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Evaluating vital rate contributions to greater sage-grouse population dynamics to inform conservation

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Abstract. Species conservation efforts often use short-term studies that fail to identify the vital rates that contribute most to population growth. Although the greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) is a candidate for protection under the U.S. Endangered Species Act, and is sometimes referred to as an umbrella species in the sagebrush (*Artemisia* spp.) biome of western North America, the failure of proposed management strategies to focus on key vital rates that may contribute most to achieving population stability remains problematic for sustainable conservation. To address this dilemma, we performed both prospective and retrospective perturbation analyses of a life cycle model based on a 12-yr study that encompassed nearly all sage-grouse vital rates. To validate our population models, we compared estimates of annual finite population growth rates (λ) from our female-based life cycle models to those attained from male-based lek counts. Post-fledging (i.e., after second year, second year, and juvenile) female survival parameters contributed most to past variation in λ during our study and had the greatest potential to change λ in the future, indicating these vital rates as important determinants of sage-grouse population dynamics. In addition, annual estimates of λ from female-based life cycle models and male-based lek data were similar, providing the most rigorous evidence to date that lek counts of males can serve as a valid index of sage-grouse population change. Our comparison of fixed and mixed statistical models for evaluating temporal variation in nest survival and initiation suggest that conservation planners use caution when evaluating short-term nesting studies and using associated fixed-effect results to develop conservation objectives. In addition, our findings indicated that greater attention should be paid to those factors affecting sage-grouse post-fledging females. Our approach demonstrates the need for more long-term studies of species vital rates across the life cycle. Such studies should address the decoupling of sampling variation from underlying process (co)variation in vital rates, identification of how such variation drives population dynamics, and how decision makers can use this information to re-direct conservation efforts to address the most limiting points in the life cycle for a given population.

Key words: *Centrocercus urophasianus*; conservation planning; elasticity; life table response experiment; population model; population stability; radio-telemetry; sage-grouse; vital rates.

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INTRODUCTION

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

In western North America, the degradation and loss of sagebrush (*Artemisia* spp.) plant communities has led to range contraction and declines in abundance of sagebrush obligate species. Most notable is the greater sage-grouse (*Centrocercus urophasianus*; sage-grouse; Schroeder et al. 2004, Garton et al. 2011), which was listed as an endangered species in Canada in 1998 (Harris et al. 2001), and in 2010, the United States Fish and Wildlife Service (USFWS) designated sage-grouse as a candidate species for protection under the U.S. Endangered Species Act (ESA) of 1973 (USFWS 2010, Stiver 2011).

Sage-grouse are a relatively long-lived galliforme with lower reproductive rates than other gallinaeous species (Schroeder et al. 1999). However, it is thought that like other ground-nesting birds (Johnson et al. 1992, Hoekman et al. 2002, Hagen et al. 2009), nest survival plays an influential role in population dynamics (Taylor et al. 2012). As such, conservation recommendations have often been focused on improving nesting habitat conditions (Johnson and Braun 1999, Connelly et al. 2000, Taylor et al. 2012, Kirol et al. 2015). However, the actual contribution of nest survival specifically, or any other given vital rate, to population dynamics has yet to be assessed over the long-term in any particular sage-grouse population.

Projection and perturbation of life-cycle models can help managers formalize their understanding of how vital rates (e.g., nest

survival, chick survival, female survival) affect population dynamics (Taylor et al. 2012), allowing for more informed conservation strategies (Akçakaya and Raphael 1998, Cooch et al. 2001, Clutton-Brock and Coulson 2002). A combination of retrospective and prospective perturbation analyses can help identify whether a species exhibits buffered demographic responses to environmental variability, whereby vital rates with the greatest potential to affect population growth (i.e., greatest elasticity) exhibit the least amount of temporal variability; a pattern thought to arise from natural selection against the potentially deleterious impacts of temporal variation in vital rates on fitness (Pfister 1998). Alternatively, a species may exhibit demographic lability to fluctuating environmental conditions if the benefits of booms in demographic performance outweigh the busts (Koons et al. 2009). Long-lived animals tend to exhibit demographic buffering (Gaillard et al. 2000, Gaillard and Yoccoz 2003, Schmutz 2009), but little is known about species such as sage-grouse, which may be intermediate on the slow-fast life history continuum (Koons et al. 2014). As such, it is difficult to make predictions based on theory as to which vital rates should most influence sage-grouse population dynamics.

Although sage-grouse are of eminent conservation concern, there remains a paucity of information needed to develop empirically based population models (Johnson and Braun 1999, Taylor et al. 2012). Population models based on meta-analyses are useful learning tools, but they confound spatial and temporal variation, which limits guidance for management actions that are directed at specific populations (Morris and Doak 2002, Koons et al. 2006, Taylor et al. 2012). Here, we used data from one of the longest continuous studies of sage-grouse demography to evaluate both retrospective and prospective vital-rate contributions to the dynamics of a population to determine the most important vital rates for conservation efforts (Caswell 2000, Dobson and Oli 2001), and to assess whether current trends in management of this candidate species may need to be reevaluated. To validate our approach using radio-marked females, we additionally compared estimates of λ from male-based lek counts to those from our female-based population model.

MATERIALS AND METHODS

Study area

Field data were collected on Parker Mountain (PM) in south-central Utah, USA. The PM sage-grouse population occupied habitat at the southern extreme of the species' range (Schroeder et al. 2004). PM is a high elevation (~ 2000–3000 m) sagebrush semidesert located on the Colorado Plateau (West 1983). PM is largely dominated by black sagebrush *A. nova*; however, there are also large areas of mountain big *A. tridentata vaseyana* and silver *A. cana* sagebrush with some Wyoming big sagebrush *A.t. wyomingensis*. PM largely consists of state and federal land. Livestock grazing was the dominant land use with stocking rates at 1.46 ha per animal unit month (AUM). Stocking rate was relatively low and livestock grazing was not considered adverse to sage-grouse habitat conditions. The PM sage-grouse population was also hunted each fall during our study period.

Field methods

Second-year (SY) and after second-year (ASY) females were captured during the spring breeding season of 1998–2009 (Giesen et al. 1982). Each captured bird was fitted with a 19 or 21-gram necklace-style VHF radiotransmitter with at least 2-yr of battery life (Advanced Telemetry Systems™, Isanti, MN, USA and Holohil™, Carp, Ontario, Canada). Age and sex were determined by wing and body size differences (Ammann 1944). Following capture, radio-marked females were monitored for nesting activities. Hens were not flushed from nests due to increased abandonment for this species, but were visually monitored with binoculars from ≥ 10 m every other day to determine fate and nests that hatched ≥ 1 egg were considered successful (Connelly et al. 2011). Flagging was used to mark monitoring locations for nests the first year, but only small rock cairns were used in all subsequent years due to concerns of observer bias by the flagging signifying nest locations to visual predators. We were unable to monitor partial depredation, though partial depredation is a rare occurrence for sage-grouse (Coates 2007). We only used clutch sizes of successful nests during our study, but recognize there is potential for

bias if clutch size differed for unsuccessful nests (Schroeder 1997). Our definition of effective clutch size (ECS) refers to the number of hatched eggs within a clutch that survived incubation, and excluded unhatched eggs in successful nests. The ECS thus defines the unbiased number of newly hatched individuals transitioning from successful nests to the chick development stage of the life cycle.

Radio-marked females with broods were monitored using telemetry every 3 d in 1998–2004. We switched monitoring of broods to every 2 d during 2005–2009 when 1.5 g backpack suture-style VHF radios (Advanced Telemetry Systems, Isanti, MN in 2005, Holohil Systems, Carp, Ontario, Canada in 2006–2008, and American Wildlife Enterprises, Monticello, FL in 2009) were used to mark all chicks (except in 2006 when three chicks were randomly selected from each brood) in broods of marked females within ~ 48 h of hatch (Dahlgren et al. 2010a, Guttery et al. 2013a). Throughout the study period, brood success was estimated as the proportion of broods where ≥ 1 chick was observed alive ≥ 42 d post hatch. If at 42 d no radio-marked chicks remained in broods, pointing dogs were used to detect if unmarked chicks were present (Dahlgren et al. 2010b, 2012). Survival of juveniles (from August in the hatch year until the following March) was monitored from 2008 to 2010 (Caudill et al. 2014).

Vital-rate estimation

We fit generalized linear mixed models (GLMM) to vital-rate data with fixed age effects and random-year effects. The mixed-effect structure allowed for direct decomposition of temporal variance in each response variable into sampling and process components. Consequently, we obtained annual 'shrinkage' estimates of each vital rate attributable to process variance and not confounded by sampling variance (Royle and Link 2002). We then used the shrinkage estimates to estimate temporal 'process correlation' among vital rates; a statistic that has been difficult to isolate from empirical studies of demography (Morris and Doak 2002). Analyses were performed in program R using the 'RMark' package or directly in Program MARK unless otherwise specified (Laake and Rexstad 2012, R Development Core Team 2012, Cooch and White 2014).

For marked females, we modeled the probability of nest initiation in R using a logit link GLMM with a binomial distribution and the model structure described above. Variation in ECS was modeled similarly using a GLMM in R, but with log-normal errors. We estimated daily survival rates (DSR) of nests using the nest survival model (Cooch and White 2014). Due to convergence issues with maximum likelihood optimization of the temporal random effect, nest survival was modeled using the MCMC routine in MARK. The nest survival probability was estimated as DSR^{38} representing an incubation period of 27 d (Schroeder 1997) and 1.5 d per egg laid (Schroeder et al. 1999). Corresponding estimates of standard errors were attained using the delta method (Seber 1982).

We modeled radio-marked chick survival from hatch to 42-d using a mixed-effect Cox proportional hazard model and the 'coxme' package in R (Therneau et al. 2003). In addition to a random effect for year, we also included a 'correlated frailty' random effect to control for fate dependence among marked chicks within broods. Brood survival was modeled from 1998 to 2009 using a GLMM with a logit-link and binomial distribution in R. We then determined brood survival estimates from 2005 to 2009 to be highly correlated with chick survival estimates ($P > 0.7$). Hence, we used a simple linear model to predict chick survival rates for 1998–2004 based on estimated brood survival.

Variation in monthly survival rate (MSR) between age classes (SY and ASY) and years was modeled using the logit-link and nest survival model because monitoring was 'ragged' in nature (White and Burnham 1999). We attempted to monitor radio-marked females at least monthly from April to August, and then usually during the fall and again during the winter with fixed-wing aircraft. Each spring we intensively surveyed the study area to document radio-marked female overwinter survival. Females that went "missing" or whose radio-collar failed were right-censored ($n = 125$ of 401; 62 of 125 were monitored ≥ 4 months post capture) at their last known survival period. We defined the survival year as April 1 of calendar year t to March 31 in year $t + 1$, and subsequently estimated annual survival for each year and age class as MSR^{12} . As above, we used the delta method to estimate

standard errors for annual survival. Juvenile survival in 2008 and 2009 was estimated by Caudill et al. (2014) who captured and radio-marked juveniles in the late summer and monitored them at least monthly through the following winter. Although they did not use mixed-effects models to estimate juvenile survival, we used their reported survival estimates as they represent the best available data for juvenile survival on our study site for those years. For the remaining years (1998–2007) we used the monthly survival probability for SY females (i.e., MSR_{SY}^8) as a surrogate for juvenile survival. We used SY female survival as a proxy for juvenile survival because this was the closest post-fledging age class, and juvenile, SY, and ASY females flock together through the fall and winter exposing all age classes to the same environmental conditions that affect survival (Taylor et al. 2012).

Life-cycle modeling

We constructed a female-based table from estimated vital rates (Table 1) to facilitate the development of a two-stage matrix population model (A) for each year of study using a pre-breeding census and birth-pulse reproduction format (Caswell 2001). Each matrix consisted of SY and ASY fertility (F) and hen survival (HS):

$$A = \begin{pmatrix} F_{SY} & F_{ASY} \\ HS_{SY} & HS_{ASY} \end{pmatrix} \quad (1)$$

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

$$F_x = NI_x * ECS_x * 0.50 * NS_x * CS_x * JS \quad (2)$$

where

NI_x = age-specific probability of nest initiation
 ECS_x = age-specific effective clutch size adjusted for hatch failure
 NS_x = age-specific nest survival
 CS_x = age-specific chick survival
 JS = juvenile survival

The 0.50 in the fertility equation accounts for the fraction of offspring that are female (Gutierrez et al. 2013b). Equation 2 calculates the number of females recruited to breeding age in year $t + 1$ per breeding female of age x in year t . We additionally constructed a matrix with mean vital rates across all years, and used a basic eigen-analysis

Table 1. A summary of female-based vital rates for the greater sage-grouse *Centrocercus urophasianus* population at Parker Mountain, UT, 1998–2009. SY = second year female (first breeding season); ASY = after second year female (second or more breeding season experiences); NI = nest initiation probability, where a female must have been documented on a nest using telemetry and binoculars; ECS = effective clutch size excluding hatch failures, NS = nest survival based on 1.5 d per egg of laying and a 27-d incubation period; CS = chick survival probability based on a 42-d brooding period; JS = juvenile survival for young of the year from August 1 to March 31; HS = annual female (hen) survival based on monthly survival rates (MSR¹²). All vital-rate values represent shrinkage estimates (see Methods) that are based solely on process variance and exclude sampling variance.

Year	Sample Size		NI		ECS		NS		CS ^a		JS ^b	HS	
	SY	ASY	SY	ASY	SY	ASY	SY	ASY	SY	ASY		SY	ASY
1998	19	10	0.59	0.79	5.63	6.05	0.40	0.51	0.67	0.57	0.66	0.54	0.67
1999	17	26	0.59	0.79	5.54	5.96	0.37	0.48	0.67	0.57	0.66	0.53	0.66
2000	8	19	0.62	0.81	5.64	6.07	0.40	0.51	0.64	0.55	0.68	0.56	0.68
2001	15	10	0.63	0.81	5.63	6.05	0.38	0.48	0.66	0.56	0.66	0.54	0.67
2002	14	15	0.62	0.81	5.52	5.94	0.38	0.48	0.64	0.55	0.67	0.54	0.68
2003	13	13	0.62	0.81	5.47	5.88	0.38	0.48	0.66	0.57	0.61	0.48	0.61
2004 ^c	0	9	0.59	0.79	5.56	5.98	0.39	0.50	0.65	0.56	0.66	0.54	0.65
2005	38	17	0.61	0.80	5.31	5.71	0.40	0.50	0.70	0.61	0.82	0.74	0.84
2006	13	46	0.61	0.80	5.37	5.78	0.40	0.50	0.66	0.56	0.64	0.51	0.61
2007	22	21	0.56	0.77	5.34	5.74	0.38	0.48	0.60	0.49	0.58	0.44	0.57
2008	12	32	0.56	0.77	5.61	6.04	0.40	0.51	0.69	0.60	0.42	0.50	0.62
2009	8	31	0.60	0.79	5.47	5.89	0.35	0.46	0.68	0.59	0.61	0.48	0.59
	Mean		0.60	0.80	5.51	5.92	0.39	0.49	0.66	0.56	0.64	0.53	0.65
	Process variance		0.0005	0.0003	0.0140	0.0158	0.0080	0.0057	0.0080	0.0057	0.0082	0.0055	0.0046

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

b: Estimates for 1998–2007 were calculated using the corresponding monthly survival rate for SY females (MSR⁸), whereas survival estimates for 2008 and 2009 were directly estimated from radio-marked juveniles (Caudill 2011).

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

of the mean matrix to calculate the asymptotic finite population growth rate (λ), stable stage distribution, reproductive values, expected lifetime number of replacements for each age class (R_0), and generation time (μ_1 , the mean age of parents for a cohort of newborn offspring; Caswell 2001). We calculated statistical error for estimates of the study mean and annual λ using 10 000 Monte Carlo simulations of uncorrelated annual vital rates and their associated standard errors (Taylor et al. 2012).

We calculated the sensitivity of λ to each lower level vital rate x according to:

$$s_x = \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x} \quad (3)$$

where a_{ij} is the i, j th entry of the mean matrix A (Caswell 1978). We calculated the elasticity of λ

to proportional changes in lower level vital rates as (de Kroon et al. 2000):

$$e_x = \frac{x}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x} \quad (4)$$

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

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

where $\text{cov}(x,y)$ is the process covariance of lower level vital rates x and y , and S_x and S_y are the vital

rate sensitivities evaluated at a reference matrix (average matrix across study years; Caswell 2001). We set the process correlation, and thus covariance, to 0 for pairs of vital rates that were not directly related (Table 3). Contributions of a single vital rate to process variance in λ (χx) were calculated as (Horvitz et al.1997):

$$\chi x \approx \sum_y \text{cov}(x,y) s_x s_y \quad (6)$$

Hence, vital-rate contributions to variation in λ are a function of λ 's sensitivity to changes in a vital rate, vital rate variation over time, and its correlation with other vital rates. LTRE contributions can also be estimated with elasticities and mean-standardized coefficients of variation (CV; Gaillard et al. 2000, Coulson et al. 2005):

$$\chi x \approx \sum_y \text{cov}(x,y) s_x s_y \approx \sum_y CV_{\text{matrix}}(x,y) e_x e_y \quad (7)$$

We performed the prospective and retrospective analyses of the life cycle model in R.

Lek count analyses

From 1998 – 2003 12 to 14 leks were monitored each spring. In 2004, 2005, and 2006 17, 22, and 25 leks were monitored, respectively. In 2007 a concerted effort to locate all leks within the study area resulted in 35, 34, and 36 leks being monitored in 2007, 2008, and 2009. Many of these previously unknown leks were located far away from main roads but in association with livestock watering areas. A subsample of these leks was used to trap female sage-grouse. Male sage-grouse attending each lek were counted ≥ 3 different mornings each spring during the last week of March and the first 3 weeks of April (Bernales et al. 2012). We used the maximum male lek count for each lek to estimate $\lambda_{\text{lek}, t}$ from year t to $t + 1$ as:

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

Where $M_i(t)$ = maximum number of males counted at lek i in year t , and then we summed across n leks surveyed in both years t and $t + 1$.

Variance and standard error were estimated using a standard ratio estimator (Scheaffer et al. 1996):

$$\text{Var}(\lambda_t) = \pi \frac{fpc}{n\bar{M}(t)^2} \frac{\sum_{i=1}^n [M_i(t+1) - \lambda(t)M(t)]^2}{n-1} \quad (9)$$

where fpc is assumed to be 1.0. Annual model- and lek-derived λ estimates with associated uncertainty, where then plotted against each other for visual comparison. A Z-test was also performed to assess if annual estimates of female model-based λ 's were different from those attained from male-based lek data. An alpha level of $P \leq 0.05$ was used in the Z-tests.

RESULTS

We captured, radio-marked, and monitored 180 females from 1998 to 2009, totaling 276 annual life histories accounting for females that graduated age classes (ASY $n = 136$, SY $n = 140$). We monitored NS and ECS for 153 nests. We captured and radio-marked 335 chicks in 76 broods. From 2008 to 2009, we captured 91 juvenile sage-grouse in late summer after they fledged and monitored their survival. Estimated vital rates are reported in Table 1. Inter-annual variation in nest initiation and nest survival estimates was notably higher in fixed vs. mixed-effect models, indicating the potentially strong influence of sampling variation on annual estimates attained from fixed-effect models (Fig. 1).

Life cycle modeling

Given the mean matrix, the estimated long-term λ indicated that the PM sage-grouse population was generally stable during our study ($\lambda = 0.972$, $SE = 0.025$). The stable age distribution for SY and ASY females was 0.373 ($SE = 0.015$) and 0.627 ($SE = 0.015$), respectively, and corresponding reproductive values were 0.432 ($SE = 0.011$) and 0.568 ($SE = 0.011$). Expected lifetime reproductive output was 0.916 ($SE = 0.073$), and the generation time was 3.045 yr ($SE = 0.166$).

According to our LTRE analysis, temporal process variation in JS made the largest contribution to λ , followed by variation in ASY female survival, ASY ECS, SY female survival, ASY chick

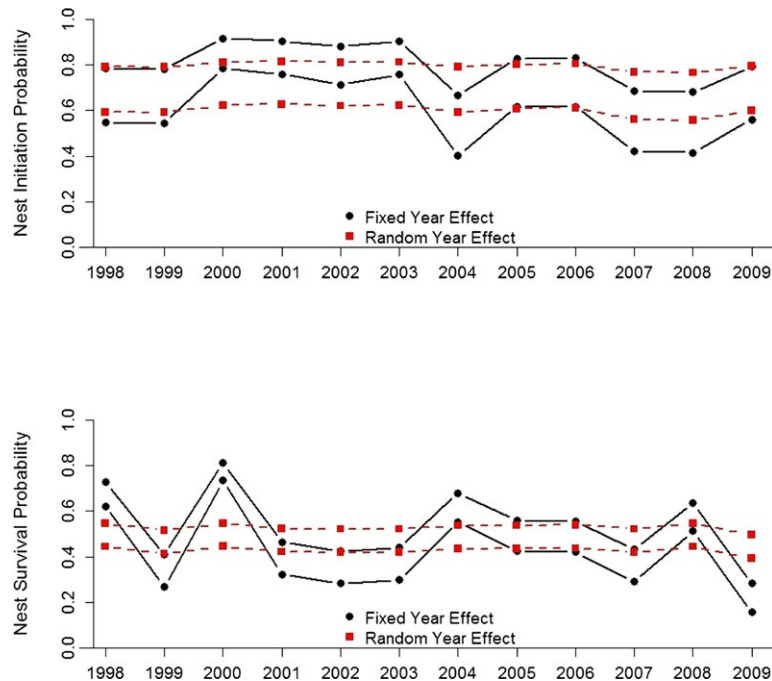


Fig. 1. Greater sage-grouse *Centrocercus urophasianus* annual estimates of nest initiation and nest survival for after second year female (top probability values) and second year female (bottom probability values) for fixed-year effects and random-year effects models where sampling error was removed for random-year effect results, 1998–2009, Parker Mountain, Utah, USA.

survival, SY ECS, SY chick survival and then the remaining vital rates associated with nesting (Table 2). Thus, past changes in λ were influenced most by postfledging (i.e., ASY, SY, and juvenile) survival transitions, and the next greatest contributions came from variation in ECS and CS (Table 2). In total, past variation in the postfledging survival parameters made more than a two times greater contribution (0.008) to past fluctuations in λ than summed contributions of prefledging vital rates (0.003).

In the prospective perturbation analyses, λ was most sensitive to per unit (sensitivity) and proportional (elasticity) changes in the annual survival of ASY females. Given the multiplicative fashion of our fertility equation (Eq. 2), elasticities for several prefledging vital rates were constrained to be equal (Table 2). Given comparable numeric scaling of vital rates, however, we found the unconstrained sensitivities to be useful in comparing prospective impacts of potential vital-rate perturbations on λ . For example, JS and ASY nest survival had the next highest sensitivity and elasticity values, respectively, followed

closely by SY HS and CS of ASY brood hens, then the remaining components of fertility (Table 2).

Vital rate covariance showed a positive relationship between all postfledging female (i.e., ASY, SY, and juvenile) survival rates (Table 3). A slight negative covariance occurred for both reproductive age classes (i.e., ASY and SY) between survival and clutch size (Table 3). All other vital rate covariance values were small and not notable (Table 3).

Lek count growth rates

The estimated mean λ from lek counts ($\lambda_{\text{male lek}} = 1.07$, SE = 0.10) did not statistically differ from mean λ estimated from our female-based population model. Moreover, Z-test results indicated that annual fluctuations in λ based on lek counts were similar to estimates attained from the female-based life cycle models, except in 1998 (Fig. 2).

DISCUSSION

The PM sage-grouse population was stable over the duration of our demographic

Table 2. A calculation of Life Table Response Experiment (LTRE) contributions to annual process variation in population growth rate, and estimates of the sensitivity (S_x) and elasticity (e_x) of the finite population growth rate to changes in the underlying vital rates (x) evaluated at temporal mean values for the greater sage-grouse *Centrocercus urophasianus* population at Parker Mountain, Utah, 1998-2009. SY = second year female (first breeding season); ASY = after second year female (second or more breeding season experiences); NI = nest initiation probability where a female must have been documented on a nest using telemetry and binoculars; ECS = effective clutch size excluding hatch failures; NS = nest survival based on 1.5 d per egg of laying and a 27-d incubation period; CS = chick survival probability based on a 42-d brooding period; JS = juvenile survival for young of the year from August 1 to March 31; HS = annual female (hen) survival based on monthly survival rates (MSR¹²).

x	LTRE	LTRE Rank	e_x	e_x Rank	S_x	S_x Rank
JS	0.00542	1	0.3112	2	0.4728	2
ASY HS	0.00151	2	0.4641	1	0.6890	1
ASY ECS	0.00118	3	0.2250	3	0.0739	10
SY HS	0.00083	4	0.2248	4	0.4090	4
ASY CS	0.00053	5	0.2250	3	0.3876	5
SY ECS	0.00052	6	0.0862	5	0.0304	11
SY CS	0.00042	7	0.0862	5	0.1270	9
ASY NS	0.00014	8	0.2250	3	0.4462	3
SY NS	3.22e-5	9	0.0862	5	0.2169	7
ASY NI	6.44e-6	10	0.2250	3	0.2749	6
SY NI	2.35e-6	11	0.0862	5	0.1396	8

monitoring, and thus our results provide an appropriate benchmark for conserving sage-grouse and potentially other tetraonid populations. In addition, estimates of λ from male-based lek counts confirmed that our demographic estimates based on radio-marked females were representative of overall population dynamics. During our study, survival of

Table 3. The greater sage-grouse *Centrocercus urophasianus* vital rate covariance matrix for Parker Mountain, Utah, 1998–2009. Covariance values without direct biological relationships were set to zero (see text). SY = second year female (first breeding season); ASY = after second year female (second or more breeding season experiences); NI = nest initiation probability where a female must have been documented on a nest using telemetry and binoculars; ECS = effective clutch size excluding hatch failures, NS = nest survival based on 1.5 d per egg of laying and a 27-d incubation period; CS = chick survival probability based on a 42-d brooding period; JS = juvenile survival for young of the year from August 1 to March 31; HS = annual female (hen) survival based on monthly survival rates (MSR¹²). Values in gray represent process variance within each vital rate and correspond to Table 1; however, values for ECS are different because they were calculated from ECS*0.50 to represent the female portion of the population in this table (see text).

Vital Rate	SY HS	ASY HS	SY NI	ASY NI	SY ECS	ASY ECS	SY NS	ASY NS	SY CS	ASY CS	JS
SY HS	0.00550	0.00495	0.00000	0.00000	-0.00082	0.00000	0.00042	0.00000	0.00094	0.00000	0.00507
ASY HS	0.00495	0.00458	0.00000	0.00000	0.00000	-0.00048	0.00000	0.00034	0.00000	0.00100	0.00469
SY NI	0.00000	0.00000	0.00054	0.00037	0.00013	0.00000	-0.00003	0.00000	0.00002	0.00000	0.00000
ASY NI	0.00000	0.00000	0.00037	0.00026	0.00000	0.00010	0.00000	-0.00003	0.00000	0.00006	0.00000
SY ECS	-0.00082	0.00000	0.00013	0.00000	0.00349	0.00372	0.00025	0.00000	0.00008	0.00000	0.00000
ASY ECS	0.00000	-0.00048	0.00000	0.00010	0.00372	0.00396	0.00000	0.00026	0.00000	0.00025	0.00000
SY NS	0.00042	0.00000	-0.00003	0.00000	0.00025	0.00000	0.00025	0.00025	0.00003	0.00000	0.00000
ASY NS	0.00000	0.00034	0.00000	-0.00003	0.00000	0.00026	0.00025	0.00024	0.00000	0.00005	0.00000
SY CS	0.00094	0.00000	0.00002	0.00000	0.00008	0.00000	0.00003	0.00000	0.00067	0.00073	0.00016
ASY CS	0.00000	0.00100	0.00000	0.00006	0.00000	0.00025	0.00000	0.00005	0.00073	0.00081	0.00030
JS	0.00507	0.00469	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00016	0.00030	0.00824

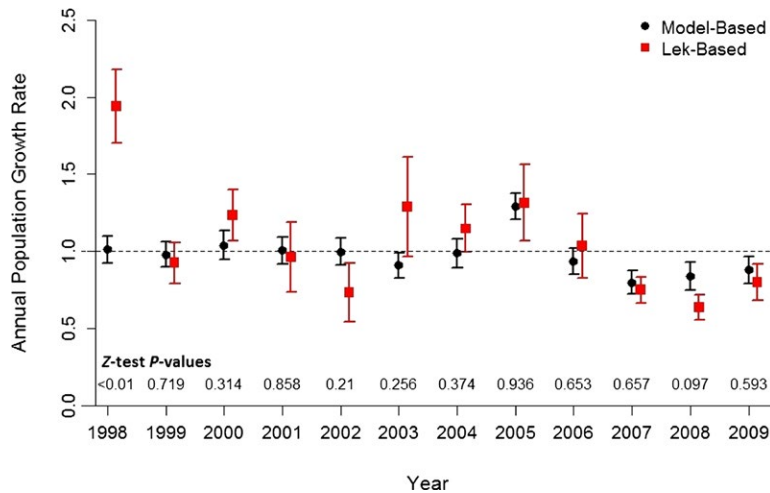


Fig. 2. Greater sage-grouse *Centrocercus urophasianus* annual estimates of radio-marked female-based matrix model and male-based lek count estimates of finite growth rate (λ), error bars represent one standard error, 1998–2009, Parker Mountain, Utah, USA.

postfledging (i.e., juvenile, SY, and ASY) females had greater prospective ability to affect λ , and made greater retrospective contributions to λ relative to equivalent changes in prefledging vital rates associated with reproductive output. Our results differ from past studies of population dynamics for other tetraonid species, which have generally concluded that reproductive success, especially nest survival, has greater prospective potential to influence λ compared to female survival (Sandercock et al. 2005, Tirpak et al. 2006, Hagen et al. 2009). This can be explained by the fact that sage-grouse are characterized by greater longevity, lower reproductive investment, and a slower overall life history than other tetraonids and most galliformes (Schroeder et al. 1999, Sæther and Bakke 2000, Taylor et al. 2012).

According to the theory of demographic buffering, the vital rates with the greatest 'potential' to affect population growth (i.e., highest elasticity) should exhibit the least amount of temporal variance because of the negative impact such variability can have on long-term fitness and population dynamics (Pfister 1998, Gaillard et al. 2000). Contrary to this theory, we found that although postfledging survival rates exhibited high sensitivity and elasticity values; they also exhibited high process variation and thus contributed the most to past changes in λ . The overall mean

estimate of λ was ~ 1.0 ; indicating population stability during our study period and that departure from the demographic buffering life history strategy is not due to a case of maladaptation to the contemporary environment (Schmutz 2009). Rather, sage-grouse may exhibit a life history that is intermediate on the slow-fast continuum, where female survival is important and lability in related traits allows them to exploit opportune environments (Koons et al. 2009), and survive at rates that, on average, are higher than most other galliformes, (Johnsgard 1983, Madge and McGowan 2002), but are also sensitive to poor environmental conditions. Postfledging survival appears malleable and therefore is likely to respond to management actions. To achieve a net long-term gain, an understanding of the impact of beneficial and detrimental years of various environmental conditions on postfledging female survival and the interaction with conservation actions is needed, especially for juvenile survival where to date information has been scarce (Beck et al. 2006, Caudill et al. 2014).

While more information is needed concerning specific management strategies that can stabilize or increase sage-grouse populations, lek counts have been widely used as an index for sage-grouse population change and to guide conservation decisions (Connelly et al. 2004, Garton et al. 2011). Although the validity

of lek counts has been questioned for monitoring changes in population numbers (Beck and Braun 1980, Walsh et al. 2004), none have evaluated their utility by comparing independent sources as has been done in assessments of other wildlife monitoring methods (Bibby et al. 1992, Pollock et al. 2002, Sandercock and Beissinger 2002, Skalski et al. 2010). Our lek and vital-rate data were male- and female-based, respectively, thus providing independent data for estimating $\lambda_{\text{female model}}$ and $\lambda_{\text{male lek}}$. We found that $\lambda_{\text{female model}}$ and $\lambda_{\text{male lek}}$ closely tracked each other over time. Standard errors and variation in $\lambda_{\text{male lek}}$ was higher compared to $\lambda_{\text{female model}}$, suggesting sampling error (e.g., observer error, differences in weather conditions within and between years, natural variation in lek attendance rates, etc.) affected our lek count analyses, though not prohibitive to providing a reliable trend to population change (Beck and Braun 1980). The number of leks counted each year on the study area was generally increasing through our study period, with significant increases in 2005 and again in 2007. Therefore, standard error usually decreased through time for $\lambda_{\text{male lek}}$ and became comparable to $\lambda_{\text{female model}}$ standard errors the last few years, highlighting the importance of locating and monitoring as many leks as possible within a population for reliable inference (Coates et al. 2013). As the trend in λ estimates from both sources generally tracked each other through time, we suggest lek counts can be a reliable index to changes in sage-grouse populations but note the caveat of larger standard errors will limit a manager's ability to detect sudden changes in abundance and the factors responsible for such changes. The overall reliability of spring lek counts is nevertheless reassuring because obtaining this index can occur at less cost and over much larger spatial areas than intensive studies of demographic vital rates.

Thus, studies of vital rates over the life cycle are needed to direct management actions in an efficient manner. Currently, there exists a paradigm of using short-term studies on sage-grouse focusing primarily on drivers of nest survival (Connelly et al. 1991, 2000, Gregg et al. 1994, Holloran et al. 2005, Moynahan et al. 2007). Consequently, it is largely thought that management directed at nest survival will yield important returns for conservation investment (John-

son and Braun 1999, Connelly et al. 2000, Kirol et al. 2015). As the emphasis is on nest survival for ground-nesting birds in general, and tetraonids specifically, we expected nest survival to be a major driver of past population change in the PM population. Nest survival did have a relatively high sensitivity value in our study and others (Taylor et al. 2012), indicating a potential to contribute to population dynamics, but in our retrospective evaluation it was relatively robust to inter-annual variation in environmental conditions. Our fixed-effect estimates of nest initiation and survival demonstrated relatively high annual variation. When estimating nest initiation and survival using mixed models that yield shrinkage estimates, however, much of the inter-annual variation was attributed to sampling variance as opposed to true process variance. Given these results, we urge caution and suggest our findings have broad implications for interpreting past short-term avian nesting studies, especially those subject to ample sampling variation that is often associated with low annual sample size. We acknowledge that large changes in nest survival resulting from, e.g., habitat degradation and fragmentation, could have contributed to population declines elsewhere and may be an important driver of actual population dynamics across the sage-grouse range (Schroeder 1997, Aldridge and Boyce 2007, Taylor et al. 2012). Ironically, the importance of nest survival, or any given vital rate, in a population can only be determined by long-term research that is able to decouple components of vital rate variation and compare the relative contributions of process variation in vital rates on population dynamics using perturbation analyses.

In a range-wide prospective perturbation meta-analysis of sage-grouse vital rates, Taylor et al. (2012) found that vital rates with the most potential to contribute to λ on a per unit basis, in decreasing order of importance, were postfledging female survival (ASY, SY, and juvenile age classes), chick survival, and then nest survival. Similarly, our prospective analyses demonstrated the importance of postfledging female survival, ASY nest survival, and ASY chick survival. However, unlike Taylor et al. (2012), we also conducted a retrospective analysis demonstrating the importance of past contributions of postfledging female survival to actual population change

as opposed to potential contributions across published studies. In particular, our results highlight the substantial contributions of the more experienced ASY females to changes in λ through higher survival and reproductive rates than other age classes. Taylor et al. (2012) stressed the importance of restoring and maintaining large intact sagebrush landscapes to support post-fledging female survival while managing shrub and herbaceous cover and height at smaller scales for nest and chick survival. Our study area is a large contiguous sagebrush landscape with few anthropogenic disturbances (e.g., low-traffic dirt/gravel roads, managed livestock grazing, limited harvest, etc.). Within our study area, a few small scale (<few hundred hectares) sagebrush management projects have been completed to improve brooding habitat conditions in high elevation mountain big sagebrush (Dahlgren et al. 2006). As λ was stable over our 12-yr study, our population provides a notable example of the benefits of maintaining large intact landscapes of sagebrush while managing at smaller scales for appropriate sagebrush and herbaceous cover to meet sage-grouse habitat needs across seasons.

Our results, and others (Taylor et al. 2012), stress the importance of female survival to sage-grouse population dynamics. Our SY and ASY female survival demonstrated a positive covariance confirming that factors affecting reproductive female survival were consistent between age classes. This is not surprising because ASY and SY females experienced similar environmental conditions year-round. Our findings suggest conservation measures that enhance survival in any one female age class will likely affect survival across age classes.

Intensive and detailed field research of marked individuals is indeed important for understanding ecological processes (Fahey et al. 2015). However, environmental dynamics influencing population change in a wide-ranging species may vary across both time and space. For example, Folk et al. (2007) demonstrated that different vital rates and temporal factors drove the dynamics of distinct populations at the northern and southern extent of northern bobwhite (*Colinus virginianus*) distribution. Similarly, there is evidence that sage-grouse demography may vary across their broad range in western North America. Consistent with avian biogeograph-

ic patterns in clutch size (Lack 1948), Blomberg et al. (2014) found that clutch size in sage-grouse decreased from north to south across the species' distribution. Our population is at the extreme southern extent of the species' distribution in western North America. Differences in latitudinal population dynamics may partially explain some of our results; for example, the important contributions of annual variations in clutch size to λ for our retrospective analysis. However, until further studies of population dynamics based on telemetry data are completed from other areas, we currently have little information to compare to at the population level. There is currently a need to better understand differences in population dynamics across gradients of latitude and anthropogenic influence for sage-grouse within their current distribution (Blomberg et al. 2014).

As an example of variation in population trajectory, some populations of sage-grouse have shown stability or only slight downward trends while others have declined more rapidly (Garton et al. 2011). Thus, to identify the conservation actions that will best improve sage-grouse population growth rates across their range, spatially replicated long-term (e.g., >10 yr) demographic studies will be needed, in conjunction with the larger repertoire of lek count monitoring, to elucidate the sources of regional differences in population dynamics (Williams et al. 2003). Our approach to demographic modeling serves as a novel guide for research and can be applied to other species of conservation concern to better understand how to reverse declining population trends. We encourage more study of stable populations that provide insight into the factors contributing to stability and sustainability (Caughley 1994).

Avian studies have generally reported low contributions of clutch size to population dynamics (e.g., Newton 1998, Cooch et al. 2001). Our population's clutch sizes were low compared to other sage-grouse studies, which may in part not only be due to the southern latitude of PM but also we monitored ECS and not absolute clutch size at the conclusion of laying (Blomberg et al. 2014). Variation in ECS during our study was likely due to increased partial hatch failure rates in certain years (Appendix A). Although ECS exhibited the lowest sensitivity in our study, we found the variation in annual ECS to be an important con-

tributor to past changes in λ . We suggest partial hatch failure could have been impacted by extreme cold temperatures at our high elevation study area during the 7–10 d laying phase, or possibly prelaying conditions of reproductive females (Stoleson and Beissinger 1999, Hassan et al. 2004), which can influence overall clutch size (Barnett & Crawford 1994). Female survival for SY and ASY age classes negatively co-varied with their respective clutch sizes, though covariance values were very small. At a minimum, we recommend that future research consider the factors that could influence hatch failure, clutch size, and the relationship of clutch size to female survival in this, and other populations (Blomberg et al. 2014).

Survival of chicks made moderate contributions to past population dynamics. Not surprisingly, chicks raised by more experienced ASY females contributed more to λ than those reared by SY females (Table 2). ASY females had higher nest initiation and nest survival, constituted a larger proportion of the population, and had higher reproductive value; thus, ASY females contributed significantly more recruitment into the population. Of note, estimates of chick survival at PM are among the highest reported for sage-grouse (Aldridge and Boyce 2007, Gregg et al. 2007, Dahlgren et al. 2010a, Blomberg et al. 2013, Guttery et al. 2013a), and in addition to focusing more on post-fledging survival, our results suggest that greater attention be paid to the factors driving variation in chick survival (e.g., forb and arthropod abundance, timing of precipitation, habitat conditions; Connelly et al. 2000, Guttery et al. 2013a) as opposed to focusing on nest survival.

Overall, our results provide evidence that: 1) telemetry-based studies can provide unbiased demographic information for analysis and monitoring, and 2) male-based lek counts of sage-grouse can be an effective index to overall population change. The integration of both types of data could provide insight into population dynamics at sites where the entire life cycle has not been studied (Davis et al. 2014), and be used to examine population dynamics at greater spatio-temporal scales. Furthermore, perturbation analyses such as ours based on long-term demographic studies are needed to enhance scientific rigor for prioritization of the most cost effective

species conservation and management actions (Akçakaya and Raphael 1998, Cooch et al. 2001, Clutton-Brock and Coulson 2002, Baxter et al. 2006).

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