



Research Article

Juvenile Greater Sage-Grouse Survival, Movements, and Recruitment in Colorado

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ABSTRACT Juvenile survival and recruitment has not been studied extensively for greater sage-grouse (*Centrocercus urophasianus*). Because there is scant information on this vital rate, the implications of management actions on specific population demographics remain unknown. We re-captured, radio-marked, and monitored the survival and recruitment of 183 domestically hatched and wild-hatched juvenile sage-grouse from 1 September to 31 March 2005–2008 at 2 study areas in northwest Colorado, USA: Axial Basin and Cold Springs Mountain. Juvenile females had higher survival than juvenile males, and survival for each was higher in Axial Basin compared to Cold Springs Mountain. Domestically hatched juveniles had comparable survival to wild-hatched juveniles. We documented differences in survival between adult females and juveniles from September to March. Juvenile survival was lowest during September and October, coinciding with brood independence and movements to winter range and integrated flocks. Average survival from hatch to recruitment into the natal breeding population (Mar) varied between areas. Our findings provide an estimate of juvenile survival and recruitment so managers can better understand and model sage-grouse population dynamics. We recommend long-term (≥ 3 yr) research to better understand spatial and temporal variation in demographic rates. © 2017 The Wildlife Society.

KEY WORDS *Centrocercus urophasianus*, Colorado, domestically reared, greater sage-grouse, juvenile survival, movements, recruitment.

Vital rates influence population dynamics and can vary spatially and temporarily, but a working knowledge of vital rates is important in understanding a species' life history and developing population models (Cézilly et al. 1996, Caswell 2001). Although there are inherent logistical and financial challenges to estimating life-history vital rates, these data are critical in elucidating population dynamics, structure, and function to assist wildlife managers in developing effective management strategies (Taylor et al. 2012, Pollentier et al. 2014).

Juvenile survival within galliformes is an important vital rate during fall movements and brood break-up. Brood break-up is a sequence of behavioral events leading to the gradual independence of the brood from the brood female (Godfrey and Marshall 1969, Bergerud and Gratson 1988). Brood break-up has been hypothesized as being linked to the influence of photoperiod (Bowman and Robel 1977) or sex (Schroeder 1986), and some authors contend that brood break-up occurs prior to dispersal (Godfrey and Marshall 1969, Bowman and Robel 1977, Pitman et al. 2006).

The presettlement distribution of greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) has declined approximately 56% (Schroeder et al. 2004). In response to this decline, research on sage-grouse has focused on population ecology, habitat relationships, and the species response to management actions (Connelly et al. 2004, Knick and Connelly 2011). Research has assisted in developing small-scale management guidelines (Braun et al. 1977, Connelly et al. 2000) to sustain healthy populations (Aldridge and Boyce 2007, Doherty et al. 2008, Connelly et al. 2011). In some cases, sage-grouse populations have become small and isolated, and are vulnerable to demographic variability and are susceptible to environmental stochasticity (Lande 1988, Caughley 1994, Williams et al. 2003, Stiver et al. 2008).

Thus, research investigating novel captive-rearing techniques to augment small and declining sage-grouse and Gunnison sage-grouse (*C. minimus*; Thompson et al. 2015; Apa and Wiechman 2015, 2016) populations have been conducted. Specifically, Thompson et al. (2015) augmented wild-reared sage-grouse broods with domestically hatched chicks that were 1–10 days of age. They reported that chick survival ≤ 28 days was comparable between wild and domestically hatched chicks. Our investigation continues to evaluate domestically hatched individual survival through the juvenile life stage ultimately to recruitment.

Received: 20 November 2015; Accepted: 12 September 2016

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Our study is unique because juvenile sage-grouse survival to the first breeding season remains essentially unexplored. Taylor et al. (2012) identified 6 studies that investigated juvenile sage-grouse survival and used data from 4 studies in their vital rate sensitivity analysis (Beck et al. 2006, Bartazzo 2007, Herman-Brunson 2007, Walker 2008). All 4 studies had different start times in the fall, sample sizes of broods ranging from 8 to 40, and were not consistent in their juvenile survival estimation approaches (e.g., radio-telemetry vs. brood counts). Additionally, Caudill et al. (2014) investigated juvenile survival in Utah. Taylor et al. (2012) concluded that there is a need for additional research investigating juvenile sage-grouse survival especially from 35 to 60 days of age.

Our objectives were to 1) use radio-telemetry to estimate sex-specific juvenile sage-grouse survival from 1 September to 31 March and evaluate factors influencing survival; 2) compare adult and juvenile survival from September through March; 3) determine recruitment rates into breeding populations; and 4) evaluate range shifts and timing of movements from brood (fall) to winter ranges in relation to natal areas. We predicted that survival rates would be lower for juveniles compared to adults, and that juvenile survival would be lowest during the initiation of and during fall movement into wintering areas (Yoder et al. 2004, Beck et al. 2006). Furthermore, we predicted that survival rates between domestically and wild-hatched chicks would be similar because of similar experiences and exposures.

STUDY AREA

We conducted our research in 2 study areas in Moffat County, Colorado, USA from 2005–2008 (Fig. 1). We delineated study areas by encompassing neighboring leks where we captured birds and included a 6.4-km buffer around each lek. For sage-grouse, because breeding is largely restricted to leks and a large proportion of nests have been observed to be within 6.4 km of leks (Autenrieth 1969, Holloran and Anderson 2005), we defined a breeding population as a complex or group of leks within 6.4 km of each other. Average straight-line distance between study areas based on distances between leks was 101 km (range = 86–114 km).

The Axial Basin study area, approximately 736.7 km², consisted of a rolling topography ranging from 1,800–2,350 m in elevation and was centered on 7 active sage-grouse leks. Lek size based on the maximum male count at each of these leks in 2005 averaged 35 ± 8 (SE) males/lek and ranged from 18 to 81. Average distance between leks was 6.7 ± 0.7 km and ranged from 2.4 km to 13.6 km.

The Cold Springs Mountain study area encompassed parts of the eastern edge of the Uinta Mountain Range that extended approximately 30 km into the northwest corner of Colorado. This area was centered on 4 active leks. Lek size based on the maximum male count at each of these leks in 2005 averaged 38 ± 4 males/lek and ranged from 34 to 50.

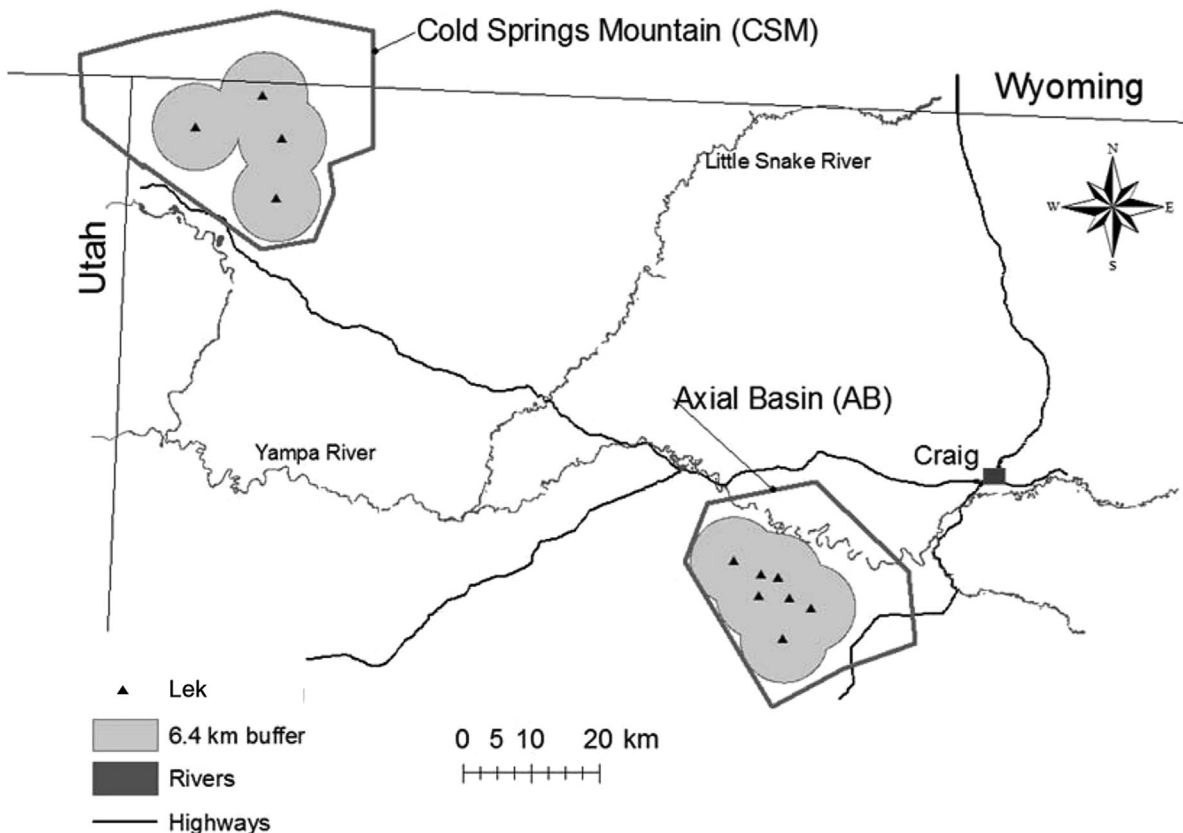


Figure 1. Study area in Moffat County, Colorado, USA depicting the Axial Basin (AB) and Cold Springs Mountain (CSM) study areas 2005–2008. Dark gray line depicts breeding season extent of radio-marked greater sage-grouse in each study area.

Table 1. Sample sizes of radio- and passive integrated transponder-marked juvenile male and female greater sage-grouse by origin (known wild-hatched, domestically hatched, or random capture) for 1 September to 31 March in northwest Colorado, USA, 2005–2008.

	F	M	Unknown	Total
Known wild-hatched ^a	59	40	5	104
Known domestically hatched ^b	7	8	1	16
Random ^c	40	10	13	63
Total	106	58	19	183

^a Juveniles for which the maternal female and natal area location (i.e., nest) are known.

^b Juveniles that were hatched and raised in captivity (1–10 days post-hatch) and released into wild surrogate broods for which the natal area location is known for the surrogate brood.

^c Juveniles that were captured opportunistically during recaptures of known wild-hatched chicks and juveniles for which the maternal female and natal area location are not known.

Average distance between leks was 11.7 ± 1.4 km and ranged from 6.8 km to 15.7 km. Topography consisted of mountainous areas, rolling hills, and mesas ranging in elevation from 1,900–2,900 m.

Both study areas support a diverse predator community and many of the species are documented predators of sage-grouse at differing life stages (e.g., eggs, juveniles, mature; Schroeder and Baydack 2001). Our study areas included, but was not limited to, golden eagle (*Aquila chrysaetos*), red-tailed hawk (*Buteo jamaicensis*), northern harrier (*Circus cyaneus*), American crow (*Corvus brachyrhynchos*), common raven (*C. corax*), black-billed magpie (*Pica hudsonia*), weasel (*Mustela* spp.), coyote (*Canis latrans*), bobcat (*Lynx rufus*), American badger (*Taxidea taxus*), red fox (*Vulpes vulpes*), and striped skunk (*Mephitis mephitis*).

The climate of northwestern Colorado was semiarid receiving 20.3–50.8 cm of precipitation annually depending on elevation (Western Regional Climate Center 2003). The

mean annual temperature for Moffat County was 6.3°C (Braun and Hoffman 1979) but was lower in areas of higher elevation like Cold Springs Mountain (4.4°C; U.S. Department of Interior 1978). Big sagebrush (*Artemisia tridentata* spp.) rangeland communities within the area comprised approximately 60% of the land area and the remainder was comprised of pinyon (*Pinus edulis*), juniper (*Juniperus* spp.), aspen (*Populus tremuloides*), spruce (*Picea* spp.), and mountain shrubs (Hausleitner 2003). Low elevation areas were dominated by Wyoming big sagebrush (*A. t.* subsp. *wyomingensis*), whereas higher elevation areas were mainly mountain big sagebrush (*A. t.* subsp. *vaseyana*) with pockets of mountain shrub communities. Land uses included cattle and sheep grazing, irrigated, and non-irrigated alfalfa (*Medicago sativa*), wheat (*Triticum aestivum*), Conservation Reserve Program (CRP) fields, mineral exploration and extraction, and ecotourism.

METHODS

Radio-Marking and Monitoring

All protocols for sage-grouse capture and transmitter attachment were approved by the University of Idaho Institutional Animal Care and Use Committee (protocol 2005-45). We captured females at night with spotlights and nets (Giesen et al. 1982, Wakkinen et al. 1992) near known leks during mid-March through late-April. We fitted females with an 18-g, 540-day necklace-mounted transmitter (model A4050, Advanced Telemetry Systems, Isanti, MN, USA) and an individually numbered aluminum leg band. We classified females as yearling (<1 yr old) or adult based on primary feather wear on feather number 9 and 10 (Eng 1955, Cruden 1963). We monitored 60–65 radio-marked females every 3–4 days in each study area during the spring, 2005–2007, until localization and confirmation of nest incubation. We determined nest

Table 2. Candidate models to predict survival (*S*) of known greater sage-grouse juveniles ($n = 114$), all juveniles ($n = 164$), and known greater sage-grouse adults (>1 yr old; $n = 223$) and juveniles ($n = 183$) from 1 September to 31 March in northwestern Colorado, USA, 2005–2008, including number of parameters (*K*), Akaike's Information Criterion values adjusted for small sample sizes compared to the best model (ΔAIC_c), deviance, and Akaike weights (w_i). We present competitive models ($\Delta AIC_c < 2$) plus the next ranked model.

Model description ^a	<i>K</i>	<i>AIC_c</i>	ΔAIC_c	Deviance	w_i
Known juveniles ^b					
<i>S</i> (study area + month)	8	290.74	0.00	274.48	0.32
<i>S</i> (sex + study area + month)	9	291.15	0.41	272.82	0.26
<i>S</i> (month)	7	292.16	1.42	277.96	0.15
<i>S</i> (sex + month)	8	292.36	1.62	276.10	0.14
<i>S</i> (sex × study area + month)	10	293.13	2.39	272.73	0.10
All juveniles ^c					
<i>S</i> (sex + study area + month)	9	388.40	0.00	370.19	0.53
<i>S</i> (sex × study area + month)	10	389.87	1.47	369.61	0.26
<i>S</i> (study area + month)	8	390.66	2.26	374.49	0.17
Adults and juveniles					
<i>S</i> (age × study area × year + month)	18	791.53	0.00	60.37	0.94
<i>S</i> (age + month)	8	805.15	13.62	94.23	0.00

^a Main effect models include the effects of time (month) and the grouping of variables of study area (Axial Basin or Cold Springs Mountain), and sex (female of male). Covariate models include the explanatory variable year (2005–2006, 2006–2007, 2007–2008).

^b Juveniles for which the maternal female and natal area location (i.e., nest) are known.

^c Known juveniles and random juveniles (those captured opportunistically with unknown natal area locations).

Table 3. Model-averaged survival rates (\hat{S}), standard error, and 95% confidence intervals from 1 September to 31 March for radio-marked male and female greater sage-grouse juveniles in the Axial Basin (AB) and Cold Springs Mountain (CSM) study areas in northwestern Colorado, USA, 2005–2008.

Model set ^a	Study area	Sex	<i>n</i>	\hat{S}	SE	95% CI
Known	AB	F	42	0.657	0.051	0.391–0.843
		M	28	0.598	0.077	0.313–0.810
	CSM	F	24	0.540	0.065	0.243–0.779
		M	20	0.477	0.089	0.182–0.742
All	AB	F	60	0.754	0.052	0.552–0.875
		M	31	0.621	0.070	0.359–0.805
	CSM	F	46	0.549	0.062	0.307–0.741
		M	27	0.410	0.081	0.169–0.648

^a Known = juveniles for which the maternal female and natal area location (i.e., nest) are known. All = known juveniles and random juveniles (those captured opportunistically with unknown natal area locations).

incubation by behavior of the female and by visually observing the female on the nest with binoculars from a distance of >5 m.

We estimated hatch date based on a 27-day incubation period (Schroeder 1997) and when we determined females

were no longer incubating. We documented nest fate and clutch size at the conclusion of nesting efforts. We considered a nest successful if ≥ 1 egg hatched as determined by the condition of the nest (i.e., disturbed, empty) and egg shell remains (Rearden 1951, Klebenow 1969).

We captured all chicks in the brood within 1–3 days post-hatch. We located radio-marked females <1 hour after sunrise or 1 hour before sunset while the female was brooding. We flushed the brood female and gathered chicks by hand and placed them in a cotton cloth bag or in small coolers with hand warmers. We weighed chicks to the nearest 0.1 g on an electronic scale, and estimated hatch date based on nest monitoring data and morphological characteristics of chicks (i.e., presence of an egg tooth, feather development; Gregg and Crawford 2009). We randomly selected 3 chicks from each brood to radio-mark with a 1.4-g, 40–60-day radio-transmitter (model A4330, modified, Advanced Telemetry Systems). We sutured the transmitter onto the back along the dorsal midline between the chick's wings (Burkpile et al. 2002) with monofilament suture

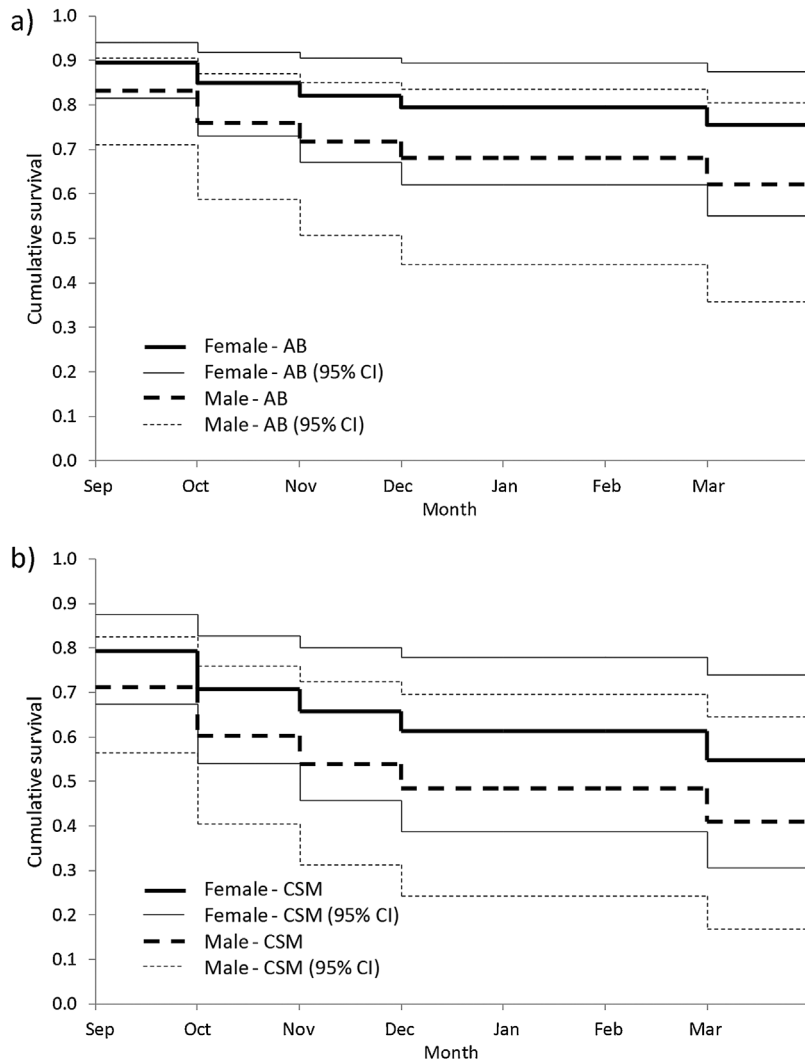


Figure 2. Model-averaged cumulative survival from 1 September to 31 March for all radio-marked female and male juvenile greater sage-grouse ($n = 164$) in a) Axial Basin (AB) and b) Cold Spring Mountain (CSM) study areas in northwest Colorado, USA, 2005–2008.

thread (Braunamide;polyamide 3/0 white and non-absorbable). We marked the remaining chicks within the brood by subcutaneously injecting mid-dorsally just above the wings an 11×2 -mm 0.078-g Passive Integrated Transponder (PIT) tag (Biomark, Boise, ID, USA) via a 12-gauge needle (Carver et al. 1999). After processing the brood (20–30 min), we released chicks to the female at the capture site and monitored (<1 hr and >50 m away) to confirm the return of the female to the brood.

Each year we placed approximately 3 ($\bar{x} = 3.0 \pm 0.2$, range = 1–8) domestically hatched 1–10-day-old ($\bar{x} = 3.9 \pm 0.2$) chicks into a subset of wild surrogate broods. Domestically hatched chicks were produced in a facility near Craig, Colorado (Thompson et al. 2015). We randomly selected available successful wild females (i.e., with brood) for placement of domestically hatched chicks. We radio-marked domestically

hatched chicks using the same transmitter attachment procedure used on wild-hatched chicks before placing them into wild surrogate broods. We released chicks into wild surrogate broods either <1 hour after sunrise or <1 hour before sunset. First, we located a radio-marked female brooding her wild chicks. We then flushed the female, collected all the wild chicks and placed them in the cooler with the domestically hatched chicks for approximately 10 minutes. We then released all chicks together from the location where the female flushed and monitored the return of the female back to the brood from a distance of >50 m.

We monitored radio-marked females and chicks daily for the first 28 days. We then monitored surviving radio-marked broods and chicks at least twice weekly through November. At 45–60 days of age, depending on functioning of the chick transmitter, we re-captured surviving chicks (now juveniles)

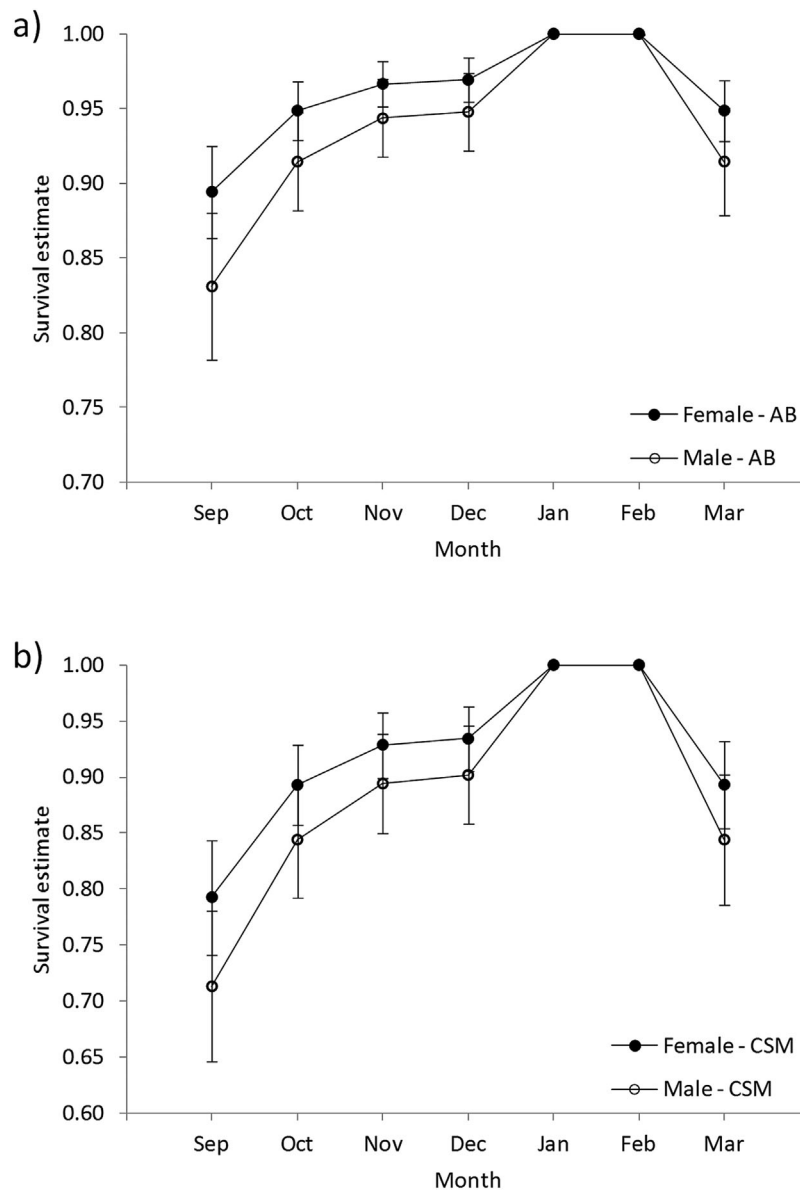


Figure 3. Model-averaged monthly survival estimates (\pm SE) from 1 September to 31 March for radio-marked female and male juvenile greater sage-grouse in the a) Axial Basin (AB) and b) Cold Springs Mountain (CSM) study areas in northwest Colorado, USA, 2005–2008.

Table 4. Model-averaged survival rates (\hat{S}), standard error, and 95% confidence intervals from 1 September to 31 March for radio-marked adult and juvenile greater sage-grouse in the Axial Basin (AB) and Cold Springs Mountain (CSM) study areas in northwestern Colorado, USA, 2005–2008.

Yr	Study area	Age	<i>n</i>	\hat{S}	SE	95% CI
2005–2006	AB	Adult	28	0.820	0.073	0.635–0.923
		Juvenile	41	0.671	0.075	0.512–0.798
	CSM	Adult	32	0.872	0.060	0.704–0.951
2006–2007	AB	Juvenile	16	0.540	0.127	0.301–0.762
		Adult	53	0.848	0.049	0.725–0.922
	CSM	Juvenile	31	0.622	0.086	0.446–0.770
2007–2008	AB	Adult	47	0.677	0.068	0.532–0.795
		Juvenile	39	0.385	0.083	0.239–0.555
	CSM	Adult	40	0.824	0.060	0.674–0.914
2007–2008	AB	Juvenile	24	0.876	0.067	0.678–0.959
		Adult	23	0.956	0.043	0.747–0.994
	CSM	Juvenile	32	0.354	0.084	0.211–0.528
All years	AB	Adult	121	0.831	0.061	0.678–0.920
		Juvenile	96	0.723	0.076	0.545–0.843
	CSM	Adult	102	0.835	0.057	0.661–0.913
		Juvenile	87	0.426	0.098	0.250–0.615

and replaced the original chick transmitter with a 3.9-g, 195-day juvenile transmitter (model A1080, Advanced Telemetry Systems). We located juveniles via radio-telemetry and recaptured them using long-handled hoop nets and spotlights at night in a similar fashion to females. Once captured, we removed the chick transmitter and attached the juvenile transmitter using the same chick transmitter suture technique. We scanned all captured juveniles with a handheld PIT tag reader to determine origin (i.e., known chick originally PIT-tagged with the brood after hatch or unknown and no PIT tag). We radio-marked and PIT-tagged all unknown juveniles captured.

In late-summer and early-fall (Aug through Oct) each year, we recaptured all surviving known radio-marked juveniles (i.e., those chicks radio-marked at hatch or at 40–60 days of age and actively monitored). We captured juveniles at night by locating them with telemetry equipment in a similar fashion to female and younger juveniles. We weighed each captured juvenile with an electronic scale and for those ≥ 900 g, we removed the 40–60-day transmitter and fitted them with an 18-g, 540-day adult necklace-mounted transmitter in a similar fashion to females. We scanned all juveniles with a handheld PIT-tag reader to determine origin. We radio-marked and PIT-tagged any unmarked random juvenile (natal nest location and maternal female unknown) that was captured and included them in the analyses.

We attempted to located juveniles from the ground at least once a week from 1 September through 1 April the following year using a portable receiver and 3-element yagi antennae. If we could not detect the transmitter signal of an individual, we systematically searched the surrounding areas from the ground or we made a fixed-wing aerial survey approximately every 2 weeks, or as needed, from September through April to search for missing individuals. Individuals that we detected during flights were located within 1 day from the ground to confirm that they were alive and the location.

Survival Analyses

Our most consistent detection occasion was a monthly basis; thus, we estimated monthly juvenile survival using the known fate option in Program MARK and modeled the effects of explanatory variables on survival (White and Burnham 1999). We included data from individuals only if their fate was known; the known fate model allows for staggered entry (Pollock et al. 1989). We right censored all individuals that went missing or had an unknown fate. We estimated survival for the 7-month period from late brood-rearing (1 Sep) to recruitment (31 Mar) into the breeding population. We constructed 3 *a priori* model sets to test for the effects of grouping and covariates on survival. We modeled monthly survival using only individuals with known nest sites by the groupings of study area (i.e., Axial Basin, Cold Springs Mountain) and sex (F, M), and including the covariates of year (2005, 2006, 2007), weight1 (body mass [g] at 40–65 days of age), weight2 (body mass [g] at 90–120 days of age), ordinal day of hatch, and juvenile type (wild, domestically hatched). In the second model set, we estimated monthly survival for all radio-marked juveniles by the grouping of study area and sex and the covariates year, weight2, and juvenile type.

For the third model set, we modeled the effect of age (juvenile or adult), study area, and year with no covariates. The adult individuals used in this model set were females originally radio-marked in the spring of a given year and consistently monitored thereafter. We included all individuals >1 year of age as adults in the final model set.

We developed a series of *a priori* hypotheses for each model set (Burnham and Anderson 2002) and used Akaike's Information Criterion corrected for small sample sizes (AIC_c) to compare within our candidate set of models. We assessed support for each model in a candidate set by the differences in AIC_c scores (ΔAIC_c) between the model with the lowest score in the set and each competing model and the weight of evidence for each model (w_i ; Burnham and Anderson 2002). We used the logit link to run all models. If no model was clearly superior to all others (AIC_c weight $>90\%$ and $\Delta AIC_c >2$), we performed model averaging of the model set to reduce the uncertainty in our parameter estimates. We calculated the model-averaged parameter estimates (β) and unconditional confidence intervals (Anderson 2008) for each covariate. Because correlated predictor variables can result in misleading parameter estimates when using model-averaging techniques (Cade 2015, Fieberg and Johnson 2015), we excluded models with covariates that co-varied ($|R| > 0.70$) to reduce the effects of multicollinearity (Kutner et al. 2004, Dormann et al. 2013).

Recruitment Analyses

We estimated recruitment (i.e., survival) using the known fate option in Program MARK (White and Burnham 1999), and staggered entry (Pollock et al. 1989) as previously described in our survival analyses. We estimate recruitment for the 11-month period from hatch (May and Jun) to entering (31 Mar) into the breeding population the following year. Our model included the main effects of study area and

year on monthly survival, and we ran 2 models: 1) for all juveniles (both wild-hatched known and domestically hatched); and 2) based on juvenile type (wild-hatched known vs. domestically hatched).

Movement Analysis

To determine seasonal range shifts of juveniles based on spatial locations from the natal nest to late-brood and winter ranges, we used the multi-response permutation procedure (MRPP; Mielke and Berry 1982, Biondini et al. 1988) in program BLOSSOM (Cade and Richards 2001). The MRPP is a powerful non-parametric method to detect differences in the distribution of spatial locations (Mielke and Berry 1982, Biondini et al. 1988). This procedure tests whether 2 or more sets of locations come from a common distribution by comparing the observed intra-group average distances between locations with the average distance that would result from all possible combinations of locations (Cade and Richards 2001, Yoder 2004). Because the MRPP can detect slight shifts in space use that may not be

biologically significant (White and Garrot 1990), we *a priori* defined 2 distinct periods for seasonal ranges (late-brood or fall and winter ranges) and set that any locations ≤ 1 km between these seasonal ranges were biologically insignificant even if the shift in location was statistically significant ($P < 0.01$; Yoder 2004). The late-brood period was from 15 August through 30 November and the winter period was 1 December through 15 March. We calculated the mean and median for the defined late-brood/fall and winter based on MRPP tests and visual inspection of locations to determine the straight-line movement distances between these periods and the natal nest or capture location. We defined the initiation of fall movements as the date a juvenile bird permanently moved >1 km from its mean late-brood location (Aug–Oct).

RESULTS

We monitored 183 juveniles from 1 September through 31 March in 2005–2008 (Table 1). We also monitored 223

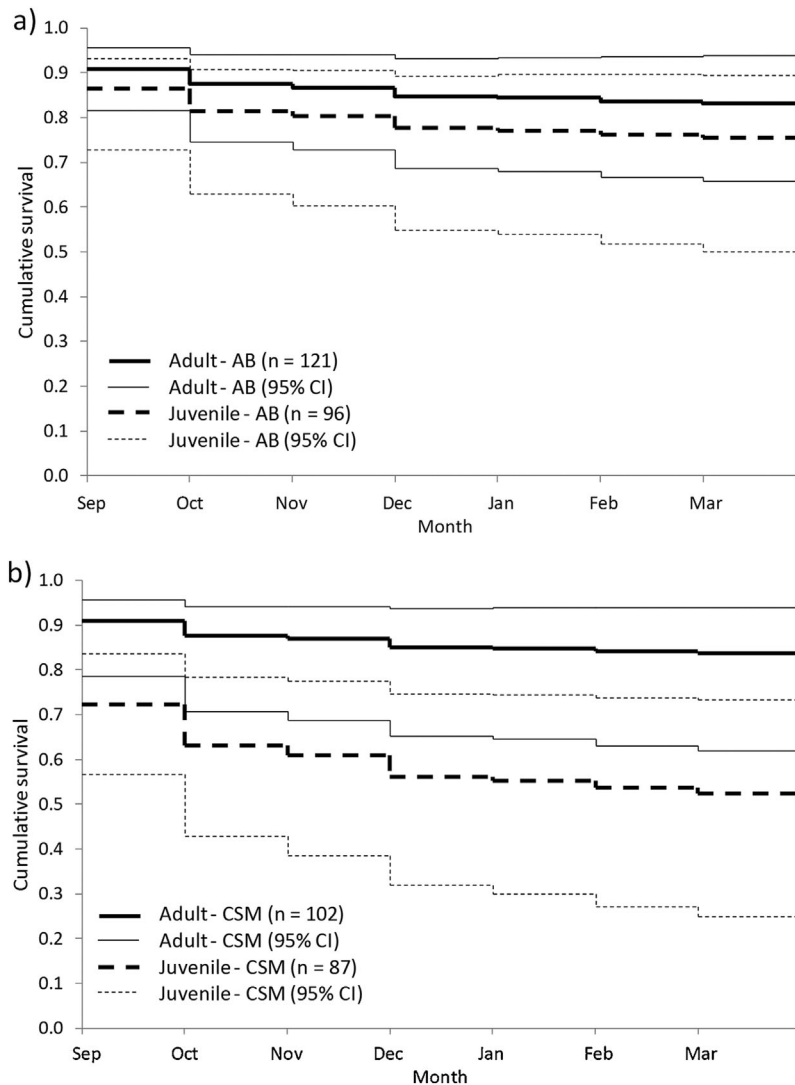


Figure 4. Model-averaged cumulative survival and 95% confidence intervals from 1 September to 31 March for radio-marked adult (>1 yr old) and juvenile greater sage-grouse in the a) Axial Basin (AB) and b) Cold Springs Mountain (CSM) areas of northwest Colorado, USA, 2005–2008.

adult female sage-grouse during the same time period. We determined the sex of 89.6% (164/183) of juveniles via direct observation of individuals during recaptures in the fall or through DNA genotyping (Thompson 2012). Juvenile body mass at 40–65 days of age was comparable between the 2 study areas (Axial Basin = 565.6 ± 22.3 g, Cold Springs Mountain = 565.8 ± 25.2 g; $F_{1, 111} = 0.0004$, $P = 0.99$), whereas juvenile body mass at 90–120 days post-hatch differed between the sexes ($F_{1, 96} = 142.1$, $P \leq 0.001$); $\bar{x} = 1,618.9 \pm 22.4$ g (range = 1,280–1,953) for males and $\bar{x} = 1,139.6 \pm 12.0$ g (range = 849–1,356) for females.

Survival

We right-censored 8 (4.4%) juveniles from our dataset because of transmitter failure or undetermined fate (e.g., mortality, but transmitter undetected or disappeared from the study area). We assumed censoring to be random and

because the numbers censored were identical between study areas (Axial Basin = 4, Cold Springs Mountain = 4), and 10–15% of the overall and within-year samples sizes (Winterstein et al. 2001, Murray 2006).

We used 3 candidate model sets to investigate the survival rates for 212 days of juveniles from late-brood status (1 Sep) through fall and winter, and recruitment into the breeding population (31 Mar). Model set 1 included only known juveniles ($n = 114$) grouped by study area and sex and incorporated the covariates of ordinal date of hatch, weight1, weight2, juvenile type, and year. There was model selection uncertainty within the top 4 models ($\Delta AIC_c \leq 2$; Table 2). All top models suggest that survival varies by monthly interval and 3 of the 4 models suggested that the additive effects of study area or sex were important factors (Table 2). We found no evidence that survival varied solely by study area or sex, or that there was an interaction (Appendix A).

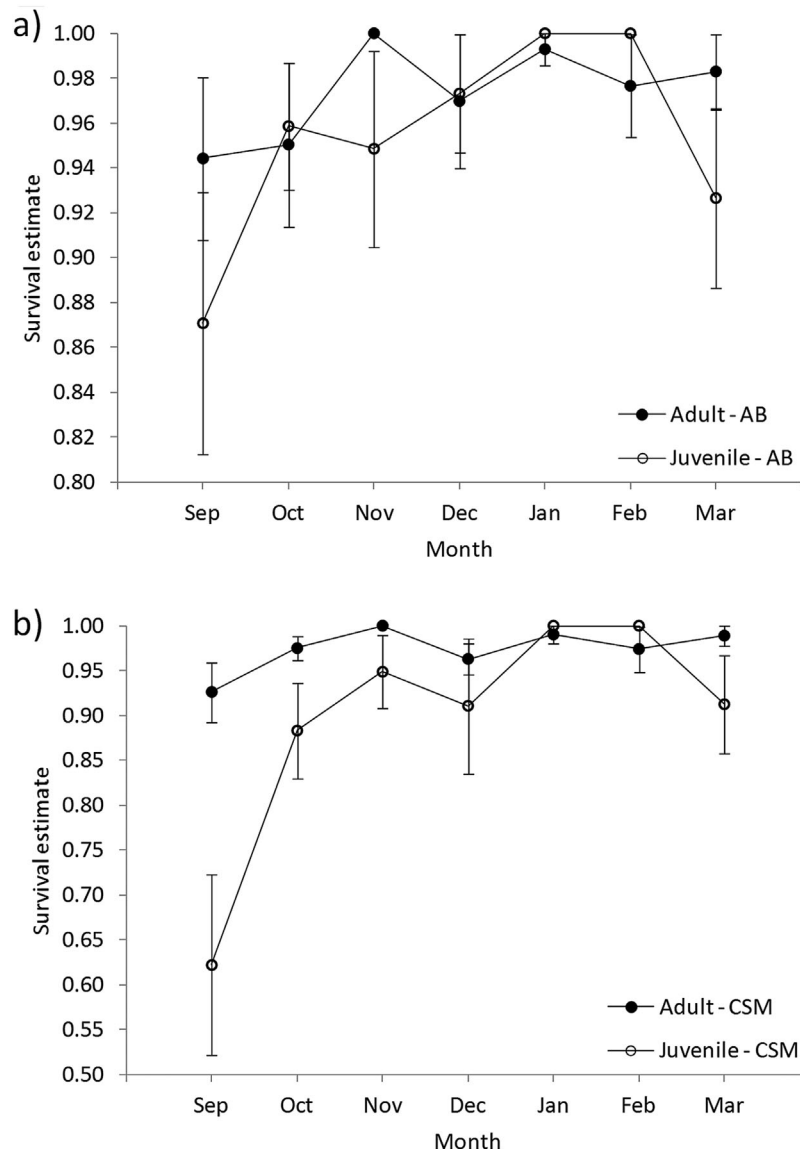


Figure 5. Model-averaged monthly survival (\pm SE) from 1 September to 31 March for radio-marked adult (>1 yr old) and juvenile greater sage-grouse in the a) Axial Basin (AB) and b) Cold Springs Mountain (CSM) study areas in northwest Colorado, USA, 2005–2008.

We also found no evidence of any univariate model effect on survival ($\Delta AIC_c > 29$) with inclusion not improving the fit of the data compared to the null model (Appendix A). In addition, the 95% confidence intervals for the estimated β coefficients for these covariates all overlapped 0 (ordinal date of hatch: $\beta = -0.018$, $SE = 0.012$, 95% CI = -0.042 to 0.005 ; weight2: $\beta = 0.001$, $SE = 0.001$, 95% CI = -0.002 to 0.001 ; weight1: $\beta = -0.001$, $SE = 0.001$, 95% CI = -0.002 to 0.0003 ; study area: $\beta = -0.092$, $SE = 0.456$, 95% CI = -0.985 to 0.801 ; year: $\beta = -0.029$, $SE = 0.197$, 95% CI = -0.415 to 0.357).

Model set 2 included all juveniles that were radio-marked, had confirmed sex determination after 1 September ($n = 164$; both known and random individuals), and were grouped by study area and sex. In addition, we included 3 covariates (weight2, juvenile type, and year) in model set 2. The best model based on AIC_c indicated that survival varied between sexes in a parallel pattern with study area and monthly interval (Table 2). This model accounted for 53% of the AIC_c weight of all models considered and was 2 times more likely

than the only other competing model (Table 2; Appendix B). The competing model indicated an interaction between study area and sex with the additive effect of monthly intervals. Similar to model 1, we found no evidence for an effect of the covariates year, juvenile type, and weight2 on survival ($\Delta AIC_c > 45$; Appendix B) and they did not improve the fit of the data compared to the null model. The 95% confidence intervals for the estimated β coefficients for these covariates also overlapped 0 (weight2: $\beta = -0.001$, $SE = 0.001$, 95% CI = -0.002 to 0.000 ; juvenile type: $\beta = 0.318$, $SE = 0.218$, 95% CI = -0.110 to 0.745 ; year: $\beta = 0.087$, $SE = 0.168$, 95% CI = -0.243 to 0.417).

We found no support in the model sets for the juvenile type covariate (Appendix A and B). Although our sample sizes were low for domestically hatched juveniles ($n = 16$), survival (\hat{S}) from 1 September through 31 March (7 months) was similar to wild-hatched chicks ($\hat{S} = 0.63$, $SE = 0.12$, 95% CI = 0.38 – 0.82 and $\hat{S} = 0.63$, $SE = 0.05$, 95% CI = 0.53 – 0.71 , respectively). We could not compare survival between wild-hatched and domestically hatched

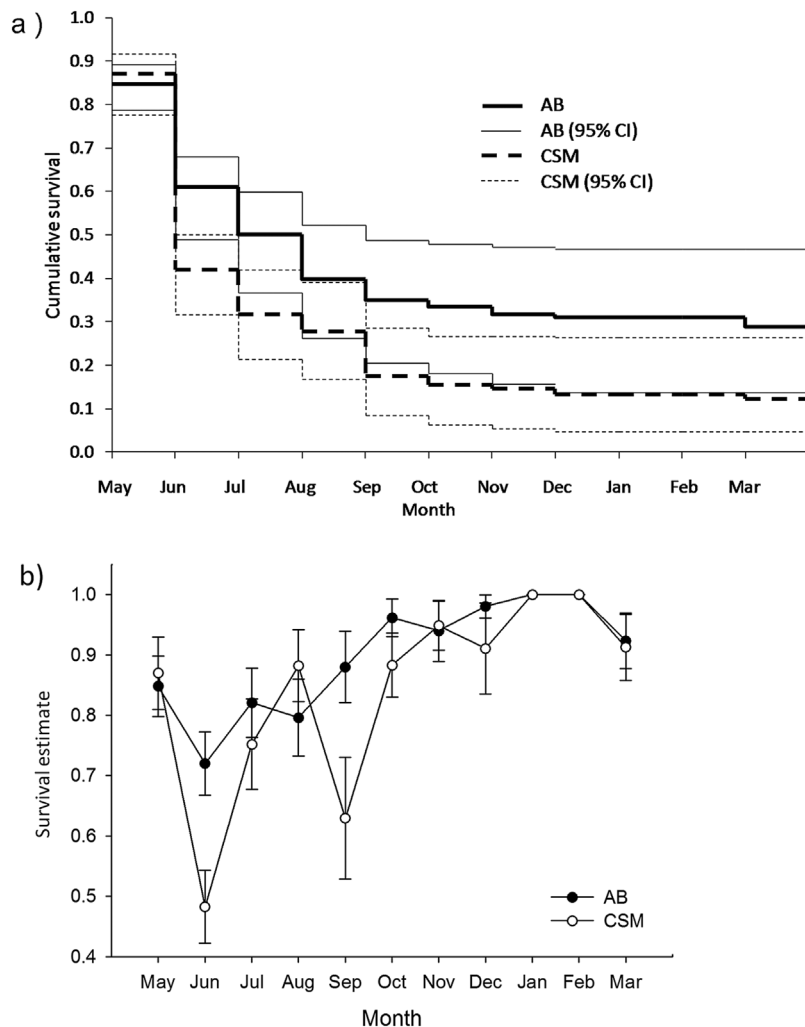


Figure 6. a) Recruitment based on monthly survival estimates (and 95% CI) and b) individual monthly survival estimates ($\pm SE$) from hatch to 31 March (11 months) for wild-hatched greater sage-grouse radio-marked as chicks and juveniles ($n = 517$) in the Axial Basin (AB) and Cold Springs Mountain (CSM) study areas in northwest Colorado, USA, 2005–2008.

Table 5. Descriptive statistics for distances moved between natal nest and late-brood (LB) and winter ranges for known and random female (F) juvenile radio-marked greater sage-grouse at 2 study areas (AB = Axial Basin, CSM = Cold Springs Mountain) in northwest Colorado (NWC), USA, 2005–2008.

Group ^a	Study area	Range shift	<i>n</i>	\bar{x} (km)	Median (km)	SD	SE	Min.	Max.
Known F	AB	LB	40	5.76	5.86	4.72	0.75	0.09	14.05
		Winter	37	9.38	5.29	10.32	1.70	1.75	43.17
	CSM	LB	16	2.93	2.16	2.20	0.55	0.56	7.43
		Winter	15	20.59	19.84	10.67	2.76	4.36	48.08
	NWC	LB	56	4.95	2.64	4.33	0.58	0.09	14.05
		Winter	52	12.62	7.70	11.52	1.60	1.75	48.08
Random F	AB	Winter	11	8.03	7.18	3.03	0.91	3.44	13.10
		Winter	14	19.03	19.17	8.74	2.34	3.88	33.58
	CSM	Winter	25	14.19	11.60	8.73	1.74	3.44	33.58
		Spring	23	3.91	3.23	2.44	0.51	1.27	11.76
	NWC	Nest	19	3.86	2.86	2.71	0.62	1.43	11.85
		Winter	48	8.71	6.24	6.78	1.31	1.75	43.17
Combined F	CSM	Winter	29	19.81	19.51	9.71	2.55	3.88	48.08
	NWC	Winter	77	13.13	8.54	10.66	1.22	1.75	48.08

^a Known = juveniles for which the maternal female and natal area location (i.e., nest) are known. Random = juveniles that were captured opportunistically with unknown natal area locations.

juveniles between study areas because no domestically hatched individuals survived to 1 September at Cold Springs Mountain; domestically hatched chicks were incorporated into our model-averaged survival estimates.

Model-averaged survival estimates of all known individuals from model set 1 tended to be higher for juveniles in the Axial Basin, and higher for females when compared to males (Table 3). For both sexes of known juveniles within study areas, September had the lowest average survival rates ($\hat{S} = 0.79$, SE = 0.02, range = 0.74–0.84) compared to the other 6 months; however, both sexes at Cold Springs Mountain continued to experience lower survival rates during October compared to individuals in Axial Basin.

Similar to model set 1, model-averaged survival estimates of all individuals from model set 2 tended to be higher for juveniles in Axial Basin, and higher for females than males within study areas (Table 3; Fig. 2). For both sexes within study areas, September had the lowest average survival rates ($\hat{S} = 0.81$, SE = 0.04, range = 0.71–0.89) followed by survival increases through December with survival remaining lower for males compared to females (Fig. 3). During January

and February neither sex experienced any mortalities, but this was followed by lower survival rates in March for males and females (Fig. 3).

In model set 3, we included the effect of age on survival. This model set included all juveniles ($n = 183$) and all adults (>1 yr old; $n = 223$) grouped by age, study area, and year with no covariates. The best model for the data was S (age \times study area \times year + month), indicating that survival rates varied between juveniles and adults, and between study areas and among years in a parallel pattern with monthly intervals (Table 2). In this model set, there were no other models within 2 AIC_c units of the top model, with the top model accounting for 94% of the weight of all models considered and 16 times more likely than the next model (Table 2; Appendix C).

Within and among the 3 years of our study, adults had higher survival than juveniles; however, these estimates varied within and among years and between study areas (Table 4; Fig. 4). Juveniles generally had lower but increasing survival rates compared to adults during the fall (especially during Sep and Oct), with high survival during the winter (Jan and Feb) within

Table 6. Descriptive statistics for distances moved between natal nest and late-brood (LB) and winter ranges for known and random male (M) juvenile radio-marked greater sage-grouse at 2 study areas (AB = Axial Basin, CSM = Cold Springs Mountain) in northwest Colorado (NWC), USA, 2005–2008.

Study area ^a	Range shift	<i>n</i>	\bar{x} (km)	Median (km)	SD	SE	Min.	Max.	
Known M	AB	LB	16	4.57	2.25	4.77	1.19	0.09	13.42
		Winter	14	8.05	6.24	5.59	1.50	2.08	23.28
	CSM	LB	8	1.72	1.19	1.53	0.54	0.48	5.18
		Winter	6	18.00	17.25	8.86	3.62	5.43	28.35
	NWC	LB	24	3.62	1.44	4.17	0.85	0.09	13.42
		Winter	20	13.03	11.75	7.23	2.56	2.08	28.35
Random M	AB	Winter	1	14.24					
	CSM	Winter	4	15.62	15.64	5.04	2.52	9.48	21.72
	NWC	Winter	5	14.93	14.23	4.87	2.49	9.48	21.72
Combined M	Winter	25	11.90	10.61	7.55	1.51	2.08	28.35	

^a Known = juveniles for which the maternal female and natal area location (i.e., nest) are known. Random = juveniles that were captured opportunistically with unknown natal area locations.

study areas (Fig. 5). However, survival differences between ages were greatest at Cold Springs Mountain, with juveniles having significantly lower survival rates compared to adults from September through November, and in March (Fig. 5). Juveniles in Axial Basin showed a similar pattern to Cold Springs Mountain juveniles, although differences in survival estimates with adults were not as large (Fig. 5).

Recruitment

We estimated recruitment of wild juvenile sage-grouse using monthly survival estimates from hatch (May and Jun; Thompson et al. 2015) to 31 March. Average recruitment in Axial Basin was 0.29 (SE = 0.04, 95% CI = 0.05–0.55) and 0.12 (SE = 0.05, 95% CI = 0.00–0.34; Fig. 6a) at Cold Springs Mountain. Both areas showed annual variation in recruitment. However, for all 3 years, mean recruitment was considerably higher in Axial Basin compared to Cold Springs Mountain (2005: 0.45 vs. 0.20, 2006: 0.27 vs. 0.18, 2007: 0.22 vs. 0.08). Although we found the 11-month survival pattern was generally similar between study areas, indicating significantly lower survival in June and again in September and March, the magnitude of these events

differed between areas (Fig. 6b). The recruitment of domestically hatched juveniles was 0.19 (SE = 0.05, 95% CI = 0.11–0.31) in the Axial Basin, but we could not estimate recruitment at Cold Springs Mountain for domestically hatched juveniles because no individuals survived past September.

Juvenile Movements and Timing

Distances of winter locations (~Dec–Mar) of juveniles from the natal nest varied by study area, rather than by sex or juvenile type (Tables 5 and 6). The distance of winter areas to natal nests in the Axial Basin was variable (range = 1.75–48.08 km) but on average were closer to the natal nest (\bar{x} = 8.48 km, SD = 7.14, n = 63) than at Cold Springs Mountain (\bar{x} = 18.32 km, SD = 8.44, n = 39; t_{64} = -2.67, P = 0.010).

Within each study area and sex, both known juveniles and random juveniles exhibited similar dates for the initiation of movements in the fall, although dates differed between study areas (W = 451.0, P < 0.001, n = 102; Fig. 7). The average date for the initiation of fall movements in the Axial Basin was 8 October (\pm 2.8 days). Females initiated fall movements 4 days earlier than males (7 Oct vs. 11 Oct, respectively; Fig. 7a).

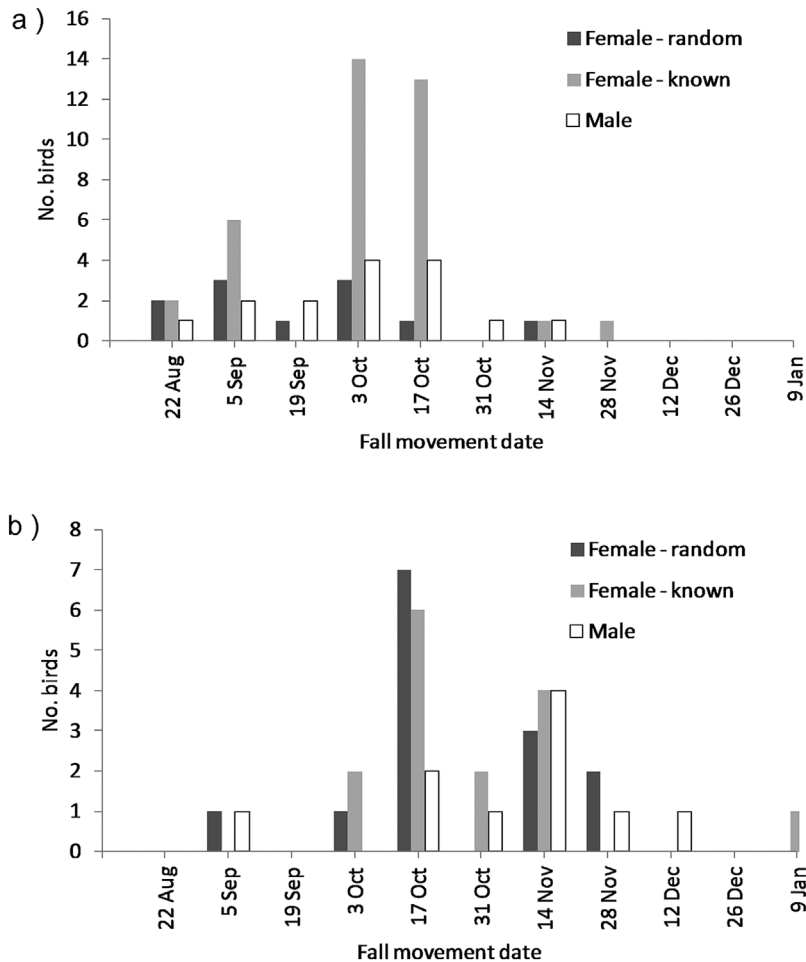


Figure 7. Timing of fall movements for female known (natal area know) or random (natal area unknown) and male radio-marked juvenile greater sage-grouse in the a) Axial Basin (n = 63) and b) Cold Springs Mountain (n = 39) study areas in northwest Colorado, USA, during 2005–2008. Dates are in 2-week increments.

At Cold Springs Mountain, the average fall movement initiation date was 6 November (± 3.9 days; Fig. 7b). Females also initiated fall movements 6 days earlier than males (5 Nov and 11 Nov, respectively; Fig. 7b). Average age at the start of fall movement for known juveniles was 145.5 days post-hatch (week 21). Movements for juveniles at Cold Springs Mountain ($\bar{x} = 141.2$ days, $SD = 29.7$, $n = 39$) were generally at an earlier age compared to Axial Basin ($\bar{x} = 156.7$ days, $SD = 23.5$, $n = 63$) but later for males ($\bar{x} = 146.6$ days, $SD = 28.3$, $n = 25$) than females ($\bar{x} = 142.5$ days, $SD = 30.7$, $n = 77$). These apparent differences were not statistically different between study areas ($W = 471.0$, $P = 0.073$, $n = 102$) or sexes ($W = 639$, $P = 0.996$, $n = 102$).

We found that brood independence was gradual, lasted approximately 16 days (range = 1–58 days), and was independent of brood age (range = 16–20 weeks of age). The general movements of juveniles in the Axial Basin after October tended towards the natal area (<5 km from natal nest), north of the Axial Basin, or within the late-brood areas, and movements were equally likely between females and males. Movement behaviors at Cold Springs Mountain with juveniles after October were also similar between the sexes: generally down in elevation to lower elevation xeric sagebrush and saltbrush (*Atriplex* spp.) communities north, northeast, and east of Cold Springs Mountain (3.9–48.1 km from natal areas or late-brood capture locations).

DISCUSSION

Survival

Our results are 1 of 2 studies to report evidence of sex-specific survival. Our results agree with Caudill et al. (2014) that juvenile females had higher survival rates than juvenile males. This was true in both of our study areas. In addition, Axial Basin male and female juveniles had higher survival compared to Cold Springs Mountain. These differences occurred predominately during September and to a lesser extent in October. Other studies using radio-marked individuals have reported no survival differences between juvenile female and male grouse (Hines 1986, Beck et al. 2006, Hannon and Martin 2006). We suggest that the overall lower survival of males could be related to the dimorphism in mass between sexes, and the increased nutritional demands and stresses males incur during the transition to a sagebrush-dominated diet (Remington and Braun 1985), sexual maturation, and flock integration (Swenson 1991). It takes nearly 2 years for males to achieve their adult mass and at the age of brood independence, juvenile males have achieved 57% of their yearling body mass (Beck and Braun 1978). We suggest that our observed difference in survival during early fall (on late brood-rearing areas) between the sexes is due to the increased nutritional requirements to reach adequate body mass, an increased development of sexual characteristics and maturation, and the social and behavioral changes related to brood independence and flock integration.

Our juvenile survival rate in the Axial Basin for September to March was comparable to survival (0.64 and 0.86) reported for juvenile greater sage-grouse at 2 study areas in Idaho (Beck et al. 2006). However, at Cold Springs Mountain, survival was considerably lower than reported in Idaho. Similar to Beck et al. (2006), we found that juvenile survival differed between study areas, suggesting that there are specific differences between areas (e.g., habitat conditions or spatial habitat configurations could influence survival rates). Beck et al. (2006) concluded that the observed differences in juvenile survival between study areas was a result of a 20% increase in distances moved between seasonal ranges in one study area compared to the other ($\bar{x} = 12.6$ km compared to $\bar{x} = 9.8$ km), thereby increasing exposure to predators. In our study, distances between late-brood range and winter range were more than twice as far at Cold Springs Mountain compared to Axial Basin, suggesting that this could potentially affect survival. However, the lowest juvenile survival in both areas occurred prior to this seasonal movement. Thus, some factor other than distance between seasonal ranges is likely contributing to the differences we observed between study areas. As such, our findings do not directly support the conclusions of Beck et al. (2006).

We found comparable patterns of survival between wild and domestically hatched juveniles into the fall and through brood break-up. Our findings further support Thompson et al. (2015) who suggested that captive-rearing techniques could be used to augment demographically challenged sage-grouse populations (Apa and Wiechman 2015, 2016), but the technique could be less successful in extreme environments (e.g., Cold Springs Mountain).

We also documented differences in survival between adult females and juveniles in both study areas from September to March. Juvenile survival was lower than adult survival during the early fall (Sep and Oct) and early spring (Mar), although juvenile survival was comparable to adult female survival from November through February. Previous research suggests that differences between adult and juvenile survival may be result of a greater vulnerability of juveniles to predation during these spring and fall transition periods (Hannon and Martin 2006). Our estimates of survival from September through March for adult females in both areas (0.83) was within the range or higher than previously reported studies across the range of sage-grouse, although survival estimates were estimated over differing time periods (Wik 2002, Hausleitner 2003, Moynahan, 2004, Anthony and Willis 2009). Warren and Baines (2002) attributed lower survival rates of juvenile black grouse (*Tetrao tetrix*) when compared to adults as a result of predation by raptors and stoats (*Mustela ermine*). Similarly, Small et al. (1991, 1993) reported survival in ruffed grouse (*Bonasa umbellus*) was lower during fall and winter for juvenile than adults. They concluded that the lower survival was due to higher predation rates by northern goshawks (*Accipiter gentilis*) and mammal species (Small et al. 1991, 1993). Our results support these conclusions; predation, primarily by mammals, accounted for 86.7% of all mortalities during this period (Thompson 2012).

We observed that juvenile sage-grouse survival was lowest during the early fall (Sep and Oct) and then again in late-winter (Mar) and corresponded to timing of brood independence and shifts in seasonal habitat use. Other research (Hannon and Martin 2006) support our findings. Hannon and Martin (2006) suggest that lower survival rates of juveniles during the fall and winter were not associated with distances traveled between seasonal ranges but concluded that movement is not the primary reason for lower survival. Caizergues and Ellison (1997) also observed lower survival of juvenile black grouse during the fall and winter but attributed the lower survival to juvenile inexperience with predators as independence from the brood increased. A majority of our radio-marked juvenile movements at Cold Springs Mountain occurred on or near late brood-rearing areas. To a lesser extent, we observed this among juveniles in Axial Basin, although some movements were to wintering areas. We suggest that the lower survival in September may be due to juveniles becoming independent from their brood and joining winter flocks prior to movement. Integrating into winter flocks could help reduce risks during migration between seasonal ranges for 2 reasons: flocking would reduce the risk of predation because of increased number of individuals (e.g., to detect predators or to dilute predation risk; Clark and Mangel 1986), and joining flocks with older more experienced individuals could reduce the exposure time of juveniles to unfamiliar or risky areas, especially because older individuals show fidelity to wintering areas and more efficiently exploit food resources (Swenson et al. 1995).

During the 3 years of our study, we recorded 2,714 locations of juveniles between October and March with 48.3% of these locations being in flocks or areas with ≥ 1 unrelated radio-marked adult individual. As such, we suggest that the lower survival we observed in September could be a result of the gradual disintegration and break-up of the natal brood before the ultimate integration of juveniles into winter flocks. This transition period could expose juveniles to greater predation risk making them more susceptible to stressors, thereby increasing those risks if the exposure is prolonged.

Recruitment

In both study areas, the majority of chicks maturing to the juvenile life-stage and entering the breeding population were recruited locally into their natal populations (Thompson 2012). We documented only 1 male in Axial Basin moving into a new breeding population. We estimated recruitment of juvenile sage-grouse from hatch to entering the breeding population as 0.29 in Axial Basin and 0.12 at Cold Springs Mountain, although estimates varied greatly among years within areas. The differences in recruitment rates between study areas occurred after hatch and during the beginning of fall, with Cold Springs Mountain having lower survival during June and September. The average recruitment estimates in our study areas may be insufficient to replace adult losses or to sustain population levels if they were to decline significantly. Our conclusion of low recruitment

could also be supported by comparing our recruitment estimate to a management lek count index, which tracks long-term male counts on strutting grounds. We caution regarding the inference by comparing demographic rates with a population index, but these data suggest that the decline in the number of males counted on leks could lend credence to our suggested low levels of recruitment (Fig. 8). The results of our study, and the eventual increase in the number of males counted (Fig. 8), indicate that there is a need for long-term vital rate studies. If management decisions to correct for low recruitment rates were made at the conclusion of our study, the decisions would have been premature. Our findings provide a much needed, although short-term, estimate of juvenile survival to develop meaningful demographic models that can rigorously evaluate sage-grouse population dynamics and better understand population persistence.

Juvenile Movement Timing

We observed that brood independence started primarily in early September and continued through the first week of October, thereby supporting other findings (Godfrey and Marshall 1969, Bowman and Robel 1977) that suggested brood break-up and recruitment were temporally specific behavioral activities, and the period between them was the most stressful time for juveniles. Additionally, for those broods using higher elevation late-brood habitats ($>2,000$ m) at Cold Springs Mountain and Axial Basin,

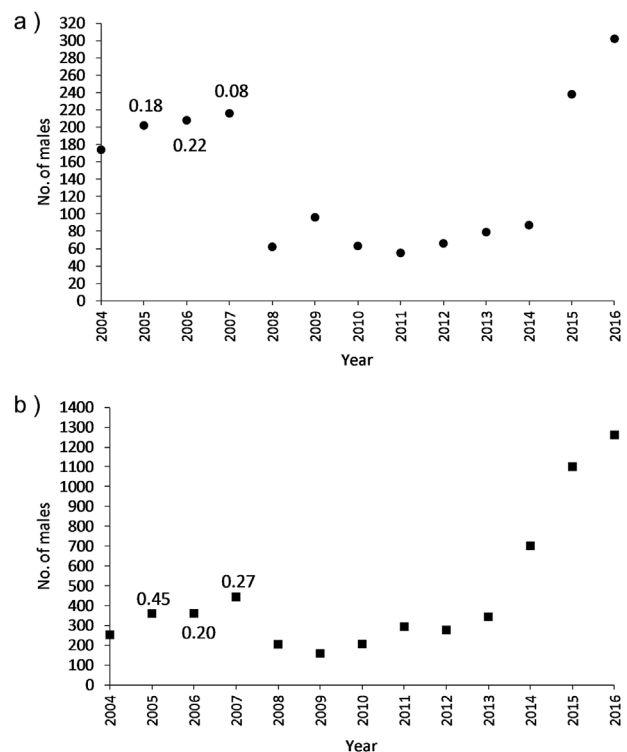


Figure 8. Number of male greater sage-grouse counted annually at a) Cold Springs Mountain and b) Axial Basin from 2004 through 2015 (Colorado Parks and Wildlife, unpublished data) and corresponding recruitment estimates from this study in northwest Colorado, USA, 2005–2008.

we observed that weather events (e.g., cold fronts and snowfall), seemed to ultimately trigger the final dissolution of broods and integration into wintering flocks.

MANAGEMENT IMPLICATIONS

Wildlife managers need a better understanding of age-specific demographic rates and how they are related to local and regional landscapes in relation to movement patterns, population levels, and habitat use to manage sage-grouse. We further support recommendations by Thompson et al. (2015) that captive-reared sage-grouse can recruit to the population and that captive rearing could be used as a potential management strategy for demographically challenged sage-grouse populations (Apa and Wiechman 2015, 2016). Although demography research is expensive and logistically challenging, long-term studies are needed to account for spatial and temporal variability. If managers use information from short-term (≤ 3 yr) studies, they risk incorrect decisions that could lead to premature management actions.

ACKNOWLEDGMENTS

We thank L. P. Waits, L. A. Vierling, A. M. Wiese (Coy), E. R. High (Duvuvuei), N. W. Gruber, A. M. Vande Vort, L. and D. Brittan, E. Wengert, A. J. Gmyrek, J. B. Stiver, S. Florin, N. Dryer, L. A. Wiechman, M. R. Shardlow, N. P. Gould, M. Christinson, B. Voelker, J. Sinclair, K. B. Howe, B. A. Miller, K. J. Rider, K. M. Tadvick, C. Yarrow, O. Bartell, O. Duvuvuei, and S. A. Vincent. We also thank the following agencies, organizations and individuals for logistic and technical support: Colorado Division of Parks and Wildlife, Colowyo Coal Company, Bureau of Land Management, Vermillion Ranch (Dickinson family), Diamond Peak Cattle Company, Simpson Ranch, Moore family, K. Bekkedahl, Cook family, Seely Land and Livestock Company, D. Griffin, A. Mead, Cross Mountain Ranch, Deakins Ranch, N., and A. Charchalis, Visintainer Sheep Company, Brannan Brothers, L. Earl, Kourlis Ranch, Moffat County Grazing Board, and Colorado State Land Board. This manuscript benefited from the reviews of R. C. Conrey and T. E. Fulbright and 2 anonymous reviewers. Financial and logistical support was provided by the Colorado Division of Parks and Wildlife, the National Fish and Wildlife Foundation, and the University of Idaho.

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Associate Editor: Timothy Fulbright.

Appendix A

Candidate models to predict survival (S) of known greater sage-grouse juveniles ($n = 114$) from 1 September to 31 March in northwestern Colorado, USA, 2005–2006, 2006–2007, and 2007–2008. Including number of parameters (K), Akaike's Information Criterion values adjusted for small sample sizes compared to the best model (ΔAIC_c), deviance, and Akaike weights (w_i).

Model description ^a	K	AIC_c	ΔAIC_c	Deviance	w_i
S (study area + month)	8	290.74	0.00	274.48	0.32
S (sex + study area + month)	9	291.15	0.41	272.82	0.26
S (month)	7	292.16	1.42	277.96	0.15
S (sex + month)	8	292.36	1.62	276.10	0.14
S (sex \times study area + month)	10	293.13	2.39	272.73	0.10
S (t, t ²)	3	295.34	4.60	289.30	0.03
S (t)	2	299.57	8.84	295.55	0.00
S (study area \times month)	14	301.73	11.00	272.97	0.00
S (sex \times month)	14	302.81	12.08	274.05	0.00
S (sex + study area)	3	317.70	26.96	311.66	0.00
S (study area)	2	317.88	27.14	313.86	0.00
S (sex \times study area)	4	319.66	28.92	311.58	0.00
S (sex)	2	320.13	29.39	316.11	0.00
S (ohd)	2	320.34	29.60	316.32	0.00
S (.)	1	320.57	29.83	318.56	0.00
S (sex \times study area \times month)	28	321.89	31.16	262.85	0.00
S (weight2)	2	321.98	31.25	317.96	0.00
S (weight1)	2	322.40	31.66	318.38	0.00
S (juvenile type)	2	322.54	31.81	318.52	0.00
S (year)	2	322.56	31.82	318.54	0.00

^a Main effect models include the effects of time (month, linear [t], quadratic [t, t²], and constant [.] time trends), in addition to the grouping variables of study area (Axial Basin or Cold Springs Mountain) and sex (F or M). Covariate models include the explanatory variables year (2005–2006, 2006–2007, 2007–2008), weight2 (weight [g] at 90–120 days of age), weight1 (weight [g] at 40–65 days of age), ohd (ordinal hatch date), and juvenile type (known wild-hatched or domestically hatched juveniles).

Appendix B

Candidate models to predict survival (S) of greater sage-grouse juveniles ($n = 164$; known and random) from 1 September to 31 March in northwestern Colorado, USA, 2005–2006, 2006–2007, and 2007–2008. Including number of parameters (K), Akaike's Information Criterion values adjusted for small sample sizes compared to the best model (ΔAIC_c), deviance, and Akaike weights (w_i).

Model description ^a	K	AIC_c	ΔAIC_c	Deviance	w_i
S (sex + study area + month)	9	388.40	0.00	370.19	0.53
S (sex \times study area + month)	10	389.87	1.47	369.61	0.26
S (study area + month)	8	390.66	2.26	374.49	0.17
S (sex + month)	8	394.13	5.72	377.95	0.03
S (month)	7	396.82	8.42	382.69	0.01
S (study area \times month)	14	399.56	11.16	371.06	0.00
S (sex \times month)	14	400.76	12.35	372.25	0.00
S (t, t ²)	3	406.13	17.7	400.10	0.00
S (t)	2	416.16	27.75	412.14	0.00
S (sex \times study area \times month)	28	419.32	30.92	361.34	0.00
S (sex + study area)	3	425.25	36.84	419.22	0.00
S (sex \times study area)	4	426.83	38.43	418.78	0.00
S (study area)	2	429.17	40.76	425.15	0.00
S (sex)	2	431.32	42.92	427.31	0.00
S (weight2)	2	434.57	46.17	430.56	0.00
S (juvenile type)	1	435.53	47.12	431.51	0.00
S (.)	1	435.63	47.22	433.62	0.00
S (year)	2	437.37	48.96	433.35	0.00

^a Main effect models include the effects of time (month, linear [t], quadratic [t, t²], and constant [.] time trends), in addition to the grouping variables of study area (Axial Basin or Cold Springs Mountain) and sex (F or M). Covariate models include the explanatory variables year (2005–2006, 2006–2007, 2007–2008), juvenile type (wild-hatched, domestically hatched, or random juveniles), and weight2 (weight [g] at 90–120 days of age).

Appendix C

Candidate models to predict survival (S) of greater sage-grouse adults (>1 yr age; $n = 223$) and juveniles ($n = 183$) from 1 September to 31 March in northwestern Colorado, USA, 2005–2006, 2006–2007, and 2007–2008. Including number of parameters (K), Akaike's Information Criterion values adjusted for small sample sizes compared to the best model (ΔAIC_c), deviance, and Akaike weights (w_i).

Model description ^a	K	AIC_c	ΔAIC_c	Deviance	w_i
$S(\text{age} \times \text{study area} \times \text{year} + \text{month})$	18	791.53	0.00	60.37	0.94
$S(\text{age} + \text{month})$	8	805.15	13.62	94.23	0.00
$S(\text{age} \times \text{month})$	14	811.85	20.33	88.81	0.00
$S(\text{study area} + \text{month})$	8	825.52	34.00	114.61	0.00
$S(\text{study area} \times \text{month})$	14	830.61	39.09	107.58	0.00
$S(\text{month})$	7	833.13	41.61	124.23	0.00
$S(t, t^2)$	3	835.99	44.47	135.13	0.00
$S(t)$	2	856.62	65.09	157.76	0.00
$S(\text{age} \times \text{study area} \times \text{year})$	12	860.52	69.00	141.53	0.00
$S(\text{age} \times \text{study area})$	4	862.41	70.88	159.54	0.00
$S(\text{age} \times \text{study area} \times \text{year} \times \text{month})$	84	869.47	77.95	0.00	0.00
$S(\text{age})$	2	877.41	85.89	178.56	0.00
$S(\text{age} \times \text{year})$	6	880.00	88.48	173.11	0.00
$S(\text{study area} \times \text{year})$	6	898.03	106.51	191.14	0.00
$S(\text{study area})$	2	899.00	107.48	200.15	0.00
$S(.)$	1	909.04	117.51	212.19	0.00

^a Main effect models include the effects of time (month, linear [t], quadratic [t, t²], and constant [.] time trends), in addition to the grouping variables of age (adult or juvenile), study area (Axial Basin or Cold Springs Mountain), and year (2005–2006, 2006–2007, 2007–2008).