates. Lastly, our results suggested a modest

Table 7. Mean annual survival estimates (s) of all females (yearling and adult) from Strawberry Valley and each of the translocated groups in the year they were captured and moved to Strawberry Valley, Utah, USA from April 1, 1998 to March 31, 2011.

Year ^a	Strawberry Valley (all F)				Parker mountain				Diamond mountain				Desert				Box elder			
	s	SE	LCI	UCI	s	SE	LCI	UCI	s	SE	LCI	UCI	s	SE	LCI	UCI	s	SE	LCI	UCI
1998	0.38	0.11	0.20	0.61																
1999	0.63	0.10	0.42	0.79																
2000	0.79	0.10	0.53	0.92																
2001	0.77	0.10	0.54	0.90																
2002	0.75	0.12	0.45	0.91																
2003	0.69	0.09	0.50	0.83	0.63	0.07	0.48	0.75												
2004	0.62	0.09	0.44	0.78	0.56	0.07	0.43	0.68												
2005	0.76	0.06	0.62	0.87	0.72	0.05	0.61	0.81	0.75	0.05	0.63	0.84								
2006	0.52	0.09	0.34	0.69	0.44	0.07	0.31	0.59					0.51	0.07	0.37	0.65	0.46	0.07	0.32	0.61
2007	0.53	0.09	0.36	0.70	0.46	0.07	0.33	0.60	0.51	0.07	0.37	0.65	0.53	0.07	0.40	0.66	0.48	0.07	0.34	0.62
2008	0.29	0.10	0.13	0.52									0.28	0.09	0.14	0.50				
2009	0.84	0.07	0.66	0.93																
2010	0.62	0.09	0.43	0.77																

^a Mortality year from 1 April of listed year to 31 March of subsequent year.

positive influence on sage-grouse survival from a predator control program. The lack of a control site and other potential confounding factors, however, limits the extent of our inference. For this reason, we suggest caution be exercised when interpreting our results or considering predator control.

ACKNOWLEDGMENTS

Funding and support for this project was provided by the Utah Reclamation, Mitigation, and Conservation Commission, the Utah Division of Wildlife Resources, the United States Forest Service, and Sportsmen for Fish and Wildlife. We thank Brigham Young University for their funding and logistical support. We thank K. Bunnell, D. Bambrough, J. Hennefer, R. Peck, J. Baxter, and countless field technicians for assisting in field data collection. We also thank the 2 anonymous reviewers and associate editor whose suggestions and comments improved this manuscript.

LITERATURE CITED

- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267–287 in B. N. Petrov and F. Csaki, editors. Second international symposium on information theory, Akademiai Kiado, Budapest, Hungary.
- Aldridge, C. L., and M. S. Boyce. 2008. Accounting for fitness: combining survival and selection when assessing wildlife-habitat relationships. *Israel Journal of Ecology and Evolution* 54:389–419.
- Anthony, R. G., and M. J. Willis. 2009. Survival rates of female greater sage-grouse in autumn and winter in southeastern Oregon. *Journal of Wildlife Management* 73:538–545.
- Bambrough, D. J. 2002. Greater sage-grouse winter and male and female summer habitat selection in Strawberry Valley, Utah. Thesis, Brigham Young University, Provo, Utah, USA.
- Barber, H. A. 1991. Strutting behavior, distribution, and habitat selection of sage grouse in Utah. Thesis, Brigham Young University, Provo, Utah, USA.
- Baxter, R. J. 2003. Greater sage-grouse brood and non-reproductive female habitat selection and population dynamics in Strawberry Valley, Utah. Thesis, Brigham Young University, Provo, Utah, USA.
- Baxter, R. J., J. T. Flinders, and D. L. Mitchell. 2008. Survival, movements, and reproduction of translocated greater sage-grouse in Strawberry Valley, Utah. *Journal of Wildlife Management* 72:179–186.
- Baxter, R. J., J. T. Flinders, D. G. Whiting, and D. L. Mitchell. 2009. Factors affecting nest-site selection and nest success of translocated greater sage grouse. *Wildlife Research* 36:479–487.
- Beck, J. L., K. P. Reese, J. W. Connelly, and M. B. Lucia. 2006. Movements and survival of juvenile greater sage-grouse in southeastern Idaho. *Wildlife Society Bulletin* 34:1070–1078.
- Bromley, C., and E. M. Gese. 2001. Surgical sterilization as a method of reducing coyote predation on domestic sheep. *Journal of Wildlife Management* 65:510–519.
- Buckland, S. T., K. P. Burnham, and N. H. Augustin. 1997. Model selection: an integral part of inference. *Biometrics* 53:603–618.
- Bunnell, K. D. 2000. Ecological factors limiting sage grouse recovery and expansion in Strawberry Valley, Utah. Thesis, Brigham Young University, Provo, Utah, USA.
- Bunnell, K. D., J. T. Flinders, D. L. Mitchell, and J. H. Warder. 2004. Occupied and unoccupied sage grouse habitat in Strawberry Valley, Utah. *Journal of Range Management* 57:524–531.
- Burnham, K. P., and D. A. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Connelly, J. W., and C. E. Braun. 1997. Long-term changes in sage grouse *Centrocercus urophasianus* populations in western North America. *Wildlife Biology* 3:229–234.
- Connelly, J. W., S. S. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming.
- Connelly, J. W., K. P. Reese, W. L. Wakkinen, M. D. Robertson, and R. A. Fischer. 1994. Sage grouse ecology. Study I: sage grouse response to a controlled burn. Idaho Department of Fish and Game, Pocatello, Idaho, USA.
- Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage-grouse populations and their habitats. *Wildlife Society Bulletin* 28:967–985.
- Crunden, C. W. 1963. Age and sex of sage grouse from wings. *Journal of Wildlife Management* 27:846–849.
- Fedy, B. C., and C. L. Aldridge. 2011. The importance of within-year repeated counts and the influence of scale on long-term monitoring of sage-grouse. *Journal of Wildlife Management* 75:1022–1033.
- Gehrt, S. D. 2005. Seasonal survival and cause-specific mortality of urban and rural striped skunks in the absence of rabies. *Journal of Mammalogy* 86:1164–1170.
- Giesen, K. M., T. J. Schoenbert, and C. E. Braun. 1982. Methods for trapping sage grouse *Centrocercus urophasianus* in Colorado, USA. *Wildlife Society Bulletin* 10:224–231.
- Griner, L. A. 1939. A study of sage grouse (*Centrocercus urophasianus*) with reference to life history, habitat requirements, and numbers and distribution. Thesis, Utah State Agriculture College, Logan, Utah, USA.
- Goodrich, S., E. D. McArthur, and A. T. Winward. 1999. Sagebrush ecotones and average annual precipitation. Pages 88–94 in E. D. McArthur, W. K. Ostler, and C. L. Wambolt, compilers. Proceedings: shrubland ecotones. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research, Station, RMRS-P-11, Ephraim, Utah, USA.
- Hagen, C. A. 2011. Predation on greater sage-grouse: facts, process, and effects. Pages 95–100 in S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology, Vol. 38, University of California Press, Berkeley, California.
- Jarvis, J. M. 1973. The Parker Mountain sage grouse study. Proceedings of the 53rd Annual Conference of the Western Association of State Game and Fish Commissioners 53:345–352.
- June, J. W. 1963. Wyoming sage grouse population measurement. Proceedings of the Western Association of State Game and Fish Commissioners 43:206–211.
- Knerr, J. S., and T. A. Messmer. 2005. Greater sage-grouse ecology in western Box Elder County, Utah. Utah State University, Logan, Utah, USA.
- Laycock, W. A., and P. A. Conrad. 1981. Responses to vegetation and cattle to various grazing on seeded and native mountain rangelands in eastern Utah. *Journal of Range Management* 34:52–58.
- Lebreton, J. D., K. P. Burnham, J. Clobert, and D. A. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- Miller, M. W., and M. M. Conner. 2005. Epidemiology of chronic wasting disease in free-ranging mule deer: spatial, temporal, and demographic influences on observed prevalence patterns. *Journal of Wildlife Diseases* 41:275–290.
- Moynahan, B. J., M. S. Lindberg, and J. W. Thomas. 2006. Factors contributing to process variance in annual survival of female greater sage-grouse in Montana. *Ecological Applications* 16:1529–1538.
- Musil, D. D., J. W. Connelly, and K. P. Reese. 1993. Movements, survival and reproduction of sage-grouse translocated into Central Idaho. *Journal of Wildlife Management* 57:85–91.
- Oyler-McCance, S. J., S. E. Taylor, and T. W. Quinn. 2005. A multilocus population genetic survey of the greater sage-grouse across their range. *Molecular Ecology* 14:1293–1310.
- Ralphs, M. H., and F. E. Busby. 1979. Prescribed burning: vegetative change, forage production, cost, and returns on six demonstration burns in Utah. *Journal of Range Management* 32:267–270.

- Reese, K. P., and J. W. Connelly. 1997. Translocations of sage grouse *Centrocercus urophasianus* in North America. *Wildlife Biology* 3:235–241.
- Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage grouse: *Centrocercus urophasianus*. *Birds of North America* 425: 1–28.
- Sedinger, B. S., J. S. Sedinger, S. Espinosa, M. T. Atamian, and E. J. Blomberg. 2011. Spatial-temporal variation in survival of harvested greater sage-grouse. *Studies in Avian Biology*, No. 39. University of California Press, Berkeley and Los Angeles, California, USA.
- Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. *Wildlife Society Bulletin* 20:425–426.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study Supplement* 46:120–138.
- White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, London, United Kingdom.
- Wik, P. A. 2002. Ecology of greater sage-grouse in south-central Owyhee County, Idaho. Thesis, University of Idaho, Moscow, Idaho, USA.
- Zablan, M. A., C. E. Braun, and G. C. White. 2003. Estimation of greater sage-grouse survival in North Park, Colorado. *Journal of Wildlife Management* 67:144–154.

Associate Editor: Peter Coates.