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Effects of climatic variation and reproductive trade-offs vary by measure of reproductive effort in greater sage-grouse

DANNY CAUDILL,[1,6,]† MICHAEL R. GUTTERY,[2] BRENT BIBLES,[3] TERRY A. MESSMER,[1] GRETCHEN CAUDILL,[4]
ERIN LEONE,[4] DAVID K. DAHLGREN,[1] AND RENEE CHI[5]

[1]*Department of Wildland Resources, Utah State University, Logan, Utah 84322 USA*
[2]*Department of Forest and Wildlife Ecology, University of Wisconsin, Madison, Wisconsin 53706 USA*
[3]*Center for Natural Resources Management and Protection, Unity College, Unity, Maine 04988 USA*
[4]*Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, Gainesville, Florida 32601 USA*
[5]*Bureau of Land Management, Salt Lake City, Utah 84145 USA*

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Abstract. Research on long-lived iteroparous species has shown that reproductive success may increase with age, until the onset of senescence, and that prior reproductive success may influence current reproductive success. Such complex reproductive dynamics can complicate conservation strategies, especially for harvested species. Further complicating the matter is the fact that most studies of reproductive costs are only able to evaluate a single measure of reproductive effort. We systematically evaluated the effects of climatic variation and reproductive trade-offs on multiple reproductive vital rates for greater sage-grouse (*Centrocercus urophasianus*; sage-grouse), a relatively long-lived galliforme of conservation concern throughout western North America. Based on over a decade of field observations, we hypothesized that reproduction is influenced by previous reproductive success. We monitored hen reproductive activity from 1998 to 2010, and used generalized linear mixed models to assess effects of climate and previous reproductive success on subsequent reproductive success. Reproductive trade-offs manifested as chronic effects on subsequent reproduction and were not apparent in all measures of subsequent reproduction. Neither nest initiation nor clutch size were found to be affected by climatic variables (either year $t-1$ or t) or previous reproductive success. However, both nest and brood success were affected by climatic variation and previous reproductive success. Nest success was highest in years with high spring snowpack, and was negatively related to previous brood success. Brood success was positively influenced by moisture in April, negatively associated with previous nest success, and positively influenced by previous brood success. Both positive and negative effects of previous reproduction on current year reproduction were observed, possibly indicating high levels of individual heterogeneity in female reproductive output. Our results support previous research in indicating that climatic variability may have significant negative impacts on reproductive rates.

Key words: *Centrocercus urophasianus*; climate; cost of reproduction; generalized linear mixed model; greater sage-grouse; trade-offs; Utah.

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[6] Present address: Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, Gainesville, Florida 32601 USA.

† **E-mail:** charles.caudill@myfwc.com

INTRODUCTION

Life history theory predicts trade-offs or costs occur between competing demographic variables (Reznick 1985). Cost of reproduction is one such trade-off (Reznick 1985), where reduced current reproductive capacity (Williams 1966, Røskaft 1985, Gustafsson and Sutherland 1988) or increased mortality (Williams 1966, Erikstad et al. 1998, Blomberg et al. 2013) result from increased resource allocation to previous reproduction. Conversely, positive trade-offs between life history traits have also been documented (e.g., Cam et al. 1998, Barbraud and Weimerskirch 2005), and may be the consequence of the "heterogeneity in individual quality" hypothesis. Individual heterogeneity in reproductive output and cost of reproduction is common in avian taxa (e.g., Aubry et al. 2009, Aubry et al. 2011, Cam et al. 2013). Evaluation of trade-offs and costs associated with reproduction is vital to conceptualization of the population ecology of a species, and consequently species conservation. Species evolve traits conducive to persistence under the environmental conditions to which, over evolutionary history, selective pressure was exerted upon the species. As such, reproductive costs likely vary in magnitude as a result of environmental conditions (Erikstad et al. 1998, Barbraud and Weimerskirch 2005, Bårdsen et al. 2011). Identification and estimation of the linkage between climatic variables and demographic rates is vital to conservation, particularly for species with limited dispersal opportunities in the face of climate change (Norris 2004, Thomas et al. 2004).

We evaluated the effect of previous reproductive success and climatic variation on subsequent reproduction using a greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) population in south-central Utah. Sage-grouse are relatively long-lived (9 years maximum reported longevity; Zablan et al. 2003) sagebrush (*Artemesia* spp.) obligate galliformes (Patterson 1952, Dalke et al. 1963, Connelly et al. 2011). Currently, sage-grouse are a species of conservation concern throughout their endemic range in western North America because of precipitous population declines and habitat degradation (Schroeder et al. 2004, Connelly et al. 2011, Garton et al. 2011, Miller et al. 2011; J. W. Connelly, S. T. Knick, M. A. Schroeder, and S. J. Stiver, *unpublished manuscript*). Consequently, sage-grouse were designated as endangered by the Canadian Committee on the Status of Endangered Wildlife and a candidate for protection under the Endangered Species Act (ESA) by the U.S. Fish and Wildlife Service (USFWS) in 1998 and 2010, respectively (Harris et al. 2001, USFWS 2010). Climatic related parameters have been identified as affecting reproduction in sage-grouse populations, where increased moisture or decreased drought positively influenced brood success (Blomberg et al. 2013), nest success (Holloran et al. 2005), and chick survival (Guttery et al. 2013). Furthermore, increased snow depth has been found to be associated with increased recruitment (Blomberg et al. 2012).

Reproductive costs to survival exist in both female (Blomberg et al. 2013) and male sage-grouse (Boyko et al. 2004), and have also been documented in black grouse (*Tetrao tetrix*; Angelstam 1984, Caizergues and Ellison 1997), lesser prairie-chickens (*Tympanuchus pallidicinctus*; Hagen et al. 2005, 2007), and willow ptarmigan (*Lagopus lagopus*; Hannon et al. 2003). Further, physiological reproductive costs have been detected in male black grouse (Angelstam 1984, Kervinen et al. 2012) and sage-grouse (Vehrencamp et al. 1989). Trade-offs between past and subsequent reproductive success have not been evaluated in female sage-grouse, with the exception of the influence of past brood success on subsequent brood success where positive trade-offs were documented (Blomberg et al. 2013).

Knowledge of the factors affecting population growth is vital to optimize the effectiveness of conservation efforts, particularly for harvested species. Taylor et al. (2012) concluded sage-grouse conservation should focus on increasing nest success, chick survival, and hen survival. Many of these parameters and the factors affecting them (e.g., habitat, environmental conditions) have been reported (see Connelly et al. 2011; e.g., Lyon and Anderson 2003, Holloran et al. 2005, Dahlgren et al. 2010, Guttery et al. 2013). However, evaluation of reproductive trade-offs and climatic effects are absent or rare in many taxa, but are vital to the conceptualization of natural systems and therefore population ecology. Precise understanding of population ecology is vital to conservation, particularly for declining and harvested species where repercussion of direct (e.g., harvest) and indirect (e.g., habitat manipulation or conservation) management actions have large effects on species conservation.

The purpose of our research was to estimate the effects of past reproductive success and climatic factors on subsequent reproductive parameters. We hypothesize: (1) reproductive costs manifest in sage-grouse nest success, brood success, and clutch size, but do not influence nest initiation; (2) positive trade-offs occur for complete reproductive success (i.e., brood success) due to the individual heterogeneity hypothesis; (3) decreased drought positively influences the likelihood of reproductive success.

METHODS

Habitat

Our study was conducted at the southern extent of the sage-grouse range (Schroeder et al. 2004) on Parker Mountain in south-central Utah, where elevation ranges 2,200–3,000 m. The area received 40–50 cm of precipitation annually, most during the winter as snow (60%), and the remainder as rain in late summer (Jaynes 1982). Parker Mountain typically experienced 65–80 frost-free days, and the mean maximum and minimum temperatures for January and July were 1°C, −13°C and 27°C, 9°C, respectively (Jaynes 1982). The site is dominated by black sagebrush (*A. nova*) flats and ridges with mountain big sagebrush (*A. tridentata tridentata*) and silver sagebrush (*A. cana*) in swales and at higher elevations. Parker Mountain is predominately publicly owned, and private lands accounted for 1% (1,363 ha) of the study area. The primary land-uses are grazing by domestic livestock and recreation (e.g., hunting, camping, off-highway vehicles).

Field methods

Hens were captured at roost sites proximal to leks using spotlights and long handled nets (Giesen et al. 1982, Wakkinen et al. 1992) during March and April 1998–2009. Once captured, birds were fitted with 15–19 g necklace-style radio transmitters (Advanced Telemetry Systems, Isanti, MN, USA in 1998–2004; Holohil Systems, Carp, Ontario, Canada in 2005–2009) equipped with mortality sensors. Hens were classified as second year (SY) or after second year (ASY) based on condition of the outer primaries (Dalke et al. 1963) and wing characteristics (Beck et al. 1975). Beginning in May, hens were located at least once every 5 days to document the onset of incubation. Nesting was confirmed visually, but hens were not intentionally flushed due to the species' propensity to abandon nests if disturbed (Holloran et al. 2005, Baxter et al. 2008), and consequently clutch size was measured post-hatch or after depredation. Nests were checked every 1–2 days to determine fate. Once hatched, broods were monitored using one of two techniques. From 1998–2004 and in 2010 brood hens were located every 3 days to determine brood fate. Non-brood hens were located every 5–7 days. From 2005 to 2009 broods were captured within 1 week of hatch (most within 48 hours of hatch), and chicks were marked with suture-anchored 1.5-g backpack-style radio transmitters (Burkepile et al. 2002) without mortality sensors (Advanced Telemetry Systems, Insanti, MN, USA in 2005; Holohil Systems, Carp, Ontario, Canada in 2006–2008; American Wildlife Enterprises, Monticello, FL, USA in 2009). Radio marked chicks were located every other day. Broods were considered successful if $\geq$1 chick survived to $\geq$50 days in 1998–2004 and $\geq$42 days in 2005–2010. Brood success could be slightly biased in years without marked chicks (1998–2004) due to brood mixing (see Dahlgren et al. 2010). Regardless, brood success in both years with and without marked chicks was measured using direct observations and apparent success. Non-brood hens were not monitored regularly during the breeding season 2005–2009.

Model covariates

We compiled year-specific covariate data for drought and climate on our study area. We included monthly and seasonal values of the Palmer Z-index of drought severity (PZ). Winter, early summer, late summer, and summer were defined as 1 November to 31 March, 1 May to 30 June, 1 July to 31 August, and 1 May to 31 July, respectively. PZ data were downloaded from the National Oceanic and Atmospheric Administration's National Climate Data Center (http://www.ncdc.noaa.gov/temp-and-precip/time-series/index.php). We included climatic variables on average temperature and total precipitation accumulation for monthly and seasonal time periods. Additionally, we include a proximate measure of spring snowpack (wteq). By our definition, wteq is the maximum snow water equivalent measured in the spring of each year. Climatic data was downloaded from the Natural Resources Conservation Service SNOTEL website (http://www.wcc.nrcs.usda.gov/snow/). All SNOTEL covariate data were averaged across the two proximal and representative stations to our study site (Black Flat–U.M. Creek, site number 348; Donkey Reservoir, site number 452).

Model implementation

We used generalized linear mixed models implemented with the "glmer" function from the lme4 package in program R 3.0.0 (R Core Team 2013) for all analyses. Four separate modeling procedures were implemented to evaluate the effects of climatic variation, previous reproductive success, and hen age (in year $t-1$) on nest initiation, clutch size, nest success, and brood success. Previous reproductive success was defined as reproductive parameters (e.g., nest initiation, nest success, brood success) in the immediately preceding year. In all analyses, the unique identity for each individual hen was used to specify an individual random effect (intercept), to account for repeat observations within each individual's reproductive history. Individual random effects aid in capturing differences in individual quality by accounting for unobserved variability in reproductive quality across individuals. Data for nest success and brood success models was subset to isolate the direct effect of each parameter (i.e., only individuals that actually attempted the reproductive stage in year t). For nest initiation, nest success, and brood success modeling procedures we used a binomial distribution, a logit link, and fit models using an adaptive Gaussian Hermite approximation procedure. For the clutch size modeling procedure, we used a Poisson distribution, a log link, and fit models using the Laplace approximation procedure.

Model selection

We used a sequential approach to candidate model set building for nest initiation, clutch size, nest success, and brood success. We first evaluated the effect of previous reproductive parameters (e.g., nest success year $t-1$) on current reproduction (e.g., brood success year t). Once the best performing previous reproductive effects models were selected, we then modeled the effects of climatic variables (in year t and $t-1$) on reproduction in year t. Candidate models were ranked using Akaike's Information Criterion adjusted for sample size (AIC_c; Akaike 1973, Burnham and Anderson 2002), and models with $\Delta AIC_c \leq 2$ were considered equally supported by the data (Burnham and Anderson 1998). When calculating AIC_c we counted all fixed effect parameters, and counted random effects where the variance was greater than zero. Our final candidate model set included the best performing ($\Delta AIC_c \leq 2$) parameter structures for reproductive variables in year $t-1$ and climatic variables (in year t and $t-1$), while testing for their effects on reproductive output in year t. We used likelihood ratio tests to evaluate parameters in competing nested models.

RESULTS

We marked 248 hens, monitored 313 nests, and tracked 142 broods from 1998 to 2010. Nest initiation models were based on 123 two-year observations (i.e., 246 nest initiation attempts) of 100 individuals (i.e., 23 individuals had $\geq$3 years of data); clutch size models on 77 two-year observations of 67 individuals; nest success models on 97 two-year observations of 83 individuals; brood success models on 58 two-year observations of 50 individuals.

Both the nest initiation models and clutch size models in our candidate models set failed to outperform the null model (intercept only). Consequently, we could not detect a relationship between either nest initiation rate or clutch size in year t and reproductive success in year $t-1$ or climatic variables in year $t-1$ or t. Further, we found no evidence to support effects of hen age, nest initiation in year $t-1$, or time lag effects of climatic variables in any of the models. Previous reproductive success and climatic variation were, however, found to affect both nest success and brood success (Tables 1 and 2).

Our nest success modeling procedure (Table 1) suggested the existence of one competing model ($\Delta AIC_c \leq 2$). However, this model ($\Delta AIC_c = 1.94$) only differed from the top model with the

Table 1. Candidate models evaluating the effects of climate and past reproductive success on subsequent hatch success of greater sage-grouse (*Centrocercus urophasianus*) on Parker Mountain, Utah, USA, 1998–2010.

Model†	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	ωi	Deviance	np	σ_R^2
BS_{t-1} + WTEQ_t	108.55	0.00	0.32	102.29	3	0
BS_{t-1} + May PZ_t	110.49	1.94	0.12	104.23	3	0
BS_{t-1} + Winter PZ_t	111.17	2.62	0.09	104.91	3	0
BS_{t-1}	111.52	2.97	0.07	107.39	2	0
BS_{t-1} + Precipitation Winter_t	111.90	3.35	0.06	105.64	3	0
BS_{t-1} + Precipitation Winter_{t-1}	112.73	4.18	0.04	106.47	3	0
BS_{t-1} + Temperature May_t	112.75	4.20	0.04	106.49	3	0
Null	112.75	4.20	0.04	110.71	1	0
BS_{t-1} + Winter PZ_{t-1}	113.03	4.48	0.03	106.78	3	0
BS_{t-1} + March PZ_t	113.23	4.68	0.03	106.97	3	0
BS_{t-1} + Summer PZ_{t-1}	113.36	4.81	0.03	107.10	3	0
BS_{t-1} + Temperature April_t	113.40	4.85	0.03	107.14	3	0
BS_{t-1} + Precipitation Late Summer_{t-1}	113.55	5.00	0.03	107.29	3	0
BS_{t-1} + April PZ_t	113.63	5.09	0.03	107.38	3	0
BS_{t-1} + Temperature Winter_t	113.64	5.09	0.03	107.38	3	0
BS_{t-1} + Precipitation Early Summer_{t-1}	113.65	5.10	0.02	107.39	3	0

Notes: $\mathrm{AIC_c}$ = Akaike's Information Criterion adjusted for sample size; $\Delta\mathrm{AIC_c}$ = difference in AIC_c values between each model and the best model; ωi = AIC_c weight; np = number of parameters (fixed effects + random effects > 0); σ_R^2 = random individual intercept variance.

† HS = hatch success; BS = brood success; PZ = Palmer Z-index of drought; WTEQ = spring snowpack, t = year t; $t-1$ = year $t-1$.

substitution of the wteq in year *t* parameter (top model) for the May PZ in year *t* parameter. The May drought index and snowpack index likely reflect an effect of spring moisture on nest success, and the snowpack index (wteq) also contributes to explaining variation in our data (wteq *t*, $\beta = 0.455$, SE = 0.214, $p = 0.033$). As such, higher values of wteq in year *t* led to a higher likelihood of nest success in year *t* (Table 3). In addition to wteq, the top model included an additive effect of brood success in year $t-1$ (brood success $t-1$, $\beta = -0.954$, SE = 0.496, $p = 0.056$), indicating females with successful broods in year $t-1$ were less likely to successfully nest in year *t* (Table 3).

From our brood success candidate model set (Table 2), two models were less than 2 $\Delta\mathrm{AIC_c}$. Both models included additive effects of brood success and hatch success in year $t-1$ on brood success in year *t*, and the top ranked model included an additive effect of April PZ in year *t* on brood success in year *t*. Based on a likelihood ratio test, we determined that the additive effect of April PZ in year *t* ($X^2 = 3.525$, df = 1, $p = 0.06$) was biologically meaningful and significantly affected brood success in year *t*. We acknowledge brood success and hatch success in year *t* are both observed (correlation of fixed effects = 0.772) and logically correlated to some degree, albeit less than the 0.80 cut-off recommended by Zar (2010) for suspected collinearity. Regardless, collinearity among predictors is directional in that it overestimates standard errors and reduces power to detect significance of estimated effects (Zar 2010, Dormann et al. 2013). However, in the presence of collinearity the coefficients (β) are still estimated correctly (see Dormann et al. 2013). Thus, collinearity increases the likelihood

Table 2. Candidate models evaluating the effects of climate and past reproductive success on subsequent brood success of greater sage-grouse (*Centrocercus urophasianus*) on Parker Mountain, Utah, USA, 1998–2010.

Model	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	ωi	Deviance	np	σ_R^2
HS_{t-1} + BS_{t-1} + April PZ_t	48.62	0.00	0.52	39.87	4	0
HS_{t-1} + BS_{t-1}	50.04	1.42	0.26	43.60	3	0
Null	53.00	4.38	0.06	46.61	2	2.65
HS_{t-1}	53.06	4.44	0.06	48.78	3	1.71
April PZ_t	53.11	4.49	0.06	46.67	3	2.97
HS_{t-1} + April PZ_t	53.35	4.73	0.05	44.59	4	1.69

Note: Model parameters and column headings are as in Table 1.

Table 3. Odds Ratios for parameters in the best models of climate and past reproductive success on subsequent nest and brood success of greater sage-grouse (*Centrocercus urophasianus*) on Parker Mountain, Utah, USA, 1998–2010.

Model parameter†	Odds ratio	95% CI
Brood success top model parameters		
HS_{t-1}	0.03 (32.12)	0.00–0.29 (3.5–295.06)
BS_{t-1}	16.01	1.83–140.1
April PZ_t	1.93	1.03–3.6
Hatch success top model parameters		
BS_{t-1}	0.39 (2.6)	0.17–0.87 (1.15–5.87)
$WTEQ_t$	1.58	1.11–2.24

Notes: Model parameters are as in Table 1.Values in parentheses are the inverse of the odds ratio (i.e., odds of failure).

† April PZ_t and $WTEQ_t$ are continuous variables and odds are per unit change (1 Palmer Z-index unit and 2.54 cm for each parameter, respectively).

of a type 2 error, but not the likelihood of a type 1 error. Consequently, when both brood success and hatch success are included in a model, our standard error estimates and associated significance values should be interpreted as maximum values, and thus, conservative estimates of underlying effects. We had a strong a priori biological justification for including both parameters in the same model despite their relatedness. The respective effects represented opposing hypotheses for reproductive trade-offs, and as such, we hypothesized that the parameter estimates would have opposing signs, which was supported by our analysis. Indeed, based on the parameter estimates (brood success $t-1$, $\beta = 2.77$, SE = 1.32, $p = 0.035$) individuals that had successful broods in year $t-1$ were more likely (Table 3) to have successful broods in year t, given they hatched a brood in year t. Parameter estimates for the effect of previous nest success (hatch success $t-1$, $\beta = -3.45$, SE = 1.35, $p = 0.01$) indicated individuals that failed to hatch a nest in year $t-1$ were more likely (Table 3) to have a successful brood in year t. April PZ in year t (April PZ t, $\beta = 0.655$, SE = 0.381, $p = 0.085$) suggests that brood survival is higher (Table 3) with increased precipitation in April of year t (i.e., decreased drought). Differential effects of previous reproductive success (negative slope of hatch success year $t-1$ vs. positive slope of brood success year $t-1$) on subsequent reproductive success could indicate individual heterogeneity. Furthermore, when comparing the models with additive effects of both brood and hatch success in year $t-1$ (second ranked model; Table 2) to hatch success in year $t-1$ only (third ranked model; Table 2), the variance associated with the individual random intercept was estimated at 0 and 1.71, respectively.

DISCUSSION

Previous research has demonstrated acute reproductive costs on survival of various species (Williams 1966, Erikstad et al. 1998), including some grouse species (Tetraoninae, Angelstam 1984, Caizergues and Ellison 1997, Hagen et al. 2007, Blomberg et al. 2013). We extend the reproductive costs to a chronic effect on subsequent reproduction that, to our knowledge, has not been shown for grouse, but has been shown for other taxa (e.g., Røskaft 1985, Gustafsson and Sutherland 1988). Additionally, we were able to decompose the reproductive cycle into its various components (nest initiation, clutch size, nest success, and brood success), thereby allowing us to evaluate the effects of various stages of previous reproductive effort and climatic variability (in year t and $t-1$) on current-year stage-specific reproductive success while also controlling for repeat observations of individuals throughout their known reproductive history. For example, Blomberg et al. (2013) reported positive effects of brood success in year $t-1$ on brood success in year t for sage-grouse. Our detailed analysis indicated that previous reproductive success had varying effects on the likelihood of subsequent reproduction. Similar to Blomberg et al. (2013) we demonstrate that successful brood hens are more likely to have successful broods in the following year (given that a brood was attempted) than unsuccessful brood hens; however, we were also able to detect a negative association between nest success in year $t - 1$ and brood success in year t. Our additional level of detail revealed that both cost of reproduction and individual heterogeneity in reproductive output may be influencing a particular measure of reproductive output (brood success).

Individual heterogeneity in reproductive output and cost of reproduction has been shown in mammalian (Hamel et al. 2009) and avian (Aubry et al. 2009, Aubry et al. 2011, Cam et al. 2013) taxa and could be present in our system as evidenced by differential effects of previous brood success on subsequent hatch success (negative slope) and brood success (positive slope). The differential effects lead us to conclude that most individuals that produce a successful brood subsequently fail to achieve complete reproductive success in the following year (i.e., failed hatch success). However, successful brood hens that attain subsequent hatch success are more likely to achieve subsequent brood success. Although individual heterogeneity in reproductive output appeared to be present in our system, we believe our covariates largely described variation within individuals as evidenced by the individual random effect variance estimated at zero for the top two brood success models (Table 2) and all nest success models (Table 1). The link of reproductive costs between seasons could be tied to time and/or energy constraints reproduction puts on molt, and in turn increased energy expenditure in thermoregulation during winter (Nilsson and Svensson 1996, Dawson et al. 2000).

Our analysis, as hypothesized, did not reveal reproductive costs for all estimated reproductive parameters (e.g., nest initiation). However, in contrast to our hypothesis, costs did not manifest in clutch size. Reproductive costs can manifest as completely forgoing reproduction or abandonment of effort during a reproduction attempt (Erikstad et al. 1998). Our results suggest that the probability of a hen attempting to initiate a nest in a given year is not associated with previously accrued costs, but likelihood of reproductive failure post-nest initiation (i.e., a form of abandonment) increases when reproductive costs were incurred, which is consistent with grouse ecology. Food is not typically a limiting factor for grouse species during winter (Bergerud and Gratson 1988), which is particularly apparent for sage-grouse as evidenced by high winter survival (see J. W. Connelly, S. T. Knick, M. A. Schroeder, and S. J. Stiver, *unpublished manuscript*; e.g., Caudill et al. 2014) and observations of substantial weight gain during winter (Beck and Braun 1978). A logical conclusion is that sage-grouse generally enter the breeding season with adequate resources to attempt reproduction. However, ample high quality wintering habitats on our study site (Caudill et al. 2013) could have influenced hens' body condition and mitigated variability that has been reported in nest initiation (see Connelly et al. 2011). Our results demonstrate that multiple measures of previous reproductive effort had varying effects on reproductive trade-offs and trade-offs manifest in multiple, but not all, measures of reproductive output. Consequently, multiple measures of reproductive effort and output should be assessed when evaluating cost of reproduction and trade-offs.

Evaluation of individual heterogeneity and reproductive costs are vital to the conservation of harvested species. If "superior" individuals are removed by harvest from the population in non-random fashion, a distinct dichotomy could occur, where disproportionate removal is inversely related to effects on population size and persistence due to disproportionate contribution of "superior" individuals. For example, harvest may appear compensatory at the population level, but if "superior" individuals are removed disproportionally, effects on population size could be greater than expected. Both additive (e.g., Van Kooten et al. 2007, Sedinger et al. 2010) and compensatory (e.g., Connelly et al. 2000, Gibson et al. 2011) harvest mortality have been espoused for sage-grouse. However, harvest mortality hypotheses, as currently conceptualized, may be problematic when reproductively successful groups have differential susceptibility to harvest (Redfield 1975), contribute disproportionately to population growth rates (sensu Taylor et al. 2012), and consistently contribute to population growth (i.e., consistently successful "brood hens"; e.g., Blomberg et al. 2013). In many states, sage-grouse harvest seasons have been trending later in the year to minimize the susceptibility to harvest of reproductively successful females and their offspring (see Hornaday 1916, Patterson 1952, Reese and Connelly 2011).

Our results indicate this trend is warranted and should likely continue as in some instances harvest is still selective of juvenile birds (young of the year) and successful hens (Caudill et al. 2014). Importance of segments of the population (i.e., consistently successful "brood hens") to population growth rates was not a parameter we attempted to quantify, but is of paramount importance in understanding the effects of harvest and conceptualization of population ecology.

Climatic variables in the same year as the reproductive event influenced reproductive success. For both nest success and brood success, increased moisture resulted in increased likelihood of reproductive success. We found limited support for an effect of April drought on brood success, where brood success increased with moisture. The effect of moisture in April may be associated with soil moisture and habitat conditions during the brood-rearing period. Drought negatively affects chick survival (Guttery et al. 2013) and increased snow depth positively affects recruitment in sage-grouse (Blomberg et al. 2012). Furthermore, increased moisture in sagebrush-steppe ecosystems is positively related to abundance of insects (Wenninger and Inouye 2008), which are an important resource for sage-grouse chicks (Johnson and Boyce 1990, Gregg and Crawford 2009, Dahlgren et al. 2010). In addition, snowpack was the best climatic predictor of nest success, showing a positive relationship, and is likely linked to habitat quality during the nesting season (e.g., grass cover at nest sites). Holloran et al. (2005) also reported increased winter precipitation positively affected sage-grouse nest success. Our results suggest that reduced depth of snowpack as a result of climate change (Mote et al. 2005) could negatively affect nest success. Similarly, Guttery et al. (2013) suggest that reductions in snowpack may pose a major threat to sage-grouse populations.

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