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RESEARCH ARTICLE

Reconstructing Greater Sage-Grouse chick diets: Diet selection, body condition, and food availability at brood-rearing sites

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ABSTRACT

Growth and survival of juvenile birds is nutritionally demanding, making the availability of major foods critical to population productivity. Access to nutritious foods for juveniles has important implications because poor foraging conditions during development could result in mortality, or reduced fitness in adulthood. Selection of brood-rearing habitats by female Greater Sage-Grouse (*Centrocercus urophasianus*) thus has broad implications to survival of juveniles and persistence of populations. Previous research using crop contents demonstrated that invertebrates and forbs comprise the major portion of sage-grouse chick diets for the first few months post-hatch. We coupled stable isotope analysis of feathers and field measurements to quantify chick diet and then correlated that with measures of chick body condition. We sought to reconstruct sage-grouse chick dietary history (2013–2015) using nitrogen stable isotopes to (1) evaluate whether selection of brood-rearing habitats by female sage-grouse was related to chick diet, and (2) assess the relationship between dietary consumption and body condition. Brood-rearing females selected habitats in areas where diet resources occurred in proportion to their availability, with the exception that females selected areas with greater forb abundance 4 weeks after hatch. Diet assimilation by chicks at brood-rearing locations was unrelated to the availability of forbs and invertebrates, but consumption of forbs increased with chick age. Chicks that assimilated proportionally greater amounts of plant-derived nitrogen in their feathers during their first week of life tended to weigh more and have longer wing chords. This relationship was similar between male and female chicks. The importance of quality foods for sage-grouse is well recognized and conservation efforts should aim to maintain functioning sagebrush ecosystems containing adequate brood-rearing habitats for juvenile sage-grouse; there remains a need to identify whether desirable effects are achievable when attempting to improve big sagebrush (*Artemisia tridentata*) habitats to benefit sage-grouse populations.

Keywords: body condition, *Centrocercus urophasianus*, chick diets, dietary selection, forbs, Greater Sage-Grouse, invertebrates

Reconstrucción de la dieta de los polluelos de *Centrocercus urophasianus*: Selección de la dieta, condición corporal y disponibilidad de alimento en los sitios de cría

RESUMEN

El crecimiento y la supervivencia de las aves juveniles representa una demanda nutricional importante, lo que hace que la disponibilidad de los alimentos principales sea un aspecto crítico para la productividad de la población. El acceso de los juveniles a alimentos nutritivos tiene implicancias importantes ya que las condiciones de alimentación desfavorables durante el desarrollo podrían ocasionar mortalidad o reducir la adecuación biológica en la adultez. Por ende, la selección de los hábitats de cría de los polluelos por parte de las hembras de *Centrocercus urophasianus* tiene amplias implicancias para la supervivencia de los juveniles y la persistencia de las poblaciones. Investigaciones previas que usaron el contenido del buche demostraron que los invertebrados y los forbes componen la mayor porción de la dieta de los polluelos de *C. urophasianus* durante los primeros meses luego de la eclosión. Vinculamos el análisis de isótopos estables de las plumas con datos de campo para cuantificar la dieta de los polluelos y luego lo correlacionamos con medidas de la condición corporal de los polluelos. Buscamos reconstruir la historia de la dieta de los polluelos de *C. urophasianus* (2013–2015) usando isótopos estables de nitrógeno para: (1) evaluar si la selección de los hábitats de cría por parte de las hembras de *C. urophasianus* estuvo relacionada con la dieta de los polluelos, y (2) evaluar la relación entre el consumo de la dieta y la condición corporal. Las hembras con cría seleccionaron hábitats en áreas donde los recursos de la dieta se presentaron en proporción a su disponibilidad, con excepción de las hembras que seleccionaron áreas con mayor abundancia de forbes cuatro semanas luego de la eclosión. La asimilación de la dieta por parte de los polluelos en los sitios de cría no estuvo relacionada con la disponibilidad de forbes e invertebrados, pero el consumo de forbes aumentó con la edad del polluelo. Los polluelos que asimilaron proporcionalmente mayores cantidades de nitrógeno derivado de las plantas en sus plumas durante su primera semana de vida tendieron a pesar más y tener cuerdas alares más largas. Esta relación fue similar entre polluelos macho y hembra. La importancia de los alimentos de calidad para *C. urophasianus* es algo ampliamente reconocido, por lo que los esfuerzos de conservación deberían apuntar a mantener ecosistemas funcionales de *Artemisia* que contengan hábitats de cría adecuados para los juveniles de *C. urophasianus*. Se mantiene la necesidad de identificar si se pueden lograr efectos deseables al intentar mejorar los hábitats de *Artemisia tridentata* para beneficiar a las poblaciones de *C. urophasianus*.

Palabras clave: Centrocercus urophasianus, condición corporal, dieta de los polluelos, forbes, invertebrados, selección de la dieta

INTRODUCTION

Habitat loss and degradation are primary threats to the quality of habitats used by avian species (Johnson 2007). Maintaining or improving habitat quality has important implications to survival, reproduction, and population productivity. Food quality and availability are substantial components of habitat quality for birds and food quality may potentially influence offspring development and fitness during adulthood. Poor food resources may directly influence survival, but may also influence development during ontogeny; however, consequences of poor forage conditions during early development are less well understood (Lindstrom 1999). Poor early nutrition may have profound effects on juvenile development that may be expressed in later life stages, which could result in reduced body size, survival, and fecundity (Schluter and Gustafsson 1993, Verhulst et al. 1997, Rose et al. 1998) and negatively influence individual reproductive success (Metcalfe and Monaghan 2001). Understanding diets that produce larger juveniles in better body condition may provide important insights about the effects of diet on survival during the critical period between hatch and subsequent breeding (e.g., Owen and Black 1989, Maness and Anderson 2013, Blomberg et al. 2014).

North American prairie grouse (Tetraoninae) have experienced declines resulting from habitat loss, degradation, and fragmentation (Storch 2007), prompting a need to understand and conserve important habitats for remaining populations. Reproductive success, particularly nest and brood survival, are major contributors to population growth in grouse (Bergerud 1988). Juvenile mortality is notable, primarily occurring during the first 2 weeks of life (Hannon and Martin 2006). As such, habitat management efforts have focused on improving nest success and brood survival of grouse populations (e.g., Dahlgren et al. 2006). Gallinaceous birds are primarily herbivorous, but invertebrates are critical for proper growth and survival of dependent young during early life (Savory 1989); low food availability is a contributing factor influencing early life mortality (Hannon and Martin 2006).

Most studies that have evaluated diet associated with Greater Sage-Grouse (*Centrocercus urophasianus*) brood-rearing habitat have assessed the relationship between areas selected by females with broods compared to diet items at available locations. Female Greater Sage-Grouse (hereafter "sage-grouse") with broods select areas with greater arthropod abundance (Harju et al. 2013, Schreiber et al. 2015) and greater abundance and cover of herbaceous plants (Drut et al. 1994a, Kirol et al. 2012). Greater availability of invertebrates and forbs has been attributed to increased chick survival during this period (Gregg and Crawford 2009).

Nutritional demand is high for juvenile sage-grouse, and consumption of invertebrates and forbs is related to individual growth and body condition (Johnson and Boyce 1990, Huwer et al. 2008, Blomberg et al. 2013). Many studies have demonstrated the relationship between gallinaceous chick survival and the contribution of various foods they consume (e.g., Johnson and Boyce 1990, Moss et al. 1993, Picozzi et al. 1999). Johnson and Boyce (1990) demonstrated that captive-reared sage-grouse chicks required invertebrates in their diets for survival up to 10 days after hatch. In addition, chick body growth has been positively associated with the proportion of invertebrates consumed (Johnson and Boyce 1990) and the amount of forbs available to chicks during foraging bouts (Huwer et al. 2008). Chick growth rates have also been positively associated with more rapid transitions to primarily herbivorous diets during early life (Blomberg et al. 2013).

Reduced annual recruitment due to poor brood-rearing habitats has been considered a major factor contributing to sage-grouse population declines (Connelly and Braun 1997). Chick survival, therefore, has compelling implications for persistence of sage-grouse populations. Sage-grouse are relatively long lived with moderate reproductive rates compared to other gallinaceous birds and population growth is more sensitive to survival of adults and chicks, rather than productivity (Taylor et al. 2012). However, adult survival is generally higher and less variable than chick survival (Taylor et al. 2012), suggesting that management-directed actions to improve breeding habitat quality may have greater potential to influence chick survival (Mills et al. 1999).

Analysis of diets using stable isotopes has emerged as a powerful technique to reconstruct diets of avian taxa, provided consumer material used to estimate diet can be related to a relevant period of interest (Hobson and Clark

1992). Stable isotopes in feather tissue reflects diets during periods of feather growth; following growth, feather material becomes metabolically inert (Hobson and Clark 1992, Hobson and Wassenaar 1997, Martinez del Rio et al. 2009), providing a framework to determine potential changes in diets along a time series corresponding to feather synthesis (e.g., Blomberg et al. 2013). Sage-grouse chick secondary feathers offer a means to assess dietary consumption during early life. Secondary feathers emerge 2–3 days after hatch (Johnsgard 1983) and grow continuously until ~4 weeks after hatch (Blomberg et al. 2013, K. Smith and A. Pratt personal observation) until they are replaced during the preformative molt (Howell et al. 2003). To better understand dietary relationships of sage-grouse chicks we sought to reconstruct sage-grouse chick dietary history using nitrogen stable isotopes to (1) compare diet availability at selected brood-rearing and available habitats, (2) estimate assimilation of dietary items by chicks at selected brood-rearing habitats, and (3) assess the relationship between dietary assimilation by sage-grouse chicks and body condition.

METHODS

Study Area

We worked in 2 study areas in central Wyoming, USA. The Bighorn Basin study area (44.5°N, 107.9°W) was in Big Horn, Washakie, and northeastern Hot Springs counties, in north-central Wyoming (elevation range: 1,157–2,976 m). Major land uses in this area included bentonite mining, livestock grazing, and a variety of recreational activities. The Jeffrey City study area (42.6°N, 107.9°W) was in portions of Fremont and Natrona counties in central Wyoming (elevation range: 1,529–2,524 m). Livestock grazing was the major land use in this study area. Important vegetation communities in both study areas included big sagebrush (*Artemisia tridentata*), black sagebrush (*A. nova*), rabbitbrush (*Ericameria nauseosa* and *Chrysothamnus viscidiflorus*), and greasewood (*Sarcobatus vermiculatus*). Gardners's saltbush (*Atriplex gardneri*), and shadscale saltbush (*A. confertifolia*) were common at lower elevations in the Bighorn Basin study area. Detailed study area descriptions are found in Smith et al. (2016).

Capture and Monitoring

We captured and radio-tagged female sage-grouse near leks in spring by nighttime spot-lighting and hoop-netting (Giesen et al. 1982, Wakkinen et al. 1992). We captured additional females at summer roosting locations during July and August to supplement our sample size in subsequent years. We attached either VHF radio transmitters (22 g, Model A4060; Advanced Telemetry Systems Incorporated, Isanti, Minnesota, USA) to females with a PVC-covered wire necklace or Global Positioning System (GPS) transmitters (22-g PTT-100 Solar Argos/GPS PTT [Microwave Telemetry, Columbia, Maryland, USA] or Model 22 GPS PTT [North Star Science and Technology, King George, Virginia, USA]) via rump mount. GPS transmitters were solar-powered and uploaded locations (±10-m error) to satellites (CLS America, Lanham, Maryland, USA) every 3 days. GPS transmitters were programmed to acquire 6 locations per day from May 1 to August 24 (at 0100, 0700, 1000, 1300, 1600, and 1900 hr, local time).

We monitored VHF females weekly from late April through ~August 15, 2013–2015. Nests were located by circling each VHF-tagged female's signal until surveyors visually observed the female on a nest or isolated the nest location on the ground. We subsequently monitored nests with triangulation from a distance of at least 30 m to minimize nest disturbance. We visually inspected nest locations of GPS-equipped females after the female left a location of clustered GPS points that indicated a nest (Dinkins et al. 2016). We determined nest success (at least one hatched egg; Rotella et al. 2004) by examining eggshell and eggshell membranes after the female left the nest location. Brood productivity and survival were estimated from females with successfully hatched nests by visually observing chicks or by identifying brooding behavior of the female. We determined brood loss following 2 telemetry visits with no brooding behavior displayed by the female or lack of chick observations. We further assessed brood fate by nighttime spotlight counts at ~35–37 days post-hatch. During nighttime counts, we captured 2–3 chicks (if present) per brood and plucked the fifth secondary feather from each chick. We selected the fifth secondary wing feather because its growth begins slightly later than more distal secondary feathers and minimizes the influence of egg yolk nutrients on nutritional analysis (Romanoff 1944, Johnsgard 1983, Blomberg et al. 2013). At the time of capture, we weighed each chick to the nearest 1 g and measured its wing chord length to the nearest 1 mm. Feathers were stored individually in freezers prior to processing for isotopic and genetic analyses.

Forb and Invertebrate Sampling

For successful broods, we sampled forbs and invertebrates at 1 location and 1 dependent random location per week during the first 4 weeks post-hatch for each female (2013–2015 in Jeffrey City and 2013 in Bighorn Basin). Random locations were constrained to a random direction and distance (0.1–0.5 km) from each paired location (Aldridge and Boyce 2008). Sampling was conducted as soon as possible, but no later than 2 weeks after the brood was located. We sampled dependent random locations on the same day as brood-rearing locations. At each location, we established a sampling plot demarcated by two 30-m transects, intersecting the center of the sampling location and extending in each cardinal direction. We collected invertebrates within four 1-m^2 quadrats placed along each transect. Each quadrat was randomly placed at either 3, 6, 9, or 12 m without replacement from the center of the plot. We fitted quadrats with mesh window screening to prevent invertebrate escapement. We used an invertebrate vacuum (duration, 2 min per quadrat; Model 1612, John W. Hock Company, Gainesville, Florida, USA; Schreiber et al. 2015) to sample relative invertebrate abundance in each quadrat. We clipped perennial food forbs (see Kirol et al. 2012 for list of perennial food forbs) directly adjacent to each invertebrate quadrat with an additional 1-m^2 quadrat. Forb and invertebrate samples were combined from each quadrat to estimate mass per 4 m^2 at each sampling plot and stored in a freezer prior to processing. We dried forb and invertebrate samples in a forced-air drying oven at 60°C for 48 hr to obtain dry mass (g DM per 4 m^2; Beck and Peek 2005). We randomly selected a subset of forb and invertebrate samples to identify potential food items for our dietary mixing model (n = 25 composite samples per study area and year; described below). Samples were selected to represent dietary availability during the brood-rearing period in each study area and year, and to reflect potential yearly and seasonal changes in stable isotope composition of food items.

Stable Isotope Sample Preparation and Analysis

Feathers were cleaned in a 2:1 chloroform:methanol solution (Hopkins and Ferguson 2012) and air dried for 48 hr in a fume hood. We used model predictions derived from Blomberg et al. (2013) to determine the age of each sample. Blomberg et al. (2013) used the relationship between feather growth bars and the distance to feather tip of known-age individuals to determine the age (in days post-hatch) of each sample. This resulted in a generalized linear model with strong fit that predicted age based on the distance from the tip of the feather (Blomberg et al. 2013). We used estimated ages of broods at the time each brood-rearing female was located to compare dietary composition estimated with feathers with the timing of dietary sampling at brood locations. We removed feather vane material along one side of the rachis to correspond to approximately 1 week of feather growth for each weekly sample by estimating the position along the rachis that corresponded to the estimated age from Blomberg et al. (2013) model results (feather sample location at estimated age ~3 days of feather growth). Feather, invertebrate, and forb samples were analyzed for $\delta^{15}N$ at the University of Wyoming Stable Isotope Facility with a continuous flow Finnigan Delta + XP isotope ratio mass spectrometer. We report results in units of per mil (‰) relative to atmospheric N_2. Measured uncertainty was less than ±0.2‰.

Genetic Sample Preparation and Analysis

We included genetic analyses to determine sex of sage-grouse chicks because differential growth rates of this sexually dimorphic species (Schroeder et al. 1999) could be partially explained by dietary differences. We extracted total genomic data from feather samples using a DNeasy Blood and Tissue Kit (Qiagen, Valencia, California, USA). Samples were incubated at 56°C for at least 24 hr. Following incubation, remaining portions of the feather quill were discarded. Samples were extracted with an automated extraction using a Qiacube (Qiagen). We used a PCR assay using primers 1237L and 1272H to determine sex (Kahn et al. 1998). The assay was designed to amplify the highly conserved CHD gene, which in most birds is linked to the W and non-W sex chromosomes (Griffiths et al. 1996). PCRs were performed with 10 μL volumes of 6.85 μL dH_2O, 1 μL genomic DNA, 0.6 μL $MgCl_2$ (2.5 mM), 1.0 μL 10× PCR buffer, 0.25 μL dNTPs (10 mM for each dNTP), 0.1 μL of each primer (10 mM), and 0.1 μL AmpliTaq (5 U μL^{-1}; Applied Biosystems, Foster City, California, USA). The thermocycler reaction profile was as follows: initial denaturation at 94°C for 2 min, followed by 40 cycles of 94°C for 1 min, 56°C for 1 min, and 72°C for 1 min, then held at 60°C for 45 min and a final elongation step at 72°C for 5 min. Using the final PCR product of the amplified CHD gene, sex was determined via gel electrophoresis using a 4% agarose gel. Gels were run for at least 50 min to accentuate the short distance between the W and Z genes found in females.

Statistical Analyses

Brood feeding site selection. All statistical analyses were performed in Program R (R Core Team 2015). We used conditional logistic regression to compare diet availability at brood-rearing locations and dependent random locations with CLOGIT in the survival package (Therneau and Grambsch 2000, Therneau 2015). We were interested in selection for forbs and invertebrates during the entire brood-rearing period, rather than performing individual models to assess weekly selection. We used broods as a strata term; for each brood, we had estimates of forb and invertebrate mass at used and dependent random locations during each week. We evaluated forb mass, invertebrate mass, and the proportion of forb and invertebrate mass collected during each week as predictor variables. Because brood-rearing periods for sage-grouse are often defined as early (2 weeks following nest hatch; Thompson et al. 2006) and late (post–2 week period; Connelly et al. 2011), we also considered predictors that averaged forbs, invertebrates, and the proportion of forbs and invertebrates during the first 2 weeks and the last 2 weeks at used and dependent random locations, respectively. In addition, we evaluated the mean and range of forbs, invertebrates, and the proportion of available forbs and invertebrates across all weeks. We removed unsupported variables in single variable models based on whether 85% confidence intervals around odds ratios included 1 (Hosmer and Lemeshow

2000). We computed Pearson's correlations for remaining predictor variables to assess collinearity among predictors and evaluated all combinations of uncorrelated variables ($|r| < 0.6$) to develop candidate models. We considered the model that only included the strata term (i.e. brood) as the null model and identified the most-supported model relative to the null model using Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson 2004). We considered models within 4 AIC_c of the best-fit model competitive (Arnold 2010).

Dietary assimilation at selected brood-rearing locations. We used a single element, 2-source mixing model to evaluate the contribution of plants and invertebrates in the weekly diet of each chick estimated from $\delta^{15}N$ in feathers (consumer) relative to potential food items (source) with package SIMMR (Parnell 2016). The model output provided estimates of the relative proportion of plant-derived nitrogen assimilated into feather tissue during each week for each individual. We used discrimination factors between diet source and consumer of avian feather tissue ($\Delta^{15}N = 3.84 \pm 0.26‰$ [SE]) derived from Caut et al. (2009). Prior to running the mixture models, we used analysis of variance and linear regression models to determine if $\delta^{15}N$ of source material differed between study area, year, and sampling date within each year. We detected differences between study area and year ($P < 0.05$) but did not detect differences across sampling date. In addition, we used Student's t-tests to ensure that $\delta^{15}N$ could distinguish between plant and invertebrates for each study area and year. We performed separate mixing models for each study area and year to account for differences in $\delta^{15}N$ of source materials.

To evaluate dietary selection (estimated from feather $\delta^{15}N$) relative to dietary mass at brood use locations, we used generalized linear mixed models with package LME4 (Bates et al. 2015). We used $\delta^{15}N$ from feather samples as a proxy for the proportion of plant-derived nitrogen during each week compared to the mass of dietary items at brood-rearing locations instead of estimated proportion of plant-derived nitrogen generated from mixing models to limit potential bias from using isotope discrimination factors that were not derived from our study system (Martinez del Rio et al. 2009, Phillips et al. 2014). Moreover, estimates of feather $\delta^{15}N$ and proportion of plant derived nitrogen from mixing models were highly correlated ($r = -0.94$). We averaged $\delta^{15}N$ across chicks in each brood and included brood in all models as a random intercept term to account for a lack of independence of repeated samples over the 4-week period. We considered both linear and quadratic effects of forb, invertebrate, proportion of available plants and invertebrates, and week as predictor variables. We used AIC_c to determine the most plausible linear or quadratic model for each variable, and explored all combinations of remaining uncorrelated variables ($|r| < 0.6$; Burnham and Anderson 2004), when single variable models had parameter estimates that excluded zero. Predictors were centered and Z-transformed prior to analysis (Becker et al. 1988) to ensure model convergence.

Relative body condition. We used body mass and wing chord length separately as relative metrics of chick body condition. We used the residuals from generalized linear models with chick age and year to develop age-corrected mass and wing chord length estimates to account for individuals that were captured at different ages. We generated age-corrected mass and wing chord length estimates for males and females separately because sage-grouse are size dimorphic (Swenson 1986). We included year to account for potential environmental differences on growth during each year and determined post hoc that inclusions of year in the model did not influence our interpretation of final model results. We used generalized linear mixed models with package LME4 (Bates et al. 2015) to evaluate age-corrected relative body condition indices relative to individual $\delta^{15}N$ feather samples. We included a term that assigned each chick to sex in all models. We considered models with predictor variables including feather $\delta^{15}N$ during each week, mean feather $\delta^{15}N$ during weeks 1 and 2 (early brood-rearing) and weeks 3 and 4 (late brood-rearing), the mean $\delta^{15}N$ across all weeks, and the range of feather $\delta^{15}N$ across weeks. We considered all variables as linear and quadratic effects, retaining the most plausible linear or quadratic model for each variable based on AIC_c. We explored all combinations of remaining uncorrelated variables ($|r| < 0.6$; Burnham and Anderson 2004), when single variables had parameter estimates with 85% confidence intervals that excluded zero. All models included brood as a random intercept term to account for potential differences in diet availability by year and lack of independence among individuals among the same brood. Model support was assessed relative to the random intercepts and sex model with AIC_c.

RESULTS

To identify brood diet selection in 2013–2015, we sampled forb and invertebrate mass at 232 brood-rearing locations and 232 paired random locations from 58 females (Bighorn Basin $n = 16$; Jeffrey City $n = 42$) that successfully raised a brood to at least 35 days post-hatch. We sampled an equal number of brood-rearing and paired random locations during each week (58 brood-rearing and 58 paired random locations). We used information from 76 broods (Bighorn Basin $n = 16$; Jeffrey City $n = 60$) to evaluate dietary consumption at selected brood-rearing locations, and evaluated dietary influences on relative body condition from 128 sexed individuals (Bighorn Basin $n = 39$; Jeffrey City $n = 89$) from those broods. The overall estimated age of chicks at the time of capture (37.5 days; range = 31–49) was similar between study areas and across years. The overall sex ratio was 1.07 females to 1.00 males.

Brood Feeding Site Selection

Plausible models explaining brood-rearing site selection for dietary items included variables with forb mass during week 4, forb mass during the early brood-rearing period (weeks 1 and 2), invertebrate mass during the late brood-rearing period (weeks 3 and 4), and the average proportion of forbs and invertebrates across all weeks (Table 1). All variables in each competitive model, with the exception of forb mass during week 4, had odds ratios with 85% confidence intervals that included 1 (Supplemental Material Table S1). In general, invertebrate mass during late brood-rearing and forb mass during early brood-rearing were positively correlated with brood-rearing habitat selection. However, the model including the single variable forb mass during week 4 had the lowest AIC_c value and was the most parsimonious model; therefore, we considered this the most supported model. Forb mass during week 4 was positively correlated with brood-rearing habitat selection; model predictions suggest that for every 5 g per 4 m^2 increase in food forb abundance, relative probability of selection increased by ~2%.

Dietary Consumption at Selected Brood-Rearing Locations

Student's *t*-tests indicated that $\delta^{15}N$ differed between plant and invertebrate food items in each study area and year (Table 2). Mixing models indicated that plant food items were ~50% of the assimilated diet of sage-grouse chicks through 4 weeks post-hatch. However, this relationship varied slightly between study areas, years, and between sexes, and was highly variable among individuals (Figure 1). Competitive models explaining dietary consumption at brood-rearing locations included all variables that we assessed (Table 3). Forbs, invertebrates, and the proportion of forbs and invertebrates were positively related to feather $\delta^{15}N$ (Supplemental Material Table S2). However, we considered the top model that only included week as the most supported model because 85% confidence intervals for parameter estimates of forbs, invertebrates, and proportion of forbs and invertebrates included zero in all competitive models. Week ($\hat{\beta}$ = −0.095 ± 0.024 SE) was negatively related to feather $\delta^{15}N$, suggesting that broods were assimilating more plant-derived nitrogen as they aged.

TABLE 1. Top and competing models best explaining selection of dietary resources at brood-rearing female sage-grouse locations in the Bighorn Basin and Jeffrey City study areas, Wyoming, USA, 2013–2015.

	Model selection statistics		
Model	K	ΔAIC_c	w_i
$\text{Forbs}_{(\text{week 4})}$	1	0.00	0.27
$\text{Forbs}_{(\text{week 4})}$ + $\text{Invertebrates}_{(\text{late})}$	2	0.60	0.20
$\text{Forbs}_{(\text{week 4})}$ + $\text{Forbs}_{(\text{early})}$	2	1.73	0.12
$\text{Forbs}_{(\text{week 4})}$ + $\text{Proportion}_{(\text{mean})}$	2	2.02	0.10
$\text{Forbs}_{(\text{week 4})}$ + $\text{Forbs}_{(\text{early})}$ + $\text{Invertebrates}_{(\text{late})}$	3	2.34	0.08
$\text{Forbs}_{(\text{week 4})}$ + $\text{Invertebrates}_{(\text{late})}$ + $\text{Proportion}_{(\text{mean})}$	3	2.70	0.07
$\text{Forbs}_{(\text{week 4})}$ + $\text{Forbs}_{(\text{early})}$ + $\text{Proportion}_{(\text{mean})}$	3	3.75	0.04
NULL	0	8.94	0.00

Relative Body Condition

Competitive mixed effect models relating diet to age-corrected body mass contained variables that included feather $\delta^{15}N$ during week 1, a quadratic effect of feather $\delta^{15}N$ during week 4, and the range of feather $\delta^{15}N$ (Table 4, Supplemental Material Table S3). The most parsimonious model in the competitive model set included the single variable of feather $\delta^{15}N$ during week 1. Feather $\delta^{15}N$ during week 1 was in all competitive models, so we used this model to interpret the relationship between age-corrected body mass and diet. Feather $\delta^{15}N$ during week 1 was negatively correlated with age-corrected mass ($\hat{\beta}$ = −37.57 ± 10.23 SE), indicating that chicks assimilating a relatively higher proportion of plant-derived nitrogen during their first week of life tended to weigh more (Figure 2A).

Age-corrected body mass was similar between male and female chicks ($\hat{\beta}$ = −15.29 ± 13.72 SE). Similarly, competitive mixed effect models relating diet to age-corrected wing chord length contained variables that included feather $\delta^{15}N$ during week 1, a quadratic effect of feather $\delta^{15}N$ during week 4, and the range of feather $\delta^{15}N$ (Table 5, Supplemental Material Table S4). This was not surprising because body mass and wing chord length were highly correlated (r = 0.89). The most parsimonious model in the competitive model set included the single variable of feather $\delta^{15}N$ during week 1. Feather $\delta^{15}N$ during week 1 was in all competitive models, so we used this model to interpret age-corrected wing chord length and diet. Feather $\delta^{15}N$ during week 1 was negatively correlated with age-corrected wing chord ($\hat{\beta}$ = −7.11 ± 1.77 SE), indicating that chicks assimilating a relatively higher proportion of plant-derived nitrogen during their first week of life tended to have longer wing chords (Figure 2B). Age-corrected wing chord length did not differ between males and females ($\hat{\beta}$ = −3.11 ± 2.39 SE).

DISCUSSION

Prioritizing species conservation requires identification of critical habitats during an annual life cycle. Habitats that have disproportionately high use are particularly important for conservation. However, habitat use may not accurately reflect the importance of habitats, as species may utilize a range of habitat quality (Donovan and

TABLE 2. Mean $\delta^{15}N$ ± SE of plant and invertebrate samples collected in the Bighorn Basin and Jeffrey City study areas, Wyoming, USA, 2013–2015; *t* statistics and *P* values are from independent sample Student's *t*-tests.

Study area	Year	Invertebrate	Forb	*t*-statistic	*P*
Bighorn Basin	2013	3.60 ± 0.22	0.60 ± 0.34	7.75	<0.001
Jeffrey City	2013	4.59 ± 0.34	0.91 ± 0.33	7.71	<0.001
Jeffrey City	2014	4.51 ± 0.24	1.07 ± 0.30	9.01	<0.001
Jeffrey City	2015	4.34 ± 0.21	0.32 ± 0.24	12.41	<0.001

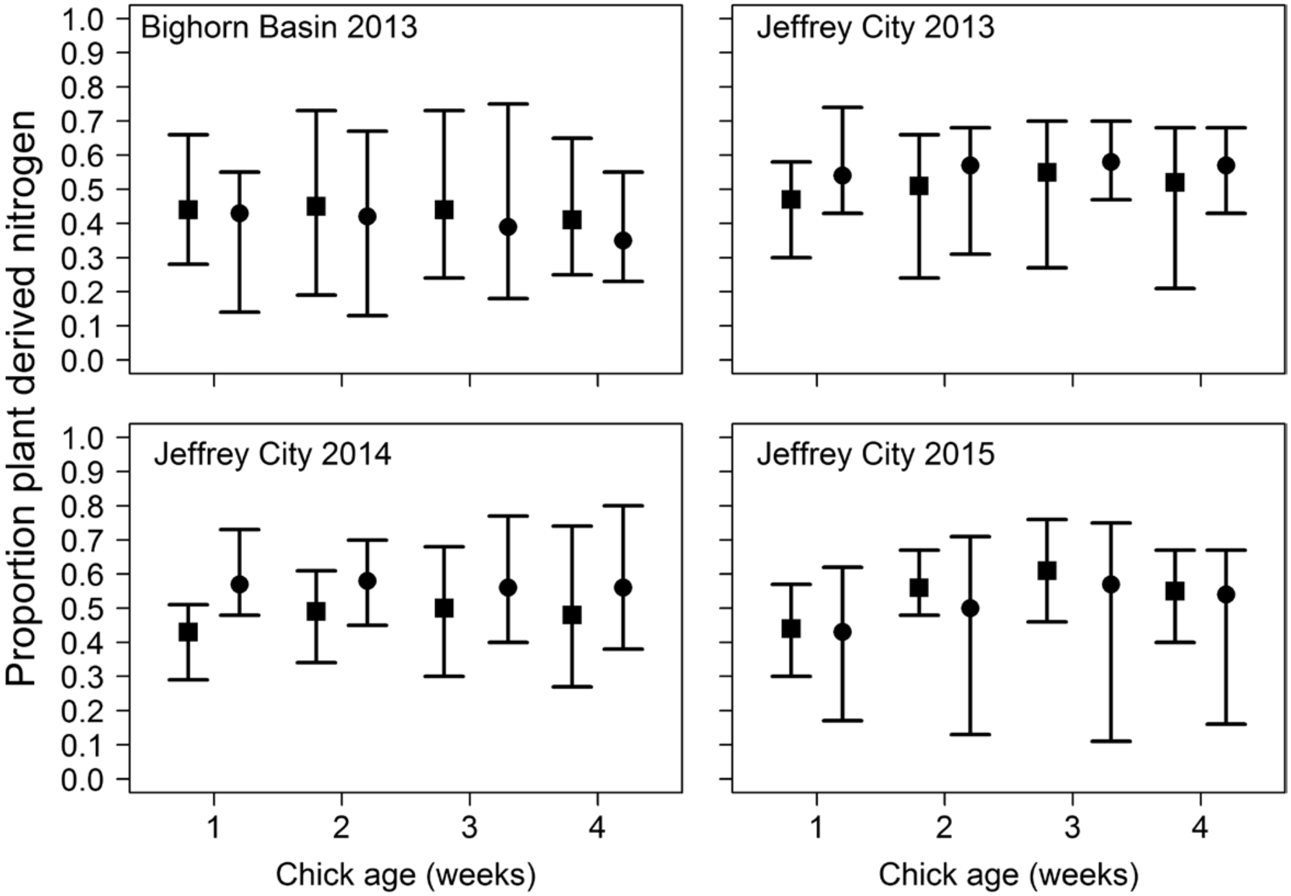

FIGURE 1. Estimated proportion of plant-derived nitrogen with chick age (weeks 1–4 post-hatch) from individual Greater Sage-Grouse chicks captured in the Bighorn Basin during 2013, and Jeffrey City study areas during 2013, 2014, and 2015, Wyoming, USA. Squares (females) and circles (males) indicate the mean and outer lines represent the range of values of plant-derived nitrogen estimated from mixing models.

Thompson 2001) and understanding habitat use or occurrence may not accurately depict fitness (Van Horne 1983). While many studies focus on structural and compositional vegetation characteristics associated with habitat use, other features, such as forage quality, influence selection (e.g., Gaillard et al. 2010). Forage quality may be directly linked to habitat preference (e.g., Frye et al. 2013) and may influence early life development and lifetime reproductive success. The negative influence of nutritional deficiencies during ontogeny on fitness during adulthood has been demonstrated in several avian taxa (Lindstrom 1999, Metcalfe and Monaghen 2001).

We sought to evaluate dietary resource availability at brood-rearing locations, understand dietary consumption by chicks estimated from feather $\delta^{15}N$ at selected habitats, and determine how diets influenced the relative body condition of sage-grouse chicks. Our findings generally suggested that females with broods were selecting habitats that contained forbs and invertebrates in proportion to their availability, with the exception that brooding females selected areas with greater forb abundance 4 weeks after hatch. In contrast, several studies have found positive associations with brood-rearing habitats and forb (Sveum et al. 1988, Drut et al. 1994a) and invertebrate (Harju et al.

TABLE 3. Top and competing mixed-effects models evaluating the relationship between dietary assimilation, estimated from feather $\delta^{15}N$, and dietary abundance at selected brood-rearing locations in the Bighorn Basin and Jeffrey City study areas, Wyoming, USA, 2013–2015.

	Model selection statistics		
Model	K	ΔAIC_c	w_i
Week	4	0.00	0.34
Week + Forbs	5	1.43	0.17
Week + Invertebrates	5	1.61	0.15
Week + Proportion	5	1.98	0.13
Week + Forbs + Invertebrates	6	3.21	0.07
Week + Invertebrates + Proportion	6	3.49	0.06
Week + Forbs + Proportion	6	3.51	0.06
NULL	3	13.59	0.00

TABLE 4. Top and competing mixed-effects models evaluating the relationship between relative diet and age-corrected mass of Greater Sage-Grouse chicks captured in Bighorn Basin and Jeffrey City study areas during 2013–2015, Wyoming, USA.

	Model selection statistics		
Model	K	ΔAIC_c	w_i
$\delta^{15}N_{(week\ 1)} + \delta^{15}N_{(week\ 4)}{}^{a}$	7	0.00	0.38
$\delta^{15}N_{(week\ 1)} + \delta^{15}N_{(week\ 4)}{}^{a} + \delta^{15}N_{(range)}$	8	0.83	0.25
$\delta^{15}N_{(week\ 1)}$	5	1.07	0.22
$\delta^{15}N_{(week\ 1)} + \delta^{15}N_{(range)}$	6	2.10	0.13
NULL	4	11.53	0.00

[a] Quadratic form.

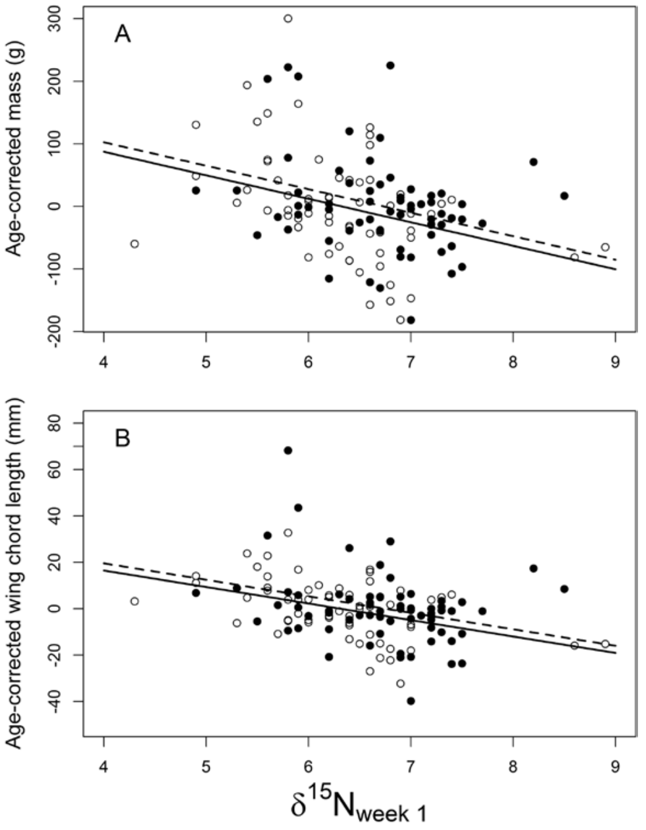

FIGURE 2. Relationship between feather $\delta^{15}N$ during week 1 and (**A**) age-corrected mass (g) and (**B**) age-corrected wing chord length (mm) for individual chicks from Bighorn Basin (n = 39) and Jeffrey City (n = 89) study areas, Wyoming, USA, 2013–2015. Hashed and solid lines represent the trend line for females (hollow circles) and males (solid circles), respectively.

2013, Schreiber et al. 2015) abundance. However, brood-rearing habitat selection is not always related to forb abundance, particularly during early brood-rearing (Thompson et al. 2006, Kirol et al. 2012). We did find a positive association with selection for forb abundance during week 4 post-hatch, which is corroborated by studies that suggest females with broods move to more forb-rich mesic habitats during late brood-rearing (e.g., Connelly et al. 2000). Selection for forbs during week 4 may signify the beginning of late brood-rearing in our study areas. Our study used a dependent random design that constrained the sample of available habitat to within 0.1 and 0.5 km of brood-rearing locations (third-order selection; Johnson 1980). This contrasts with many studies that have evaluated brood habitat selection within the lens of a study area (second-order selection; Drut et al. 1994a, Kirol et al. 2012). Spatial and temporal differences in forb and invertebrate abundance may explain the lack of selection we found for forb and invertebrate abundance during the first 3 weeks after hatch. Female sage-grouse may select nesting areas that enhance chick survival by placing nests in suitable brood-rearing habitats (Gibson et al. 2016). We speculate that females may have been selecting relatively homogeneous brood-rearing areas, which may explain the minimal differences we found in forb and invertebrate abundance between used and paired random locations. Our analysis only included females with broods that survived to ~35 days post-hatch. By excluding females who failed earlier our sample probably included higher-quality areas for brood-rearing.

Chick dietary assimilation at brood-rearing locations was generally unrelated to dietary availability of forbs and invertebrates, but assimilation of plants generally increased with chick age. Adaptive habitat selection theory suggests that females should select areas to maximize foraging opportunities while minimizing predation risk (e.g., Smith et al. 2018). Consumption of dietary items by juvenile grouse may be directly related to their availability (Savory 1989). For example, Red Grouse (*Lagopus lagopus scoticus*) chicks ate invertebrate food in relation to its availability (Savory 1977) and forbs and invertebrates were consumed by sage-grouse chicks in greater mass when availability was greater (Drut et al. 1994b). Presumably, dietary assimilation by chicks occurs opportunistically within the habitat

TABLE 5. Top and competing mixed-effects models evaluating the relationship between relative diet and age-corrected wing chord length of Greater Sage-Grouse chicks captured in Bighorn Basin and Jeffrey City study areas during 2013–2015, Wyoming, USA.

	Model selection statistics		
Model	*K*	ΔAIC_c	w_i
$\delta^{15}N_{(week\ 1)} + \delta^{15}N_{(week\ 4)}{}^{a}$	7	0.00	0.46
$\delta^{15}N_{(week\ 1)} + \delta^{15}N_{(week\ 4)}{}^{a} + \delta^{15}N_{(range)}$	8	0.90	0.29
$\delta^{15}N_{(week\ 1)}$	5	2.27	0.15
$\delta^{15}N_{(week\ 1)} + \delta^{15}N_{(range)}$	6	3.20	0.09
NULL	4	15.29	0.00

[a] Quadratic form.

patch chosen by the female. Our methods provide a coarse evaluation of dietary assimilation rather than selection for specific invertebrate or plant taxa, which have been linked to sage-grouse brood selection and survival (Gregg and Crawford 2009, Schreiber et al. 2015). In addition, it is possible that our sampling methodology did not accurately reflect foraging locations of broods as we only sampled 1 location per week and estimated dietary consumption from an entire week of feather synthesis.

Body condition of Red Grouse chicks was correlated with green heather (*Calluna vulgaris*) biomass (Moss et al. 1993). Capercaillie (*Tetrao urogallus*) chick survival was positively associated with invertebrate consumption (Picozzi et al. 1999), and the importance of invertebrates and forbs for survival has been well established for sage-grouse chicks (Johnson and Boyce 1990, Drut et al. 1994b, Blomberg et al. 2013). Drut et al. (1994b) found that sage-grouse chicks from 2 different study areas exhibited similar dietary selection, but differences in productivity were related to the relative dry mass of forbs and invertebrates, not the proportion of diet items consumed. Our methods to determine dietary consumption did not allow us to assess relative mass of consumed foods. We found that, on average, individuals assimilated a lower proportion of forbs than in previously published studies, particularly by individuals that were more than 1 week old (Klebenow and Gray 1968, Peterson 1970, Blomberg et al. 2013). For example, through analysis of crop contents, Klebenow and Gray (1968) found that invertebrates formed ~50% of the diet of 1-week-old chicks, whereas invertebrates comprised less than 25% of the diet for older individuals. Similarly, Peterson (1970) found that juvenile diets during the first 4 weeks consisted of ~70% plants. These estimates were derived from crop content (ingested diet), whereas we evaluated the assimilation of plants and invertebrates into feather nitrogen, which may explain the differences we found. Nonetheless, using similar methods to estimate diet composition as in our study, Blomberg et al. (2013) found that sage-grouse chicks in Nevada assimilated consistently higher proportions of plants during the first 4 weeks compared to our results. We found that age-adjusted mass and wing chord length of chicks captured at ~35–37 days were positively related to the proportion of plant-derived nitrogen during their first week of life and this was similar between male and female chicks. Our results indicate that the proportion of plant-derived nitrogen was ~50% across all weeks for the average individual, but this trend was variable between study areas and across years. Proportionally, invertebrates were the primary food source during an individual's first week of life, but chicks that had a greater proportion of plant-derived nitrogen in their feather tissue during their first week weighed more and had longer wing chords.

Our findings that increased assimilation of plant material during the first week was related to individual growth may be explained in several ways. First, we assumed that feather synthesis, and therefore dietary consumption, estimates from feather $\delta^{15}N$ come entirely from dietary intake and not endogenous sources. Egg yolk nutrients are thought to be absorbed at ~3–4 days after hatch (Romanoff 1944); therefore, egg yolk nutrition could have contributed to dietary estimates during this time if there was variability in absorption rates. We also assumed that nitrogen discrimination between diet and chicks was constant through time and across individuals. Differences in individual physiology, such as growth rates, may influence nitrogen discrimination (Trueman et al. 2005, Sears et al. 2009). However, the magnitude of differences in nitrogen discrimination factors is relatively small compared to trophic enrichment between forbs and invertebrates (sensu Sears et al. 2009). Further research is needed to assess the influence of egg yolk nutrients and individual physiology on dietary contributions and how these may influence the utility of stable isotope methods to infer juvenile diets. Another possible explanation for the importance of forbs during week 1 on chick body condition is the specific suite of micronutrients and vitamins that forbs contain. Invertebrates provide more protein than plant materials (Sugimura et al. 1984), but forbs contain higher levels of calcium and ascorbic acid (i.e. vitamin C; Savory 1989). Calcium is necessary for skeletal growth of juvenile birds (e.g., Tilgar et al. 2004). Ascorbic acid is synthesized by grouse; however, endogenous sources of ascorbic acid may be important for survival (Hanssen et al. 1979), and supplemental diets containing ascorbic acid have been associated with increased growth rates in juvenile poultry (Kutlu and Forbes 1993, Sahin et al. 2003). High protein–based invertebrate diets are crucial for early sage-grouse development (Johnson and Boyce 1990); however, consumption of forbs during this time may also provide important resources necessary for growth. The general shift toward proportionally greater plant diet may be related to gut morphology and development (sensu Blomberg et al. 2013), however this relationship has not been explored in sage-grouse.

Regardless of mechanisms that explain chick growth, the importance of quality foods for sage-grouse is well recognized and habitat management has aimed to increase forb and concomitant invertebrate abundance in sagebrush habitats. Management actions are unlikely to directly increase invertebrate abundance (Harju et al. 2013, Hess and Beck 2014), suggesting that increasing the abundance and availability of forbs would improve dietary conditions for sage-grouse. Improving foraging resources in degraded sagebrush habitats could potentially improve availability and abundance of critical invertebrate and forb foods; however, managers need to identify whether this can actually be achieved (Davies et al. 2012). Annual weather drives herbaceous production in sagebrush communities (Noy-Meir 1973) and invertebrate abundance is positively associated with herbaceous production (Wenninger and Inouye 2008). Precipitation positively influences population growth and individual vital rates (Blomberg et al. 2012, Guttery et al. 2013) suggesting that forage availability influences sage-grouse reproduction. Females may modify their behavior and habitat use to maintain reproductive success in drought conditions, but reproduction may still be suppressed at the population level (Gibson et al. 2017). Management and conservation practices that maintain or improve habitat quality for sage-grouse are needed to ensure sage-grouse viability in the future.

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