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RESEARCH ARTICLE

Individual and environmental effects on egg allocations of female Greater Sage-Grouse

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ABSTRACT

The average number of eggs in a clutch and the size of those eggs play a role in individual fitness. We explored sources of variation in egg allocations of female Greater Sage-Grouse (*Centrocercus urophasianus*) in the American Great Basin over a 10-yr period, as well as range-wide variation in clutch size, using our data and other published values. We tested for environmental and individual effects on clutch size ($n = 390$) and egg volume ($n = 2,486$) in a mixed-modeling framework, with random-effect terms that described variation among individual females (i.e. heterogeneity) and allowed us to calculate repeatability for clutch and egg size. The strongest influence on clutch size was the timing of nest initiation, which varied by as much as 67 days within years and showed a negative linear relationship with clutch size. Once this pervasive effect was accounted for, we also found positive effects of annual precipitation and nest-site elevation. In wetter years and at more productive high-elevation sites, females laid larger clutches, which suggests that some degree of large-scale resource availability affects clutch size. The fixed effects in our models explained $\sim 34\%$ of the total variance in clutch size, and individual random effects explained an additional 15% (repeatability = 0.15). In contrast to clutch size, little measurable variation in egg volume could be attributed to the fixed effects we considered, and $\sim 60\%$ of the variance in egg volume was associated with random effects (repeatability = 0.59). Prenesting female body condition influenced clutch size, and this effect was most pronounced for replacement clutches. We found repeatability for clutch and egg size to be within the range of published estimates for other avian taxa. Across studies, mean clutch size increased with latitude, demonstrating that Greater Sage-Grouse follow geographic patterns in clutch size that are consistent with other avian taxa.

Keywords: body condition, *Centrocercus urophasianus*, clutch size, egg volume, heterogeneity, repeatability

RESUMEN

El número promedio de huevos en una nidada y el tamaño de esos huevos juegan un rol en la adecuación biológica individual. Exploramos las fuentes de variación en las asignaciones de huevos de hembras de *Centrocercus urophasianus* en la Gran Cuenca americana a lo largo de un período de 10 años, y también exploramos la variación a lo largo del rango en el tamaño de la nidada de *C. urophasianus* usando nuestros datos y otros valores publicados. Evaluamos los efectos ambientales e individuales en el tamaño de la nidada ($n = 390$) y el volumen del huevo ($n = 2,486$) en un marco de trabajo de modelo mixto, con términos de efectos aleatorios que describen la variación entre las hembras individuales (i.e. heterogeneidad), y que nos permitió calcular la repetibilidad del tamaño de la nidada y del huevo. La influencia más fuerte sobre el tamaño de la nidada fue el momento del inicio del nido, que varió tanto como 67 días dentro del año y mostró una relación lineal negativa con el tamaño de la nidada. Una vez que controlamos este fuerte efecto, también encontramos efectos positivos de la precipitación anual y la elevación del sitio del nido. En los años húmedos y en sitios elevados más productivos, las hembras pusieron nidadas más grandes, sugiriendo que algún grado de disponibilidad de recursos a gran escala afecta el tamaño de la nidada. Los efectos fijos en nuestros modelos explicaron el $\sim 34\%$ de la varianza total en el tamaño de la nidada, y los efectos aleatorios individuales explicaron un 15% adicional (repetibilidad = 0.15). En contraste con el tamaño de la nidada, se podría atribuir poca variación mensurable en el volumen del huevo a los efectos fijos que consideramos, y casi 60% de la varianza en el volumen del huevo estuvo asociado con los efectos aleatorios (repetibilidad = 0.59). La condición corporal de la hembra antes de la anidación influenció el tamaño de la nidada y este efecto fue más pronunciado para nidadas reemplazantes. Encontramos que la repetibilidad del tamaño de la nidada y del huevo para *C. urophasianus* está dentro del rango de los estimados publicados para otros taxones de aves. A lo largo de los estudios, el tamaño medio de la nidada

aumentó con la latitud, demostrando que *C. urophasianus* sigue patrones geográficos en el tamaño de la nidada que son consistentes con otros taxones de aves.

Palabras clave: *Centrocercus urophasianus*, condición corporal, heterogeneidad, repetibilidad, tamaño de la nidada, volumen del huevo

INTRODUCTION

Individuals must balance the energy they allocate to reproduction against that necessary for maintenance and survival (Cody 1966, Stearns 1992), and life history strategies evolve to optimize this energy allocation in order to maximize fitness in a given environment (Stearns 1992, Ricklefs 2000). In birds, the production of eggs represents a major investment in reproductive activities. The number of eggs laid in a given clutch and the size of those eggs are two opportunities for females to adjust reproductive allocations and balance current reproductive effort against mortality risk and the potential for future reproduction. Females must also balance the number of eggs laid in a clutch against the energy invested in each individual egg within the clutch (Smith and Fretwell 1974). Larger eggs are likely to contain greater amounts of nutrients, and young produced from larger eggs are typically morphologically larger, have increased growth rates, and/or survive at a greater rate than young hatched from smaller eggs (Ankney 1980, Moss et al. 1981, Sandercock and Pedersen 1994, Krist 2011). Female egg allocations therefore involve both trade-offs between current reproductive success and future reproductive potential and trade-offs between the total number and the average quality of young within clutches.

A number of ubiquitous patterns related to large-scale spatial and temporal variation in clutch size have influenced questions related to why birds lay the number and size of eggs that they do (Winkler and Walters 1983, Martin 2014). Both among and within species, clutch size tends to increase with latitude (Evans et al. 2009, Musvuugwa and Hockey 2011, Martin 2014). Within species breeding at a common latitude, clutch size also tends to follow clear temporal patterns within a single nesting season (Winkler and Walters 1983, Crick et al. 1993, Evans et al. 2009, Martin 2014). The shape of this seasonal relationship differs among single-brooded versus multibrooded species, presumably because different selective pressures operate on these 2 reproductive strategies (Crick et al. 1993). In multibrooded birds, clutch size increases early in the nesting season, reaches a maximum during midseason, and declines thereafter. By contrast, for single-brooded birds, clutch size declines linearly throughout the nesting season. Hypotheses that attempt to explain the evolutionary mechanisms that produce these spatial and temporal sources of variation in clutch size are

numerous (e.g., Arnold et al. 1987, Rowe et al. 1994) and remain a subject of ongoing discussion (Ricklefs 2000, Martin 2014).

Selective pressures related to food availability (Lack 1947), risk of predation on eggs and dependent young (Martin 1995, Ghalambor et al. 2013), offspring development time (Martin 2014), and mortality of adult birds (Ashmole 1961) have all been suggested as drivers of clutch-size evolution (Martin 2014). Of these, food may not influence selection directly, but rather may serve as a proximate mechanism for realized variation in clutch size by placing a limit on the total nutrients available to breeding birds (Martin 2004, 2014). In species that feed their young (often, but not always, altricial species), food availability places a constraint on the number of dependent offspring that parents can feed (Lack 1947, 1954, Winkler and Walters 1983). Conversely, in species with self-feeding young (precocial species only), food's primary limitation is the amount of nutrients that can be allocated to eggs (Lack 1968, Winkler and Walters 1983). In these species, food availability affects egg allocations either from stored endogenous reserves obtained prior to breeding (Ryder 1970, Ankney and MacInnes 1978) or from food obtained concurrently with egg production (i.e. exogenous resources; Lack 1968, Winkler and Walters 1983, Martin 1987). Heterogeneity among individuals is also an important determinant of realized variation in demographic traits (van Noordwijk and de Jong 1986, Aubry et al. 2009, Blomberg et al. 2013), including egg allocation (Christians 2002). Some sources of heterogeneity, such as individual age, can often be measured directly, whereas others, such as social dominance or physiological condition, may be more difficult to measure. Studies of egg allocation often measure repeatability, or the degree to which clutch or egg size remains constant within individuals (Lessells and Boag 1987). Repeatability provides a method for assessing the importance of individual heterogeneity in determining the realized variation in egg allocations among individuals within populations.

We explored sources of variation in clutch and egg size of Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter "sage-grouse"; Figure 1), an endemic resident bird of shrub-steppe habitats, found throughout western North America, that are dominated by sagebrush (*Artemisia* spp.). Sage-grouse have emerged as a species of concern in both the United States and Canada following long-term declines throughout their range (Schroeder et al. 2004). Most investigations of sage-grouse nesting



FIGURE 1. Nesting female Greater Sage-Grouse. Photo credit: E. J. Blomberg

ecology have focused on nest success and habitat selection (reviewed by Hagen et al. 2007, Connelly et al. 2011a, 2011b), with less attention paid to other vital rates such as nesting propensity or factors that affect female allocation of nutrients to eggs. Sage-grouse produce a single brood of precocial young each year but often initiate replacement clutches when primary nests are lost (Schroeder et al. 1999). Several authors have reported that first clutches tend to be larger than second clutches and that experienced females tend to lay larger clutches than first-year breeders (Schroeder et al. 1999, Connelly et al. 2011a). Few studies, however, have explored variation in sage-grouse clutch size as an explicitly stated objective (e.g., Schroeder 1997), and information on variability in egg size is even more sparse (Petersen 1980).

We used 10 yr of nesting data collected from radio-tagged female sage-grouse in Eureka County, Nevada, USA, as well as a summary of range-wide estimates of sage-grouse clutch size, to evaluate variation in egg allocations and explore factors that may potentially affect clutch size and egg volume. Our objective was to evaluate variation in sage-grouse egg allocations as a result of temporal, spatial, and individual processes. We expected that sage-grouse would follow broad patterns of clutch size consistent with those often observed in single-brooded or precocial birds. That is, we predicted that clutch size would decline throughout the nesting season within our focal study population and that range-wide estimates would increase with study latitude. We also expected that variation in food resources would explain some of the

realized variation in egg allocation among individuals, so we explored relationships between large-scale drivers of resource availability, such as annual rates of precipitation and nest-site elevation, and clutch size and egg size. We also predicted that females in higher prebreeding body condition would produce larger clutches and lay larger eggs than females in lower condition. Because of trade-offs between the number and size of eggs within a given clutch, we predicted that we would find a negative association between clutch size and egg size. Other than age and condition effects, we lacked measures to fully capture heterogeneity among individual females, so we conducted all analyses in a mixed-modeling framework, which allowed us to incorporate individual random-effect terms (Dingemanse and Dochtermann 2013). This approach also allowed us to calculate repeatability, the proportional variance in a trait due to differences among individuals (Flint et al. 2001), for both clutch size and egg volume, which we compare to estimates from other species.

METHODS

Study Area

Our study was conducted in a 6,500-km² landscape located in Eureka County (Figure 2). Terrain and vegetation in this study area were characteristic of the American Great Basin (Blomberg et al. 2012, 2013). Sage-grouse nesting habitat was dominated by sagebrush steppe vegetation communities. Female sage-grouse nested at low elevations (<2,100 m) in sites dominated by Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis*) and black sagebrush (*A. nova*), and at higher-elevation sites (>2,100 m) dominated by mountain big sagebrush (*A. tridentata* ssp. *vaseyana*) and low sagebrush (*A. arbuscula*). In this study area, large-scale wildfires have resulted in recent (post-1999) conversion of sagebrush steppe habitats to grasslands dominated by exotic grasses (Blomberg et al. 2012).

Field Methods

We captured female sage-grouse near breeding leks during the spring and in seasonal high-elevation sagebrush habitat during late summer, using standard nighttime capture techniques (Connelly et al. 2003). Each female was weighed (± 0.05 kg), and we measured tarsus length (± 0.01 cm) and the length of the fifth primary feather (± 0.1 cm). We aged females as >1 yr of age (after-first-year [AFY]) or <1 yr of age (first-year [FY]) on the basis of feather characteristics (Crunden 1963). Sometimes female age could not be determined or was not recorded, and in these cases females were classified as unknown age. Females were fitted with a uniquely numbered aluminum leg band (National Band and Tag, Newport, Kentucky, USA) and a very high frequency (VHF) radio transmitter with a necklace-style attachment (Advanced Telemetry

Systems, Isanti, Minnesota, USA). The average battery life of these radio transmitters allowed us to monitor females for as many as 3 nesting seasons. The FY females and females of unknown age were graduated to AFY in the second year they were monitored.

During the nesting season, we used handheld telemetry equipment and attempted to locate each female and visually observe nesting status at least twice weekly. Upon locating a female on a nest, we flushed the female and recorded the number of eggs in the clutch. We floated at least 2–3 eggs in a plastic container filled with water to determine incubation stage, based on the position of the egg in the water column (Westerskov 1950). We used a float chart developed for Mallards (*Anas platyrhynchos*), whose incubation period (28 days; Drilling et al. 2002) is similar to that of sage-grouse (25–29 days; Schroeder et al. 1999). For the purpose of the present study, we used only data from nests found after the onset of incubation or for which final clutch size was confirmed after the onset of incubation. We used dial calipers to measure (± 0.01 cm) the length (L) and maximum diameter (D) of each egg. Egg volume (V) was then calculated as $V = K_v LD^2$, where the egg volume coefficient ($K_v = 0.497$) was as reported for Ring-necked Pheasant (*Phasianus colchicus*; Hoyt 1979).

After processing, we monitored nests biweekly from a distance >10 m to determine nest status (active vs. inactive). For the remainder of the nesting season, to detect additional nesting attempts, we continued to monitor females whose nests failed. During the study, we discovered a small number ($n = 6$) of nests known to be third nesting attempts. For the purpose of this analysis, we grouped all second or later clutches into an aggregate category that comprised replacement clutches.

Analysis

We used generalized linear mixed models (GLMMs) to evaluate relationships between explanatory covariates and clutch size or egg volume. The covariate values we considered included female age (AFY, FY, or age unknown), nesting attempt (first or replacement), nest initiation date, nest elevation, nest aspect, precipitation, year, female lek of capture, and exotic grassland footprint surrounding the nest site. To estimate the date of nest initiation, we added 1.5 days for each egg (assuming that eggs were laid at a rate of 2 eggs per 3 days; Schroeder et al. 1999) to the measured incubation stage and subtracted this value from the date of nest discovery. In practice we were generally able to predict hatch dates for successful nests to within ± 2 days using this approach, and we assume similar precision for nest initiation.

We retrieved monthly precipitation data for each year of the study from the PRISM Climate Group website (<http://www.prism.oregonstate.edu/>). We used the total amount of precipitation falling between September and April (here-

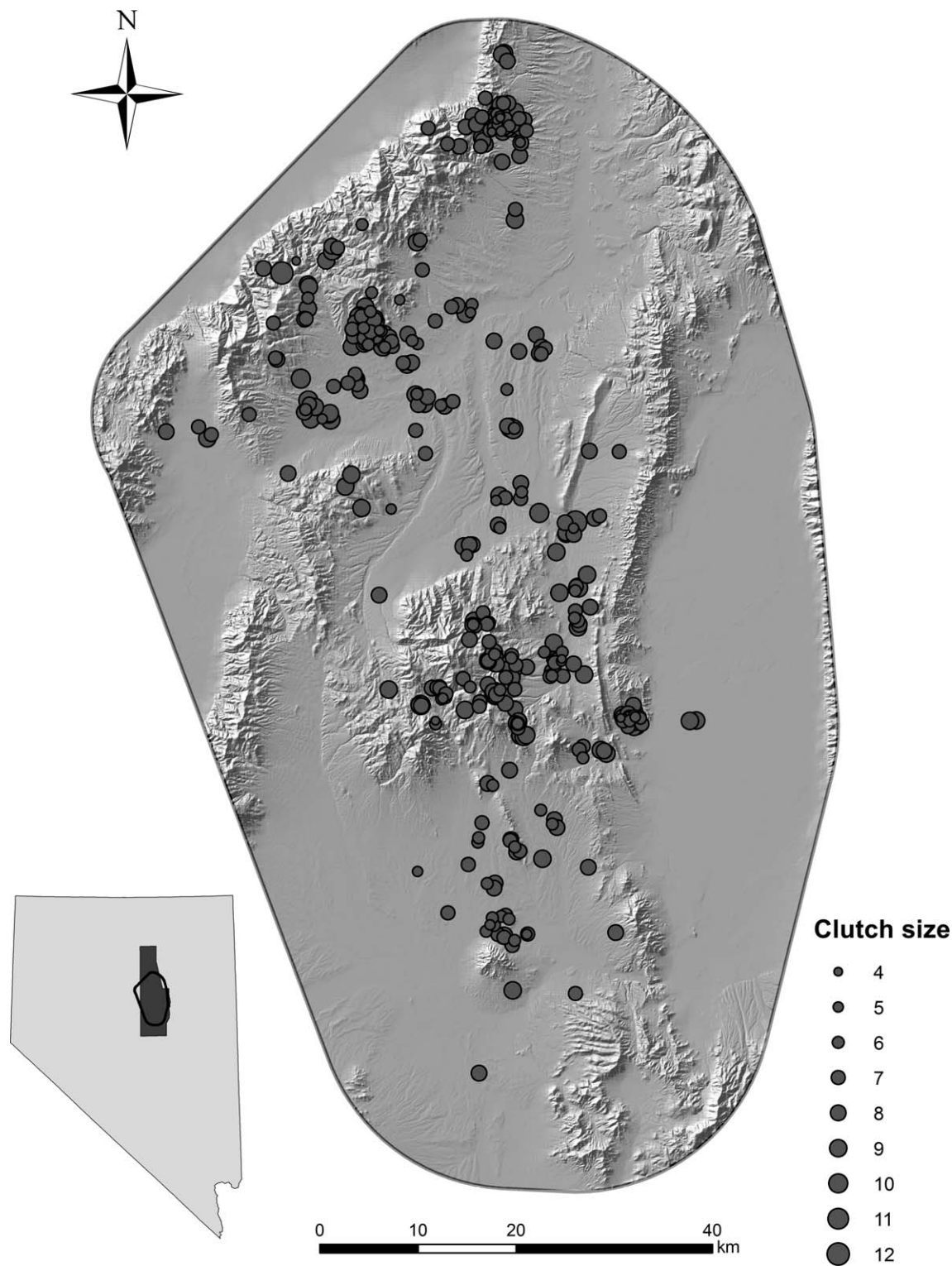


FIGURE 2. Study area, nest locations, and spatial distribution of clutch size for Greater Sage-Grouse nests located in Eureka County, Nevada, USA, 2003–2012 (inset map).

after “fall–winter”) as a precipitation metric because, we reasoned, this interval would be most likely to promote plant growth that was accessible to females during egg development. We obtained nest-site elevation (m) and aspect from a digital elevation model with 30-m resolution and converted aspect to a categorical variable associated with the cardinal directions (N = 316°–45°; E = 46°–135°; S = 136°–225°; W = 226°–315°). To evaluate the influence of sagebrush conversion to exotic grassland on egg allocation, we quantified the relative footprint of exotic grasslands within 5 km of each nest, following methods described in Blomberg et al. (2012). Year, lek of capture, nest aspect, and female age were included as discrete categorical effects to test for these sources of spatial and individual variation.

We evaluated support for covariate effects on clutch size and egg allocation in a GLMM framework implemented using the lme4 package in R (R Project for Statistical Computing; <http://www.r-project.org/>). For analyses of clutch size, we incorporated a random effect in the form of a random intercept term for each female. For analyses of egg size, we included 2 random-effect terms in a hierarchical structure that allowed the random intercept for each nest to be nested within the random intercept term for each female (Flint et al. 2001). Incorporation of these random effects allowed us to statistically account for nonindependence among measures of repeated clutches from the same female, and within clutches in the case of egg volume. We used a two-phase approach to model development and evaluation of covariates. In phase 1, we first considered univariate models that included a single additive effect for each covariate, which would reflect a simple linear relationship between the covariate and egg allocation. We then also considered that effects of certain covariates on egg allocations may be modified by the influence of other covariates. For example, AFY females may have laid larger clutches, on average, than FY females, but young females that nested in more productive high-elevation habitat may have produced clutches that were, on average, closer in size to their AFY counterparts. To account for these modifying effects, we included interactions among each pair of covariates and contrasted this model with the model that contained only additive effects of the 2 covariates in question. We also included an intercept-only model (includes random-effect terms) as a contrasting null hypothesis. To facilitate comparison of fixed effects among competing models using the lme4 package, we specified full maximum-likelihood estimation, as opposed to the restricted likelihood. We used a combination of information-theoretic model selection (Burnham and Anderson 2002) and evaluation of parameter coefficients (β) and their associated variance to determine support for each model structure. We considered variable effects on egg allocation to be meaningfully supported when their inclusion improved model fit (based

on a criterion of 2.0 Δ AIC) in relation to contrasting models, and when 85% confidence intervals (defined as $SE \cdot 1.4395$) of β did not overlap 0.0 (Arnold 2010).

In phase 2 of model development, we aggregated the covariate structures supported in phase 1 into a single comprehensive model, which maximized the variance in clutch or egg size that was described by our explanatory covariates (which represent nonexclusive hypotheses). However, we wished to ensure that this model did not overfit the data as a result of redundancy among covariates. We therefore systematically removed each covariate or interaction effect and evaluated the resulting change in model fit. If model fit was reduced when a covariate or interaction term was removed, we considered that effect important and retained the covariate. If model fit was not reduced, those covariates were discarded because they presumably did not add meaningful information to the model. This approach left us with a final “best fit” model that maximized the total amount of explained variance in egg allocation, given our model set.

Body-condition effects on egg allocation. To quantify individual body condition, which we define as mass in relation to structural size, we first conducted a principal component analysis of tarsus and fifth-primary length and used first principal component scores as an index to individual body size. We then used a generalized linear model (GLM) to relate body size to individual mass, where we also included a Julian date term (January 1 = day 1) to test for the potential of seasonal changes in mass within individuals that were related to date of capture. The residuals from this regression provided an estimate of female mass in relation to body size, standardized to a common date of capture. The values were zero-centered, such that values >0.0 reflected females in “better than average” condition, and values <0.0 reflected females in “below average” condition. Because we did not handle, weigh, and measure females during each year they were monitored, we restricted this analysis to only clutches discovered in a female’s year of capture.

We tested for body-condition effects by adding an additional body-condition term as an additive effect to the best-fit model structure identified in phase 2 above. We also expected that body condition may modify relationships between egg allocation and other explanatory covariates. For example, females in better body condition may be more buffered against drought conditions than females in poorer body condition. To explore these possibilities, we also considered models that included interactions between body condition and each of the other supported covariates. We used our best-fit model from phase 2 for the basis of comparison against model structures that contained body-condition effects, using model selection and variable support criteria as described above.

Individual heterogeneity in egg allocation. Use of a GLMM allowed us to control for the effect of heterogeneity among females (i.e. between-individual variation; *sensu* Dingemanse and Dochtermann 2013) with respect to egg allocation. In this context, we were also able to explore the extent to which heterogeneity affected egg allocations, to contrast the importance of between-individual variation with the fixed-effect component of our models, and to consider the degree of unexplained variance (a combination of unmeasured process variance and sampling error) in our data. Multiple data points are required for each level of a random effect (e.g., unique individuals) to make such interpretations (Digemanse and Dochtermann 2013), so we used only data collected from females with ≥ 2 clutches (clutch size analysis) or from clutches in which ≥ 2 eggs were measured (egg volume analysis) for the purpose of evaluating heterogeneity.

We estimated the proportional variance in egg volume and clutch size associated with our GLMMs (R^2_{GLMM}) using the MuMIn package in R, which relies on methods for partitioning variance as presented by Nakagawa and Schielzeth (2012). Here, we used the restricted maximum-likelihood estimator in lme4 to provide unbiased estimates of the model variance components. R^2_{GLMM} is analogous to the coefficient of determination (R^2) often presented in traditional statistical analysis (e.g., analysis of variance or GLM). In this case, marginal R^2 ($R^2_{\text{GLMM(m)}}$) reflects the proportional variance associated with model fixed effects (variation among clutches across individuals), whereas conditional R^2 ($R^2_{\text{GLMM(c)}}$) represents the proportional variance associated with both the fixed- and random-effect components of the model (i.e. total explained variance). The proportional variance associated with the random-effect component ($R^2_{\text{GLMM(r)}}$; variation in clutch size among individuals, i.e. heterogeneity) can then be computed as $R^2_{\text{GLMM(r)}} = R^2_{\text{GLMM(c)}} - R^2_{\text{GLMM(m)}}$, and unexplained error is estimated as $\varepsilon = 1.0 - R^2_{\text{GLMM(c)}}$. These summary statistics allowed us to evaluate the extent to which individual heterogeneity affected clutch size and egg volume in a way that was directly comparable between the 2 data types (Nakagawa and Schielzeth 2012). $R^2_{\text{GLMM(r)}}$ is also analogous to repeatability (Lessells and Boag 1987, Nakagawa and Schielzeth 2010, Dingemanse and Dochtermann 2013), which is commonly reported from field studies of egg allocation (e.g., Myrberget 1989, Flint et al. 2001), and so $R^2_{\text{GLMM(r)}}$ can also be used for the purpose of cross-study comparison.

Range-wide variation in sage-grouse clutch size. To explore whether sage-grouse conform to predictions related to latitudinal variation in clutch size, we compared mean clutch-size estimates from published studies across the species' range with study-area latitude. We used mean clutch sizes reported in the range-wide summary compiled by Taylor et al. (2012: supplemental material appendix A),

our own estimates from the present study, an additional estimate reported by Lockyer et al. (2013), and an unpublished estimate from the Pine Nut Mountains in western Nevada (P. Coates, USGS Western Ecological Research Center, personal communication). Because clutch size is commonly reported to differ among first and replacement clutches in sage-grouse (Schroeder et al. 1999, Connelly et al. 2011a), we used only estimates reported explicitly for first clutches. This allowed us to minimize bias that may have resulted from variability in reneesting rates among studies. We retrieved the latitudes ($\text{DD}^\circ \text{MM}'$) reported in each study, and in cases where latitudes were not reported, we used the latitude of a prominent nearby landmark (e.g., city or town) based on the study-area description. We converted latitudes to decimal degrees ($\text{DD}^\circ + [\text{MM}'/60]$) and used a simple linear model to evaluate the proportional variance in reported clutch size that was explained by latitude. We note that most sage-grouse researchers avoid flushing females from their nests because of the risk of nest abandonment (Connelly et al. 2011a), which may lead to undercounting if individual eggs are removed by predators or if egg shells are removed from the nest by scavengers. Assuming that this bias was uniform across studies (with the exception of ours, in which clutch size was unbiased), it should not have affected our ability to detect latitudinal effects if they existed. Results are presented as means \pm SD.

RESULTS

During our 10-yr study, we collected data on 390 clutches, of which 323 were assumed to be associated with first nesting attempts, whereas 67 were known to be replacement clutches. More nests were laid by AFY females (288) than by FYs (84) or females of unknown age (18; data summarized in Appendix Table 3). Average clutch sizes by female age class and nest attempt were as follows: AFY first clutch, 7.9 ± 1.3 ($n = 234$); AFY replacement clutch, 6.6 ± 1.5 ($n = 54$); FY first clutch, 7.2 ± 1.4 ($n = 73$); and FY second clutch, 6.4 ± 1.4 ($n = 11$). We monitored 231 unique females and obtained data for ≥ 2 nests from 101 of them. As many as 6 nests were monitored for a single female across multiple years. We measured 2,486 eggs from 341 nests, 2,141 of which were associated with first nests and 345 of which were associated with second nests.

Clutch Size

Date of nest initiation, female age, and nest attempt were all supported as univariate effects on clutch size (Appendix Table 3). Clutches that were initiated earlier in the season were larger than those laid later ($\beta = -0.08$; 85% CI: -0.09 to -0.07 ; Figure 3), and FY females laid smaller clutches than AFYs ($\beta = -0.39$; 85% CI: -0.61 to -0.18). A positive

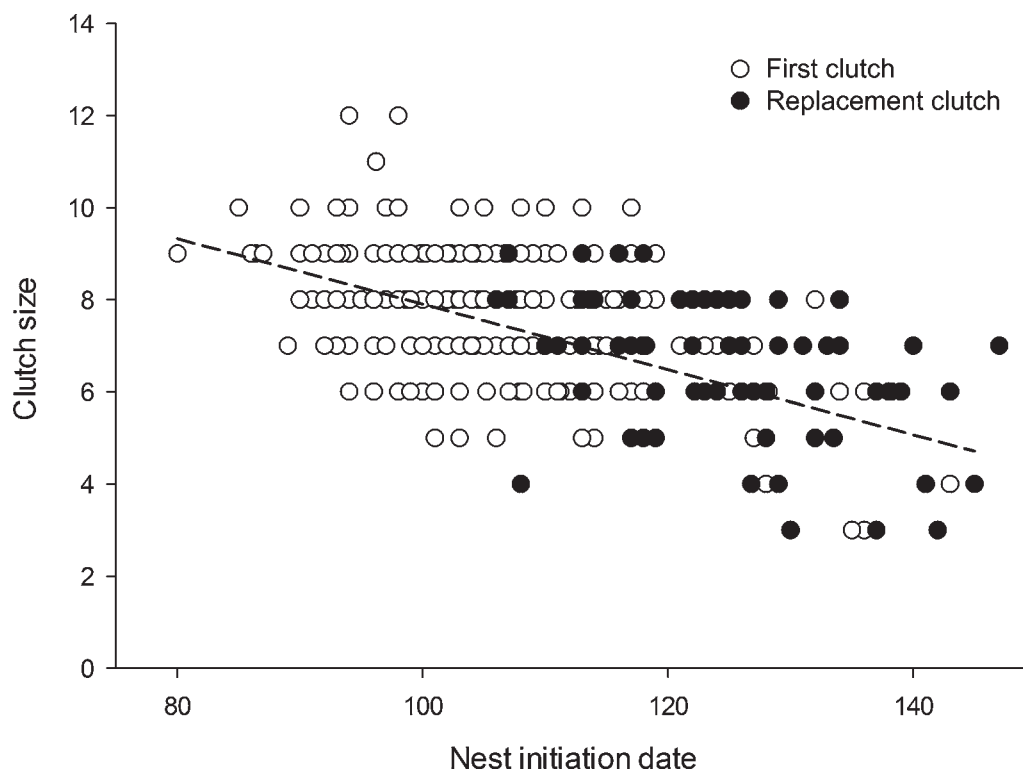


FIGURE 3. Relationship between clutch size and nest initiation date for female Greater Sage-Grouse in Eureka County, Nevada, USA, 2003–2012. Clutches associated with nests believed to be first attempts and those known to be second attempts are depicted by closed and open circles, respectively. Day 80 = March 21.

effect of nest-site elevation ($\beta = 0.27$; 85% CI: 0.16–0.37) was also revealed when considered in combination with an additive effect of nest initiation date. Because higher-elevation nests were typically laid later in the season, the positive effect of nest-site elevation was apparent only when the negative effect of initiation date was accounted for (Figure 4). Similarly, we found support for an interaction between nest initiation date and precipitation (Appendix Table 4). Drought conditions had a negative influence on clutch size, and these effects were strongest for nests that were initiated later in the season (Figure 5). By contrast, clutch size for early nests was relatively independent of precipitation rates across years (Figure 5). First clutches were, on average, larger (7.7 ± 1.4 ; $n = 323$) than replacement clutches (6.5 ± 1.5 ; $n = 67$). However, the date of nest initiation also confounded this relationship because second nests were laid relatively later in the season. If a first and a replacement clutch were initiated on a common date, our models suggest that replacement clutches were likely to be larger than first clutches ($\beta = 0.44$; 85% CI: 0.15–0.73). When we tested for an interaction between nest attempt and initiation date, AIC increased by a value of 2.5, suggesting lack of support for the interaction (Appendix Table 4). A model including additive effects of initiation date and nest attempt was 0.8

Δ AIC lower than a model that only contained the initiation date effect (Appendix Table 4), so we could not reject support for the additional positive effect of nesting attempt on clutch size. Our best-fit model therefore contained additive effects of age, initiation date, elevation, and nest attempt, as well as interactions between initiation date and precipitation and between initiation date and exotic grasslands. Removal of exotic grassland as an additive effect improved model fit, and removal of its interaction with initiation date left model fit essentially unchanged (Table 1), so we discarded the exotic grassland covariate from our final best-fit model.

The fixed-effect component of the best-fit model explained $\sim 34\%$ of the variance in clutch size ($R^2_{\text{GLMM(m)}} = 0.34$). When we reduced the data set to only individuals with >2 clutches, the overall fit to the model fixed effects remained similar ($R^2_{\text{GLMM(m)}} = 0.40$), and we found that an additional 15% of the variation in clutch size could be attributed to heterogeneity among individuals ($R^2_{\text{GLMM(r)}} = 0.15$). Clutch-size repeatability was therefore estimated as 0.15. We included 157 nests from 131 females in our analysis of effects of female body condition on clutch size. A female's date of capture did not influence her mass at capture ($\beta < 0.001$; confidence intervals overlap 0.0). Parameter coefficients suggested a positive effect of body

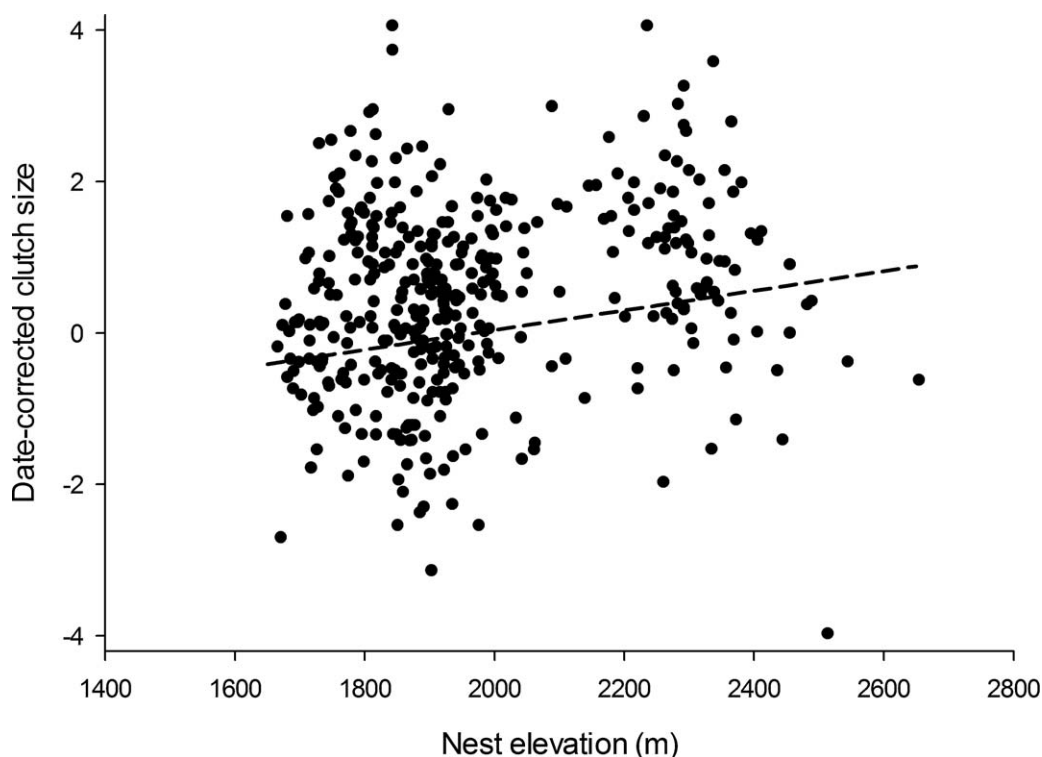


FIGURE 4. Relationships between clutch size and the elevation of nest sites selected by female Greater Sage-Grouse in Eureka County, Nevada, USA, 2003–2012. An elevational effect was apparent only when the background effect of nest initiation date was controlled for, and so here clutch size has been corrected to reflect a common initiation date.

condition on clutch size ($\beta = 1.34$; 85% CI: 0.06–2.62); however, this additive effect produced only a marginal improvement in model fit (Table 2). Including an interaction between female body condition and date of nest initiation or nest attempt produced a substantial improvement in model fit (Table 2). The best-supported model suggested that body-condition effects differed between first and replacement clutches. Females in the highest prebreeding body condition produced replacement clutches that were similar to the population average for first clutches, whereas poorer-condition females produced generally smaller replacement clutches (Figure 6). First clutches were less sensitive to female body condition (Figure 6).

Egg Volume

Model selection suggested that a number of fixed effects were associated with egg volume (Appendix Table 5). The best-supported model included an interaction between the date of nest initiation and clutch size (Appendix Table 5). Eggs laid early in the season were predicted to be the same volume regardless of clutch size, whereas eggs laid later in the season decreased in volume by $\sim 1.5\%$ for each additional egg present in the clutch. Nest initiation date and nest attempt were included in all models that outperformed the null model. Eggs laid later in the season

were smaller than earlier-laid eggs ($\beta = -0.04$; 85% CI: -0.02 to -0.06), and eggs associated with second clutches were smaller than eggs associated with first clutches ($\beta = -12.17$; 85% CI: -5.17 to -17.17). As with clutch size, these 2 effects were largely redundant, and when the effect of initiation date and attempt were considered together, the effect of nesting attempt was not supported ($\beta = 0.37$; 85% CI: -0.47 to 1.21). Also supported were effects of female age, fall–winter precipitation, nest elevation, exotic grasslands, and interactions between initiation date and exotic grasslands, nest attempt and precipitation, and nest attempt and nest-site elevation (Appendix Table 5). In general, however, all supported fixed effects explained very little of the total variance in egg size. A fully saturated model that included all supported covariates had $R^2_{\text{GLMM}(m)} = 0.04$, which suggests that although covariate effects were supported by model selection (likely a result of large sample size), they did not explain much meaningful variation in egg volume. This can be visualized in Figure 7, which shows the relatively flat modeled relationship between egg volume and nest initiation date. By contrast, the random-effect component of the model explained a large amount of the total variance ($R^2_{\text{GLMM}(r)} = 0.55$). Variance estimates for the 2 random-effect terms (clutch and individual) included in this analysis suggest that the greatest amount of variation in egg size was explained by

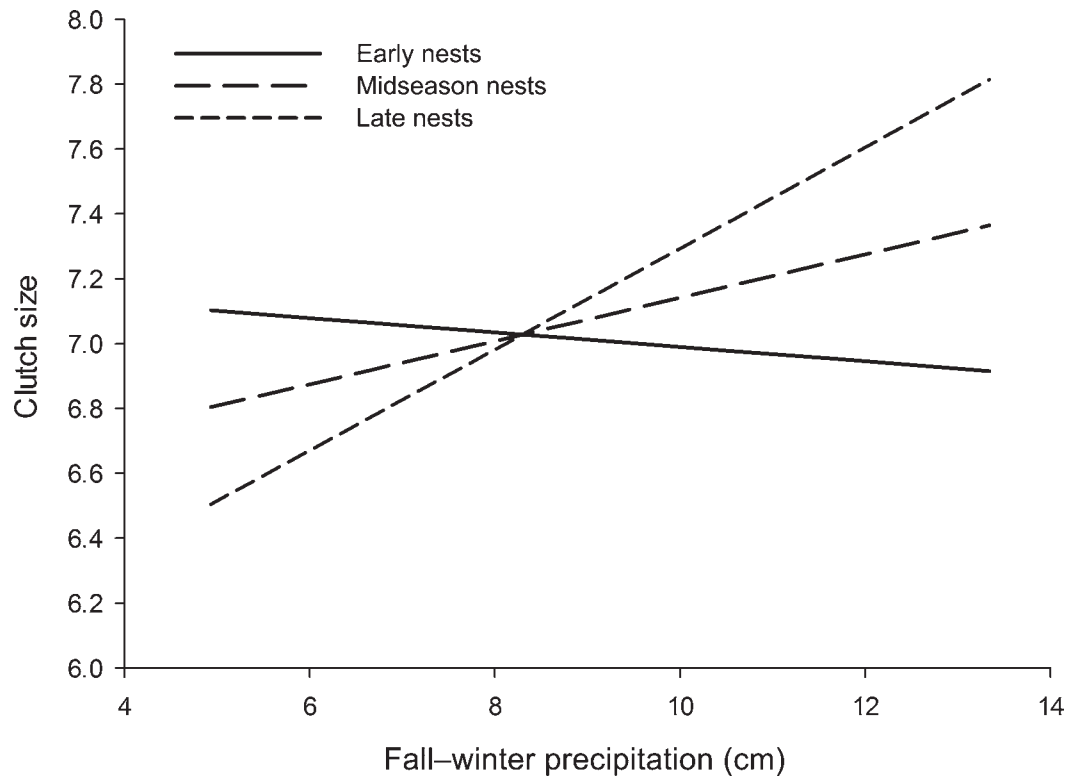


FIGURE 5. Modeled relationship between fall–winter precipitation and clutch size of nesting female Greater Sage-Grouse in Eureka County, Nevada, USA, 2003–2012. The graph depicts an interaction between the effect of fall–winter precipitation and the date of nest initiation (early = day 90; midseason = day 110; late = day 130).

TABLE 1. Model selection results for final best-fit models of Greater Sage-Grouse clutch size in Eureka County, Nevada, USA, 2003–2012. Model structure was identified in an initial phase (see Appendix Table 4), and an additional analysis was used to identify variable redundancy by systematically removing variables and/or interaction effects. All models included a random intercept term for individual females, and model selection notation follows Burnham and Anderson (2002).

Model ^a	K	ΔAIC ^b
Full – Exotic	10	0.0
Full Model	12	0.7
Full – Exotic*Initiation Date	11	0.8
Full – Precip*Initiation Date	11	4.6
Full – Attempt	7	8.5
Full – Precip	10	9.4
Full – Age	6	10.2
Full – Elevation	7	14.1
Full – Initiation Date	7	109.8
Null	3	157.0

^a Full Model = Age + Initiation Date + Exotic + Attempt + Precip + Elevation + Initiation*Precip + Exotic*Precip; Age = first-year vs. after-first-year; Attempt = first nest vs. replacement nest; Elevation = nest-site elevation (m); Exotic = footprint of exotic grasslands within 5 km of nest site; Initiation Date = Julian date of nest initiation; and Precip = total precipitation from the previous September to April.

^b Minimum AIC = 1,241.6.

TABLE 2. Model selection results for the effects of female body condition on Greater Sage-Grouse clutch size in Eureka County, Nevada, USA, 2003–2012. The base model structure (Full) was identified in an initial phase (see Table 1) and was used to evaluate body-condition effects, given other sources of variance in the data. All models included a random intercept term for individual females, and model selection notation follows Burnham and Anderson (2002).

Model ^a	K	ΔAIC ^b
Full + Body Condition*Attempt	12	0.0
Full + Body Condition*Initiation Date	12	1.6
Full + Body Condition	11	5.2
Full	10	5.4
Full + Body Condition*Age	13	5.7
Full + Body Condition*Elevation	12	7.2
Full + Body Condition*Precip	11	10.6
Null	3	56.2

^a Full Model = Age + Initiation Date + Attempt + Precip + Elevation + Initiation*Precip; Age = first-year vs. after-first-year; Attempt = first nest vs. replacement nest; Elevation = nest-site elevation (m); Initiation Date = Julian date of nest initiation; Precip = total precipitation from the previous September to April; and Body Condition = female mass in relation to a common structural size and date of capture.

^b Minimum AIC = 490.2.

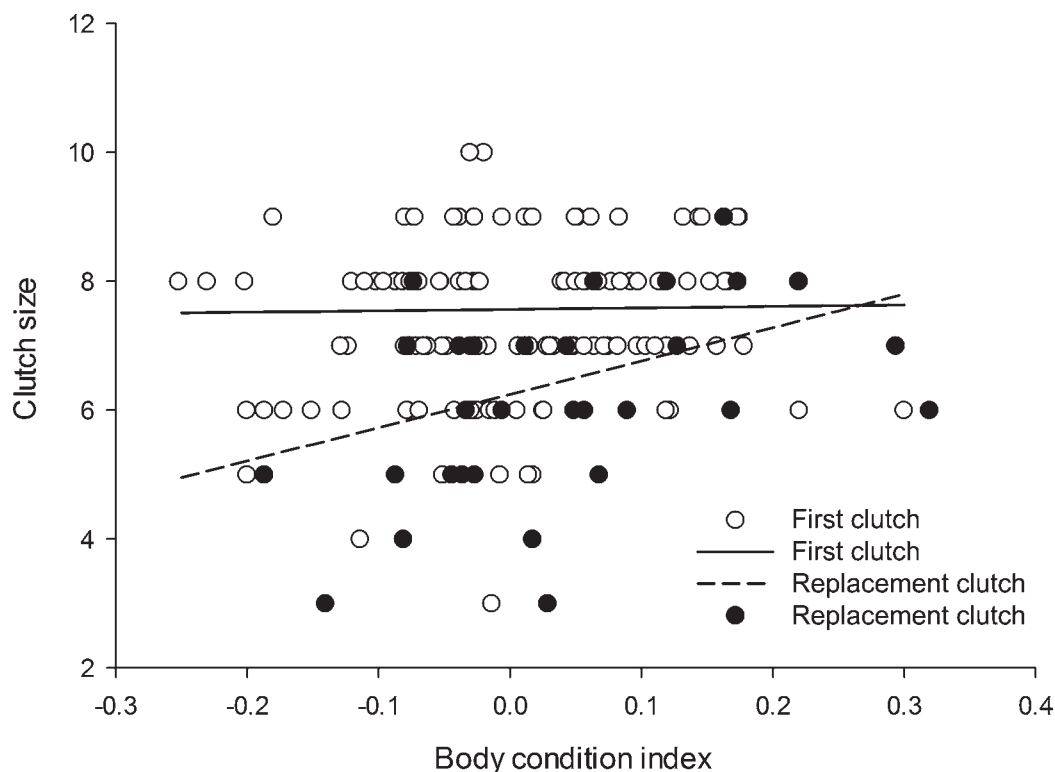


FIGURE 6. Effects of female body condition on clutch size of Greater Sage-Grouse nests in Eureka County, Nevada, USA, 2003–2012. Body-condition effects were strongest for second nesting attempts, as identified by the depicted interaction between female body condition and nest-attempt number.

repeatability within clutches ($R^2_{\text{GLMM}(r)} = 0.42$), and less variation was associated with repeatability within individual females ($R^2_{\text{GLMM}(r)} = 0.13$). We included 1,015 eggs in our analysis of female body-condition effects. Inclusion of body condition did not improve model fit, and as with other fixed effects, the body-condition covariate did not explain a meaningful amount of variance in egg volume ($R^2_{\text{GLMM}(m)} = 0.01$).

Range-wide Variation in Sage-Grouse Clutch Size

Among studies that provided estimates of mean first clutch size ($n = 12$), we found a positive relationship between the average size of first clutches and population latitude (Figure 8). This model was better supported ($\text{AIC} = 23.5$) than an intercept-only null model ($\text{AIC} = 35.6$), and parameter coefficients suggested that a 1° increase in latitude produced a 0.22-egg increase in predicted clutch size ($\beta = 0.22$; 85% CI: 0.16–0.29). Within this sample, $\sim 70\%$ of the range-wide variation in clutch size was associated with latitude ($R^2 = 0.69$).

DISCUSSION

We found that multiple sources of individual and environmental variation influenced the egg allocations of

female sage-grouse. Our results demonstrate a clear decline in sage-grouse clutch size throughout the nesting season, consistent with prior research on single-brooded species (Crick et al. 1993, Evans et al. 2009, Fletcher et al. 2013) and species with precocial young in particular (Winkler and Walters 1983). In our study, the seasonal decline in clutch size was consistent between first and replacement clutches and obscured the effects of several additional sources of environmental variation. Several prominent hypotheses have attempted to explain seasonal changes in clutch size. Original hypotheses related to the effects of food limitation (Lack 1954, Ryder 1970) were synthesized in terms of nutrient allocation by Drent and Daan (1980) and Daan et al. (1990) and were subsequently formalized by Rowe et al. (1994). Collectively, these authors suggest that females can optimize reproductive output by balancing the acquisition and allocation of nutrients against offspring reproductive value. For females in lower condition (or with access to fewer exogenous resources), delaying nest initiation is advantageous because it allows individuals to acquire additional resources to produce more and larger eggs. However, delayed initiation is beneficial only until the point at which the reductions in reproductive value of the clutch offset the benefits associated with delayed initiation. Because young from

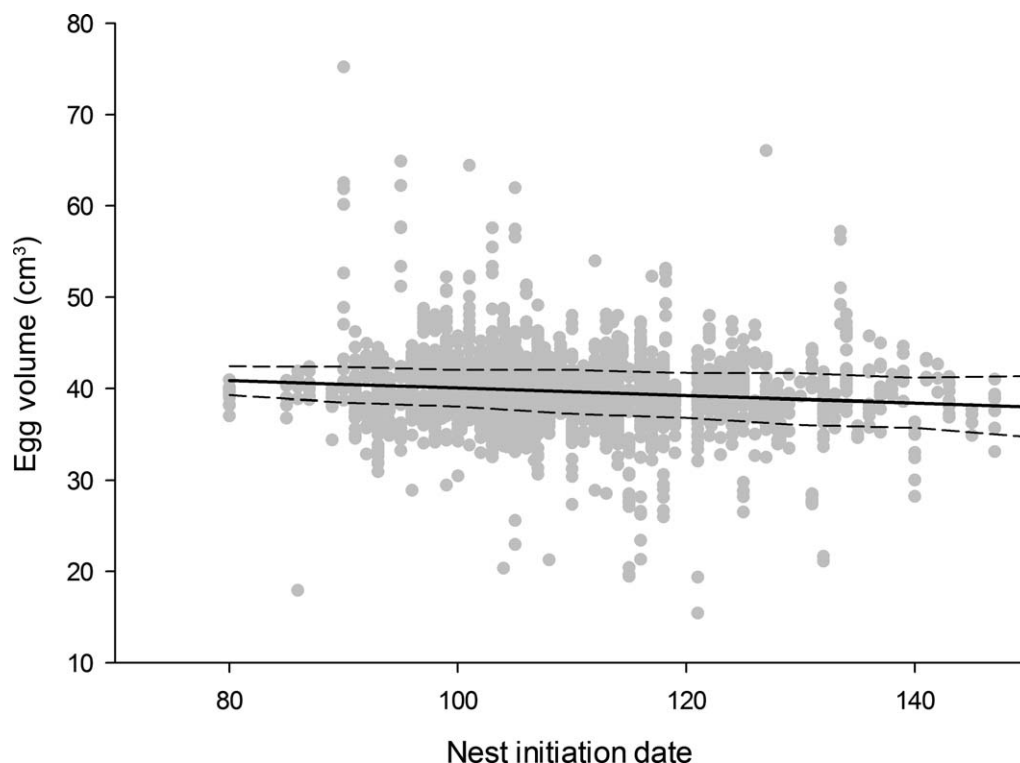


FIGURE 7. Relationship between nest initiation date and the volume of eggs laid by female Greater Sage-Grouse in Eureka County, Nevada, USA, 2003–2012. Solid line reflects the modeled relationship between initiation date and egg volume, and dashed lines represent 85% confidence intervals for this relationship.

late-laid clutches have higher mortality and lower recruitment value, females that delay nest initiation will achieve the greatest fitness benefit by laying relatively fewer eggs (Rowe et al. 1994).

Our results provide multiple lines of evidence that demonstrate the importance of nutrient limitation in driving individual variation in sage-grouse clutch size. Females that nested at higher elevations had greater-than-expected clutch sizes, given their nest initiation dates, and this effect was strong enough to produce a difference in clutch size of >1 egg along our observed gradient of nest-site elevations (Figure 4). We also found that in years of higher fall–winter precipitation, females nesting later in the season laid larger clutches than during drought years. This effect was also sufficiently strong that late-nesting females were predicted to produce clutches >1 egg larger in the wettest versus driest years (Figure 5). Higher-elevation sagebrush communities in our study system comprise more diverse plant assemblages (Blomberg et al. 2013), receive greater levels of precipitation, have greater available soil moisture, and have generally higher primary production compared with lower-elevation sites. Similarly, in years of greater precipitation, overall primary plant production increases in this semiarid region (Blomberg et al. 2012). Because female sage-grouse are almost exclu-

sively herbivorous during prenesting, a causal relationship between egg allocations and spatiotemporal variation in food resources is likely.

We found that females in higher prebreeding body condition laid larger replacement clutches than females in lower prebreeding condition. In fact, females in the highest body condition were likely to lay replacement clutches that were as large as mean first clutches (Figure 6). In tetraonids, egg nutrients are thought to be largely derived from exogenous sources (Naylor and Bendell 1989, Gregg et al. 2006). However, even if female endogenous reserves contribute a relatively small amount to egg production, the same allocation to each egg must be maintained for the length of time required to complete a clutch. The positive associations we observed between body condition and replacement clutch size may also suggest an overall effect of female quality on replacement-clutch allocation. For example, females with a greater ability to secure nutrients over winter (leading to high spring body condition) may also have been better able to secure nutrients following loss of a first nest. This may arise, for example, from variation among females with respect to social dominance in communal feeding areas, or from variation in female gut capacity or digestive efficiency. Consistent with this hypothesis, Gregg et al. (2006) found that female sage-

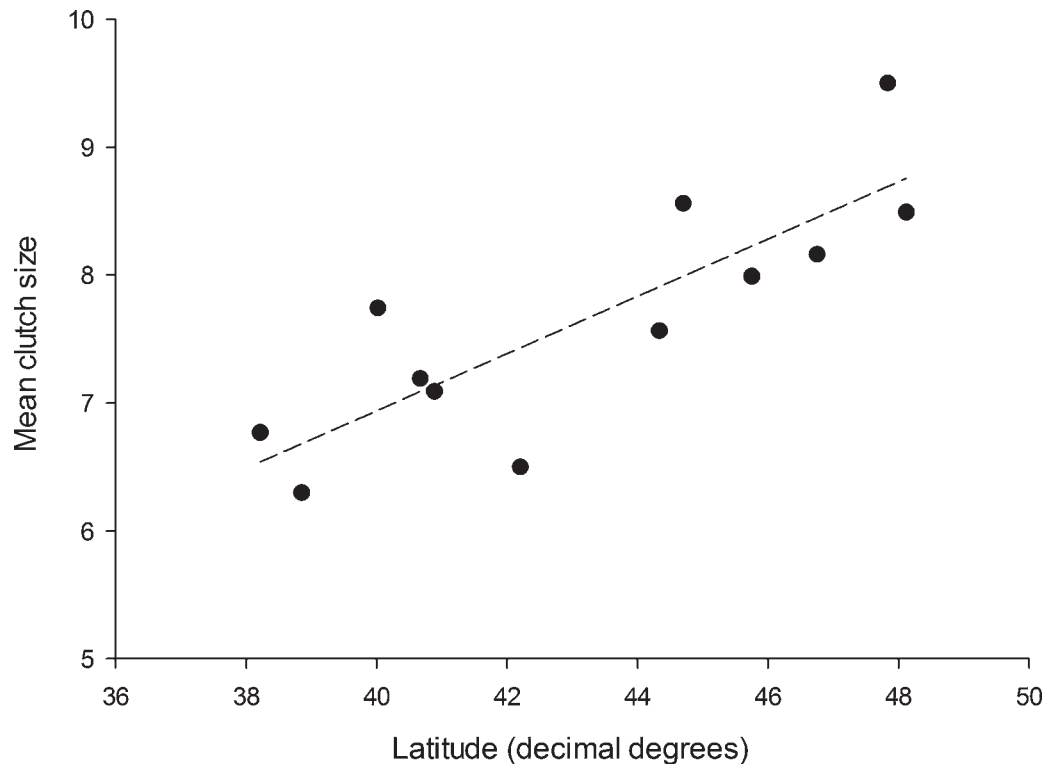


FIGURE 8. Relationship between mean first clutch size and population latitude from 12 studies of Greater Sage-Grouse nesting in which authors reported clutch sizes for first nesting attempts.

grouse with greater plasma protein levels had a higher propensity to produce a replacement clutch following nest loss.

Variation in quality may also explain our finding that once the date of nest initiation was accounted for, second clutches had slightly more eggs, on average, than would be predicted for a first clutch initiated on the same day. If “high-quality” females were more likely to initiate a replacement clutch, our sample of replacement clutches were laid by a segment of the female population that was otherwise likely to lay large clutches. To be clear, first clutches were, on average, larger than second clutches, which is consistent with values reported from other studies of sage-grouse nesting (Connelly et al. 2011a). Our results, however, suggest that the differences between first and second clutches are related more to timing of nest initiation than to individual ability to acquire the nutrients needed to produce a large second clutch of eggs. Presumably this is related to the trade-off between clutch size and offspring reproductive value that occurs at the individual level, as described earlier (Rowe et al. 1994), and may be triggered by physiological cues that are not explicitly related to nutrition (Voss and Cooper 2013). We do not mean to suggest that nutrition does not influence the clutch size of individuals—clearly it does, as we discussed above. However, we suggest that the variation

in clutch size commonly observed between first and replacement clutches (Connelly et al. 2011a) is likely a function of the evolved relationship between timing of nest initiation and clutch size (Drent and Daan 1980, Daan et al. 1990, Rowe et al. 1994), with the optimal combination for any given female determined in part by her body condition (i.e. Rowe et al. 1994: fig. 2).

Because some nests were no doubt depredated before discovery, it is likely that we misclassified some number of nests as first attempts that were, in fact, second efforts. In another analysis, we estimated that the rate of failed detection for first nests during our study was 0.09 (95% CI: 0.07–0.11) and that the average female reneesting rate was 0.34 (95% CI: 0.31–0.37; D. Gibson personal communication). On the basis of these 2 estimates, we can calculate the probability that a first nest was missed, that the hen then renested, and that we then discovered her second nest (i.e. the chain of events that would lead to misclassification) as $0.09 \times 0.34 \times (1 - 0.09) = 0.028$. We can then estimate the total number of nests during our study that were misclassified as $323 \times 0.028 = 8.99$, or 9 nests that we classified as first nests that were, in fact, replacement nests. Given this, the overall misclassification rate during our study (0.03) was relatively minor and likely did not appreciably affect our results.

Repeatability for clutch size in our study population was relatively low ($R^2_{\text{GLMM}(r)} = 0.15$) but was comparable to estimates reported by Myrberget (1989) for Willow Grouse (*Lagopus lagopus*) in Norway ($r = 0.23$) and falls within the range of values for all birds (summarized by Christians 2002). Our results therefore suggest that the majority of phenotypic variation in clutch size was associated with external forces rather than variation among individuals. The fixed-effect component of our best-fit model explained a substantial amount of this variance ($\sim 34\%$), but there was also additional variance that we could not account for, presumably due to extrinsic factors that we did not measure.

Egg size is more repeatable than clutch size (Christians 2002), and our estimate of total repeatability in egg size (0.60) fell within the range of values summarized by Christians (2002). Relatively few avian studies have partitioned egg-size repeatability into within-clutch versus within-female variance (Flint et al. 2001). We found that within-clutch repeatability explained a larger amount of proportional variance in egg volume (45%), compared with within-individual repeatability (15%). These results are consistent with those reported by Flint et al. (2001) for Black Brant (*Branta bernicla nigricans*) and suggest that although egg size is, in general, highly repeatable for sage-grouse, individual females may have some flexibility in adjusting egg size among clutches. The same fixed effects that explained a substantial amount of variance in clutch size were not strongly associated with variation in egg volume during our study. Similarly, Arnold (1991) found that egg size of American Coots (*Fulica americana*) was unrelated to laying date, year, or nesting attempt and was only slightly affected by supplemental feeding. We were unable to monitor nests throughout egg laying, so we cannot account for the influence of laying order, which often has a pervasive effect on egg size (Arnold 1991). We also cannot account for other microhabitat or microclimatic conditions that may have affected resource availability to laying females and, therefore, influenced either clutch or egg size (Christians 2002). Other external factors, such as predator densities, may have influenced either egg or clutch size, and we did not measure these variables.

We found that reported clutch size for sage-grouse increased with population latitude, consistent with our expectations. The latitudinal gradient in clutch size is one of the oldest questions in the study of avian life histories (Ricklefs 2000). Ashmole (1961) attempted to explain latitudinal variation in clutch size as a function of increased seasonality at northern latitudes. Under Ashmole's hypothesis, the effects of resource scarcity during winter in northern latitudes reduced survival of adults, leading to greater per capita resources during the breeding season compared with more southern latitudes (Martin 2014). Sage-grouse generally have high overwinter survival

in relation to other times of year (Connelly et al. 2011a, Blomberg et al. 2013), presumably because digestive adaptations (Moss 1989) allow them to persist and gain mass on a diet composed almost exclusively of sagebrush (Wallestad et al. 1975). However, not all sagebrush plants are created equal in their nutritional value for sage-grouse (Frye et al. 2013), and severe winter weather has been linked with increased mortality in some northern populations (Moynahan et al. 2006). Regardless of mechanisms, these patterns provide new insights into regional variation in sage-grouse demographics and may help explain why northern populations have been observed with above-average clutch size (Schroeder 1997). That clutches are larger at northern latitudes suggests that northern sage-grouse consistently allocate more resources toward reproduction than those in the south. This is consistent with a life-history strategy for northern populations that favors current reproduction over survival and future reproductive success (Ricklefs 2000, Ricklefs and Wikelski 2002), again in relation to more southern populations. Such regional variation could have important implications for conservation of sage-grouse populations and likely warrants further consideration.

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APPENDIX

Data Summary and Model Selection Results for Analyses of Greater Sage-Grouse Clutch Size and Egg Volume

APPENDIX TABLE 3. Numbers of nests located, by year and female age class, during a study of Greater Sage-Grouse nesting ecology in Eureka County, Nevada, USA, 2003–2012.

Year	Female age		
	Adult	Subadult	Unknown
2003	5	1	6
2004	13	1	4
2005	21	13	2
2006	28	11	2
2007	18	7	0
2008	35	0	1
2009	51	13	1
2010	53	10	0
2011	33	15	1
2012	31	13	1
Total	288	84	18

APPENDIX TABLE 4. Model selection results for generalized linear mixed models that related explanatory covariates to variation in clutch size collected from Greater Sage-Grouse nests in Eureka County, Nevada, USA, 2003–2012. All models included a nested random intercept term for individual females. Model selection notation follows Burnham and Anderson (2002).

Model	K	AIC	ΔAIC
Initiation Date + Elevation	5	1,252.7	0.0
Age + Initiation Date	6	1,254.1	1.4
Initiation Date*Precip	6	1,257.2	4.5
Initiation Date	4	1,257.7	5.0
Age*Initiation Date	8	1,257.9	5.2
Initiation Date*Exotic	6	1,258.0	5.3
Initiation Date + Precip	5	1,258.0	5.3
Initiation Date + Attempt	5	1,258.5	5.8
Initiation Date + Exotic	5	1,259.0	6.3
Initiation Date*Attempt	6	1,260.2	7.5
Initiation Date + Aspect	7	1,260.6	7.9
Initiation Date*Aspect	10	1,262.6	9.9
Initiation Date*Elevation	6	1,278.2	25.5
Age + Attempt	6	1,350.7	98.0
Age*Attempt	8	1,353.7	101.0
Attempt*Precip	6	1,366.1	113.4
Attempt + Exotic	5	1,366.2	113.5
Attempt + Elevation	5	1,366.7	114.0
Attempt + Precip	5	1,367.3	114.6
Attempt*Elevation	6	1,367.5	114.8
Attempt*Exotic	6	1,368.0	115.3
Attempt + Aspect	7	1,369.1	116.4
Attempt	4	1,370.2	117.5
Attempt*Aspect	10	1,373.2	120.5
Age + Exotic	6	1,388.7	136.0
Age*Elevation	9	1,389.0	136.3
Age + Precip	6	1,389.5	136.8
Age + Elevation	6	1,389.5	136.8
Age*Exotic	8	1,389.9	137.2
Age + Precip	8	1,392.1	139.4
Age	5	1,393.0	140.3
Null	3	1,398.6	145.9
Exotic	4	1,399.4	146.7
Elevation	4	1,400.1	147.4
Precip	4	1,400.6	147.9
Precip*Exotic	6	1,401.1	148.4
Precip + Exotic	5	1,401.4	148.7
Precip*Elevation	6	1,401.5	148.8
Precip + Elevation	5	1,402.1	149.4
Aspect	6	1,402.1	149.4
Precip + Aspect	7	1,404.1	151.4
Precip*Aspect	10	1,408.9	156.2
Lek of Capture	16	1,413.3	160.6
Year	12	1,413.7	161.1

^a Age = subadult vs. adult; Aspect = nest-site aspect; Attempt = first nest vs. replacement nest; Elevation = nest-site elevation (m); Exotic = footprint of exotic grasslands within 5 km of nest site; Initiation Date = Julian date of nest initiation; and Precip = total precipitation from the previous September to April.

APPENDIX TABLE 5. Model selection results for generalized linear mixed models that related explanatory covariates to variation in the volume of eggs laid by female Greater Sage-Grouse in Eureka County, Nevada, USA, 2003–2012. All models included a nested random intercept term for individual female and unique nesting attempts. Model selection notation follows Burnham and Anderson (2002).

Model	K	AIC	ΔAIC
Clutch Size*Initiation Date	7	12,792.3	0
Clutch Size + Initiation Date	6	12,792.6	0.3
Initiation Date* Exotic	7	12,794.8	2.5
Initiation Date	5	12,795.0	2.7
Initiation Date*Attempt	7	12,796.4	4.1
Initiation Date + Exotic	6	12,796.6	4.3
Initiation Date + Attempt	6	12,796.6	4.3
Initiation Date + Precip	6	12,796.8	4.5
Initiation Date + Elevation	6	12,796.8	4.5
Initiation Date*Elevation	7	12,797.6	5.3
Age + Initiation Date	7	12,798.4	6.1
Attempt*Elevation	7	12,798.5	6.2
Initiation Date*Precip	7	12,798.7	6.4
Attempt*Precip	7	12,800.0	7.7
Initiation Date + Aspect	8	12,800.5	8.2
Null	4	12,800.7	8.4
Elevation	5	12,801.4	9.1
Attempt	5	12,801.6	9.3
Precipitation	5	12,802.1	9.8
Attempt+ Elevation	6	12,802.2	9.9
Age*Initiation Date	9	12,802.3	10.0
Exotic	5	12,802.4	10.1
Precip + Elevation	6	12,802.5	10.2
Clutch Size	5	12,802.6	10.3
Attempt + Precip	6	12,803.1	10.8
Attempt + Exotic	6	12,803.3	11.0
Clutch Size + Attempt	6	12,803.3	11.0
Age	6	12,803.3	11.0
Clutch Size*Attempt	7	12,803.6	11.3
Precip + Exotic	6	12,803.8	11.5
Age + Attempt	7	12,804.0	11.7
Initiation Date*Aspect	11	12,804.0	11.7
Precip*Elevation	7	12,804.5	12.2
Precip*Exotic	7	12,804.7	12.4
Attempt*Exotic	7	12,804.9	12.6
Age + Precip	7	12,804.9	12.6
Age + Elevation	7	12,804.9	12.6
Age + Exotic	7	12,805.0	12.7
Age*Elevation	10	12,805.5	13.2
Aspect	7	12,805.7	13.4
Attempt + Aspect	8	12,806.6	14.3
Precip + Aspect	8	12,807.3	15.0
Age*Precip	9	12,807.8	15.5
Age*Attempt	9	12,807.9	15.6
Age*Exotic	9	12,808.8	16.5
Attempt*Aspect	11	12,809.6	17.3
Lek of Capture	17	12,810.8	18.5
Year	13	12,811.7	19.4
Precip*Aspect	11	12,812.6	20.3

^a Age = subadult vs. adult; Aspect = nest-site aspect; Attempt = first nest vs. replacement nest; Elevation = nest-site elevation (m); Exotic = footprint of exotic grasslands within 5 km of nest site; Initiation Date = Julian date of nest initiation; Precip = total precipitation from the previous September to April; and Clutch Size = number of eggs in clutch.