BioOne COMPLETE

Niche shifts and energetic condition of songbirds in response to phenology of food-resource availability in a high-elevation sagebrush ecosystem

Authors: Cutting, Kyle A. , Anderson, Michelle L. , Beever, Erik A. , Schroff, Sean R. , Klaphake, Eric, et al.

Source: The Auk, 133(4) : 685-697

Published By: American Ornithological Society

URL: https://doi.org/10.1642/AUK-16-4.1

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

The Auk
Ornithological Advances
AmericanOrnithology.org

Volume 133, 2016, pp. 685–697
DOI: 10.1642/AUK-16-4.1

RESEARCH ARTICLE

Niche shifts and energetic condition of songbirds in response to phenology of food-resource availability in a high-elevation sagebrush ecosystem

Kyle A. Cutting,[1]* Michelle L. Anderson,[2] Erik A. Beever,[3,4] Sean R. Schroff,[1] Eric Klaphake,[5] Nathan Korb,[6] and Scott McWilliams[7]

[1] U.S. Fish and Wildlife Service, Red Rock Lakes National Wildlife Refuge, Lima, Montana, USA
[2] Department of Biology, University of Montana Western, Dillon, Montana, USA
[3] U.S. Geological Survey, Northern Rocky Mountain Science Center, Bozeman, Montana, USA
[4] Department of Ecology, Montana State University, Bozeman, Montana, USA
[5] Cheyenne Mountain Zoo, Colorado Springs, Colorado, USA
[6] The Nature Conservancy, Helena, Montana, USA
[7] Department of Natural Resources Science, University of Rhode Island, Kingston, Rhode Island, USA
* Corresponding author: Kyle_Cutting@fws.gov

Submitted January 7, 2016; Accepted June 6, 2016; Published August 17, 2016

ABSTRACT

Seasonal fluctuations in food availability can affect diets of consumers, which in turn may influence the physiological state of individuals and shape intra- and inter-specific patterns of resource use. High-elevation ecosystems often exhibit a pronounced seasonal "pulse" in productivity, although few studies document how resource use and energetic condition by avian consumers change in relation to food-resource availability in these ecosystems. We tested the hypothesis that seasonal increases (pulses) in food resources in high-elevation sagebrush ecosystems result in 2 changes after the pulse, relative to the before-pulse period: (1) reduced diet breadth of, and overlap between, 2 sympatric sparrow species; and (2) enhanced energetic condition in both species. We tracked breeding-season diets using stable isotopes and energetic condition using plasma metabolites of Brewer's Sparrows (*Spizella breweri*), Vesper Sparrows (*Pooecetes gramineus*), and their food resources during 2011, and of only Brewer's Sparrows and their food resources during 2013. We quantify diet breadth and overlap between both species, along with coincident physiological consequences of temporal changes in resource use. After invertebrate biomass increased following periods of rainfall in 2011, dietary breadth decreased by 35% in Brewer's Sparrows and by 48% in Vesper Sparrows, while dietary overlap decreased by 88%. Energetic condition of both species increased when dietary overlap was lower and diet breadth decreased, after the rapid rise of food-resource availability. However, energetic condition of Brewer's Sparrows remained constant in 2013, a year with low precipitation and lack of a strong pulse in food resources, even though the species' dietary breadth again decreased that year. Our results indicate that diet breadth and overlap in these sparrow species inhabiting sagebrush ecosystems generally varied as predicted in relation to intra- and interannual changes in food resources, and this difference in diet was associated with improved energetic condition of sparrows at least in one year.

Keywords: food-resource pulse, sagebrush, diet, stable isotopes, Brewer's Sparrow, Vesper Sparrow

Cambios en el nicho y en la condición energética de aves canoras en respuesta a la fenología de la disponibilidad de recursos alimenticios en un ecosistema de *Artemisia* de alta elevación

RESUMEN

Las fluctuaciones estacionales en la disponibilidad de alimento pueden afectar la dieta de los consumidores, lo que a su vez puede afectar el estado fisiológico de los individuos y definir los patrones intra- e interespecíficos del uso de recursos. Los ecosistemas de altas elevaciones generalmente muestran un pulso estacional pronunciado en la productividad, aunque pocos estudios documentan cómo cambia el uso de los recursos y la condición energética de las aves consumidoras en relación con la disponibilidad de los recursos alimenticios en estos escosistemas. Evaluamos la hipótesis de que los incrementos estacionales (pulsos) en los recursos alimenticios en los ecosistemas de *Artemisia* de altas elevaciones resultan en dos cambios posteriores al pulso relativos al periodo anterior a éste: (a) reducción en la amplitud de la dieta y en la superposición de la misma entre dos especies simpátricas de gorriones y (b) mejora en la condición energética de ambas especies. Seguimos la dieta en la temporada reproductiva usando isótopos estables y la condición energética usando metabolitos del plasma de *Spizella breweri*, *Pooecetes gramineus* y de sus recursos alimenticios durante 2011, y sólo de *S. breweri* y sus recursos alimenticios durante 2013. Cuantificamos la amplitud de

© 2016 American Ornithologists' Union. ISSN 0004-8038, electronic ISSN 1938-4254
Direct all requests to reproduce journal content to the Central Ornithology Publication Office at aoucospubs@gmail.com

Downloaded From: https://complete.bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

la dieta y su superposición entre ambas especies, junto con las consecuencias fisiológicas de los cambios temporales en el uso de recursos. Cuando la biomasa de invertebrados incrementó luego de los periodos de lluvia en 2001, la amplitud de la dieta disminuyó 35% en *S. breweri* y 48% en *P. gramineus*, mientras que la superposición en la dieta disminuyó 88%. La condición energética de ambas especies se incrementó cuando la superposición y la amplitud de la dieta fueron menores luego del rápido incremento en la disponibilidad de recursos alimenticios. Sin embargo, la condición energética de *S. breweri* se mantuvo constante en 2013, un año con baja precipitación y falta de un pulso pronunciado en los recursos alimenticios, aunque la amplitud de la dieta de esta especie volvió a disminuir durante ese año. Nuestros resultados indican que la amplitud de la dieta y su superposición entre estas especies de gorriones habitantes de los ecosistemas de *Artemisia* generalmente varían de acuerdo a lo predicho en relación con cambios inter- e intraanuales en los recursos alimenticios, y esta diferencia en la dieta se asoció con una mejora en la condición energética de los gorriones al menos en uno de los años.

Palabras clave: Artemisia, dieta, isótopos estables, pulso en recursos alimenticios, *Pooecetes gramineus*, *Spizella breweri*

INTRODUCTION

Species coexistence within a given patch may be facilitated by a number of ecological processes, including resource partitioning (Hutchinson 1959). Whereas combined effects with other ecological drivers, such as predator–prey dynamics (Martin 1988) or limiting resources (Holt 1977, Holt 1984), are difficult to rule out, evidence of differences in sympatric species' niches are observable. Competition theory predicts that sympatric species avoid interspecific competition during periods of low resource availability by reducing the diversity of prey resources in their diet (hereafter, diet breadth) and by decreasing overlap in habitat use, time of activity, or diet with sympatric species (MacArthur 1958, Hutchinson 1959). Conversely, during times of high resource availability, niche breadth and overlap of sympatric species can increase, because resources are no longer limiting to consumers. Among other things, optimal foraging theory (OFT) predicts that a species' diet breadth should increase during times of low resource availability, because a consumer might otherwise not procure enough prey resources to meet its energy demands (MacArthur and Pianka 1966). In contrast, when resource availability is high, OFT predicts a narrowing of species' diet breadth to achieve foraging requirements. This narrowing allows sympatric species to coexist in environments with fluctuating resources by modulating their dietary niches to maximize energy gains and minimize energy loss (Pyke 1984, Perry and Pianka 1997). The dietary niche includes interactions among species within a community for shared food resources that vary in availability (Rotenberry 1980b). One way to quantify to what degree these factors influence sympatric species involves collecting data on their dietary breadth and overlap across a seasonal gradient that encompasses a food-resource pulse (Beaulieu and Sockman 2012, Correa and Winemiller 2014). In seasonal environments, food availability can fluctuate dramatically, producing a "resource pulse" in availability wherein food availability increases during a low-frequency, short-duration, large-magnitude event (figure 1 from Yang et al. 2008). Classic examples of environments with resource-pulsed systems where species are also monitored include desert environments with monsoonal rains (Warne et al. 2010), oak forests with mast production (McShea 2000), and old-growth forests with irruptions of insects (Haney 1999).

When viewed over longer time scales (multiple years to decades) in sagebrush (*Artemisia* spp.) dominated ecosystems, resource pulses predictably occur from spring to summer. However, over shorter time scales, the resource pulse in any given year may be larger or smaller, or occur earlier or later. Thus, interannual variation exists in the timing, duration, and magnitude of the spring-to-summer resource pulse during a bird's breeding season (Rotenberry and Wiens 1989, Rotenberry and Wiens 1991, Bates et al. 2006, Lowe et al. 2010). Total insect abundance in sagebrush ecosystems of the Intermountain West often peaks during June (Wenninger and Inouye 2008, Lowe et al. 2010). When combined with early-spring variability in temperature and precipitation, such abundance can strongly influence an individual's ability to gain pre-breeding body condition (Arizmendi-Mejía et al. 2013), maintain pair bonds (Chalfoun and Martin 2007), and achieve reproductive success (Rotenberry and Wiens 1989) and inclusive fitness (Luck 2003). Due to a paucity of empirical data for sagebrush-ecosystem birds, it remains largely unknown to what degree this seasonal change in resource availability affects diet breadth and overlap of sympatric species (Rotenberry 1980a).

Recent advances in stable isotope ecology and Bayesian modeling of these isotope data provide a means by which to determine resource use of animals (Parnell et al. 2010, Jackson et al. 2011). When combined with plasma metabolites, these advances can reveal how resource use of individuals affects their instantaneous physiological state (MacDade et al. 2011). For animals living in dynamic environments with different carbon and nitrogen stable isotope background in their food resources, stable isotope analyses can identify to what degree diets of sympatric species differ under various food conditions (Pearson et al.

Downloaded From: https://complete.bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

2003, Beaulieu and Sockman 2012, Correa and Winemiller 2014, Ma et al. 2014). Concomitant measures of plasma metabolites can predict direction of body-mass change in birds captured only once (Jenni-Eiermann and Jenni 1994, Jenni-Eiermann and Jenni 1997, Smith and McWilliams 2010, Stutchbury et al. 2011) and can thus potentially indicate the physiological consequences of changes in resource use over time.

Sagebrush ecosystems of the Intermountain West constitute one of the 22 most highly endangered major ecosystems of the United States (Noss and Peters 1995) due to climate change, land use, and invasive species (Bradley 2010). Within these systems, although both sparrow species inhabit sagebrush-dominated communities, Vesper Sparrows (*Pooecetes gramineus*) typically nest on or near the ground, whereas Brewer's Sparrows (*Spizella breweri*) more commonly nest in sagebrush canopy (Best 1972). Upon their arrival at the breeding grounds, both species have high energy demands and commonly consume invertebrate prey and grass seeds (Best 1972, Rotenberry et al. 1999, Jones and Cornely 2002).

Our objectives in this study were to use stable isotopes and plasma metabolites from 2 species of sagebrush-inhabiting sparrows to investigate each species' diet breadth, the dietary overlap between the 2 species, and their physiological state as resource availability substantially changed over the spring–summer seasons. We hypothesized that seasonal increases in food resources would result in the following changes, relative to the before-pulse period: (1) reduced within-species diet breadth in Vesper and Brewer's sparrows, in a given year; (2) decreased dietary-niche overlap between the 2 sparrow species; and (3) higher energetic condition in both species. To address these predictions, we quantified plant phenology, invertebrate biomass consumed by sparrow species, and both stable isotopes and metabolites in sparrow blood plasma during May–July on the western edge of the Greater Yellowstone Ecosystem. We addressed partitioning of dietary niches between Vesper and Brewer's sparrows in 2011, and compared this to a within–Brewer's Sparrow change in dietary niche breadth investigated in 2013.

METHODS

Study Species

Brewer's Sparrows and Vesper Sparrows inhabit sagebrush ecosystems across the western United States (Knick and Rotenberry 2002). North American populations of Brewer's Sparrows declined by an estimated 68% during 1966–1996, whereas Vesper Sparrows declined by an estimated 28% during 1966–1998 (Rotenberry et al. 1999, Sauer et al. 2000). Best (1972) found that Brewer's and Vesper sparrow diets (as determined by gut content analysis) consisted mainly of beetles (Coleoptera) during June. Diets during July consisted mainly of beetles, grasshoppers (Orthoptera), Hemiptera, and grass seeds for Brewer's Sparrows, and beetles, grasshoppers, and grass seeds for Vesper Sparrows.

Study Sites

Our study sites were in stands of basin big sagebrush (*Artemisia tridentata* spp. *tridentata*) across the 3,200-ha Centennial Sandhills (hereafter, Sandhills) in the Centennial Valley of southwestern Montana (44.68°N, −111.74°W). The average elevation of the Sandhills is 2,014 m. We divided the Sandhills, which are oriented east to west, into 3 sampling regions: western, central, and eastern (see Appendix Figure 5). We randomly selected 2 locations within each region to establish 500 m × 500 m study plots in 2011. We added one additional 500 m × 500 m randomly selected plot to each region in 2013 ($n_{\text{total}} = 3$ plots per region).

Flower Phenology

In high-elevation temperate ecosystems, vegetation grows rapidly following a lengthening of photoperiod during spring. This growth corresponds to complex biogeochemical changes, including increases in air and soil temperatures and moisture availability (the latter due to melting snowpack). For the purpose of this study, we used seasonal change in flower abundance to define these complex interactions. We used forb flower abundance as a proxy for grass seed development during sparrow breeding season, similarly as applied by Wood and Pidgeon (2015) for tree flower counts to reflect seasonal abundance change in food availability to migratory passerines, because both functional groups increase their abundance following the melting of snow and increases in air temperature during spring (Appendix). In addition to grass-seed counts being less accurate and less repeatable, our experience in this ecosystem is that grass seeds from the previous year vary dramatically across elevations and microsites in their detectability. We recorded abundance of flowering plants within our study plots on 5 separate survey occasions in each study-area region, once every 8 days during May 13, 2011, through June 23, 2011 (Figure 1A). We randomly selected one sampling point in a randomly selected plot distributed across each of the 3 regions and placed a permanent belt transect (25 m × 2 m). During each flower survey, we counted total number of open, non-senescent flowers from individual forb plants located along belt transects.

Invertebrate Biomass

We used grids of pitfall traps to quantify relative biomass of sparrow invertebrate prey through time, in both years of study. Though no single collection device will equally

Downloaded From: https://complete.bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

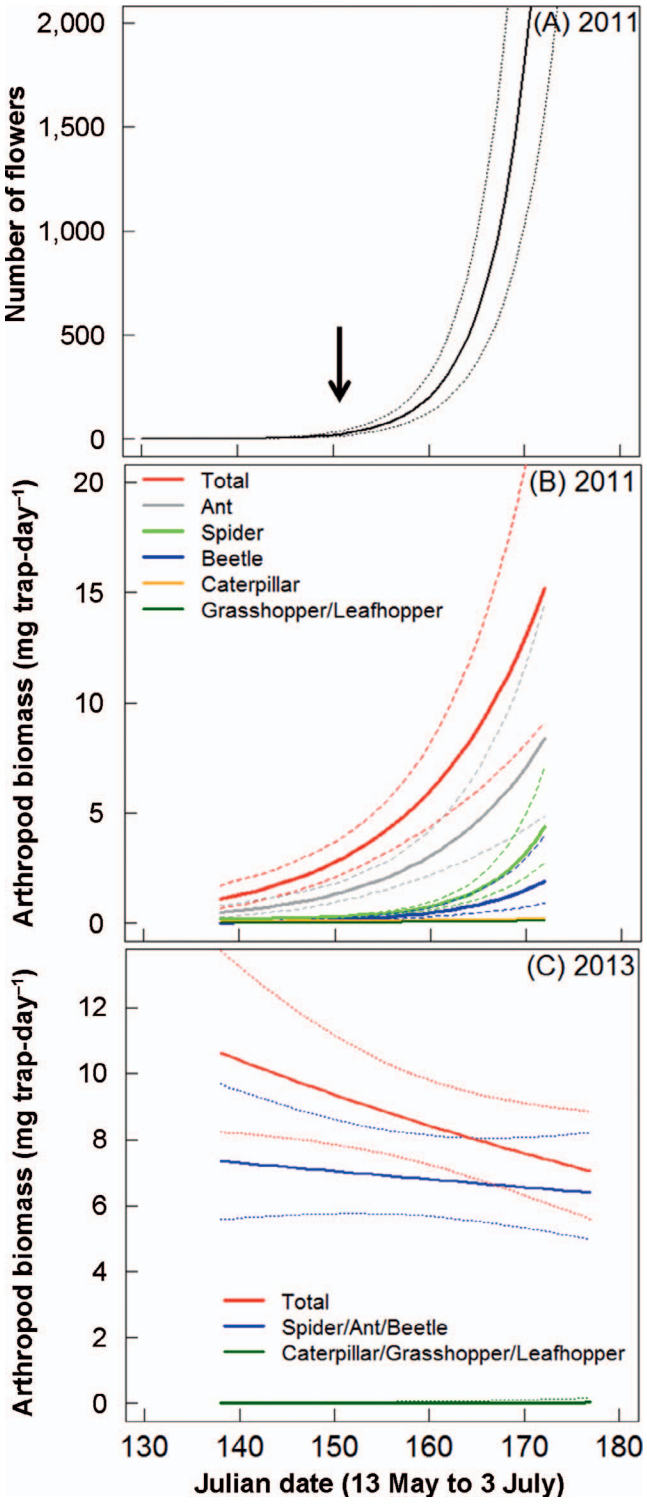


FIGURE 1. (**A**) Seasonal change in the number of flowers per 2 m × 25 m transect through time in 2011, Centennial Sandhills, Montana, USA. Arrow denotes the point of inflection of the curve as determined by a change-point analysis (Killick and Eckley 2014). This point demarcated the before-pulse from the after-pulse periods. Relative invertebrate biomass (total and for invertebrate groups based on distinct δ^{15}N values) from pitfall trap captures in 2011 (**B**) and 2013 (**C**). The dashed line indicates ± 1 SE around the average rate of change in flowers and invertebrates.

capture all invertebrate species available to foraging birds, pitfall traps collect both ground-surface– and foliage-dwelling invertebrates commonly found in the shrub canopy of sagebrush communities (Lowe et al. 2010). Lowe at al. (2010) demonstrated that non-baited pitfall traps can successfully quantify relative abundance of invertebrates consumed by sparrows (Orthoptera, Hemiptera, Coleoptera, Hymenoptera, Lepidoptera; Best 1972) over short time periods (3–5 days) in May and June. Our pitfall technique may have underestimated certain foliage-dwelling insects consumed by sagebrush sparrows, but the specificity of our trapping method is somewhat less important, because our basic objective was to test whether there were more prey items available after the food-resource pulse than before it. We placed pitfall traps at the first 6 locations of bird capture starting on May 13, 2011, and used these same (permanently marked) 6 pitfall grids in 2013, beginning on May 18, 2013. Individual pitfall grids were spaced >200 m apart. Each pitfall grid consisted of 5 plastic cups (11 cm in diameter, 14 cm deep) placed at the axis and endpoints of a † shape with 25 m spacing between cups. Saline solution was added to each cup (~3 cm deep), followed by a drop of glycerin to reduce surface tension. Invertebrate samples were collected from cups every 4–6 days, May 18 through June 29, 2011, and May 22 through July 3, 2013. Invertebrate samples were emptied from cups and preserved in 95% ethanol solution. We defined catch per unit effort (mg trap-day^{-1}) by adjusting invertebrate biomass by the number of trap nights an individual trap (cup) was deployed. We sorted invertebrate samples to taxonomic order and size class (we used only individuals of ≤10 mm total body length, based on size of prey typically consumed by these 2 sparrow species; Best 1972, Rotenberry et al. 1999, Jones and Cornely 2002). We dried samples of each invertebrate order at 60°C for 48 hours, and weighed them to the nearest 10 mg.

Sparrow Plasma Isotope and Triglycerides Sampling

Male Brewer's and Vesper sparrows were captured within the randomly selected plots distributed across the 3 regions in 2011 and 2013. We visited each plot once per day until all plots were surveyed for birds to capture. After all plots were assessed during a sample period, sampling recommenced back on the first plot; this resulted in 3–4 sample periods per year. Male Brewer's ($n = 55$ in 2011, $n = 88$ in 2013) and Vesper ($n = 32$ in 2011) sparrows were netted by luring males into one mist net (polyester mesh, each 6 m × 3 m, 30-mm cell size) using playback broadcasts of conspecific songs and calls (Sogge et al. 2001). Only male sparrows that exhibited territorial defense aggression were captured because in territorial species, males generally arrive earlier than (non-territorial) females in order to select a high-quality territory that maximizes the pair's fitness (Morbey and Ydenberg 2001).

Downloaded From: https://complete.bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

All captured sparrows were marked with a U.S. Geological Survey aluminum leg band.

A 27-gauge needle was used to puncture the brachial vein, allowing free flow of blood directly into heparinized micro-capillary tubes, to collect ~200 μL whole blood from each captured bird for both stable isotope and triglyceride analyses. Due to the constriction of the brachial vein upon capture, we could not always collect our target goal of ~200 μL of blood from each bird captured; this precluded us from analyzing both triglyceride concentrations and isotope values from every bird we captured. Each blood sample was centrifuged for 10 min at 12,000 rpm to segregate plasma from red blood cells. After tubes were centrifuged, plasma was separated from red blood cells, flash-frozen in liquid nitrogen dry shipper (Taylor Wharton CX-100, Worthington Industries, Columbus, Ohio, USA) and stored at −80°C until analysis.

Plant and Invertebrate Isotope Sampling

A sample of invertebrates from different taxonomic orders and seeds was collected to isotopically characterize diet items available for consumption to Vesper and Brewer's sparrows. However, dietary estimates are sensitive to the temporal changes in isotopic composition of their prey (e.g., Beaulieu and Sockman 2012). We therefore minimized the effect of potential temporal changes in the isotopic composition of sparrow prey (i.e. plants and insects) by timing collections to coincide with the spring and summer seasons of the study. We collected 87 individual invertebrates on June 5, 2011, and 104 invertebrates on May 23 and July 11, 2013, to characterize different prey resources available to sparrows. During the same dates, we collected grass seeds from 21 individual plants in 2011, and from 29 individual plants in 2013. Because isotope values of invertebrates submerged in saline solution for hours become degraded (Krab et al. 2012), we did not use invertebrates captured in pitfall traps to characterize the isotopic values of sparrow prey. Instead, we collected a broad array of invertebrates from potential foraging substrates by visually sampling sagebrush using forceps to collect surface-, canopy-, and foliage-dwelling invertebrates. Upon returning from the field, we immediately froze these prey samples.

Stable Isotope and Triglyceride Laboratory Analyses

All field-collected samples (i.e. vegetation, invertebrates, bird plasma) were freeze-dried and powdered with a mortar and pestle before isotopic analyses. Specimens were weighed to the nearest 1.0 ± 0.2 mg, and compressed into tin capsules. Samples were analyzed for stable-nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotopes using continuous-flow isotope-ratio mass spectrometry (following Pearson et al. 2003) at the University of New Mexico Stable Isotope Laboratory. Stable isotope values were reported in parts per thousand (‰), relative to atmospheric (AIR) nitrogen for $\delta^{15}N$ and relative to Vienna PeeDee Belemnite for $\delta^{13}C$. Estimated analytical error was ±0.3‰ for $\delta^{15}N$ and ±0.1‰ for $\delta^{13}C$, based on $n = 145$ replicate within-run measurements of organic standards.

Bird plasma triglycerides were assayed on a microplate spectrophotometer (Bio-Tek Powerwave X340, Bio-Tek Instruments, Winooski, Vermont, USA) using commercial kits modified for small volumes following Smith and McWilliams (2010). Triglycerides were measured sequentially by endpoint assay (Sigma, St. Louis, Missouri, USA: 5μL plasma, 240 μL reagent A, 60 μL reagent B) by first measuring free glycerol and then subtracting free glycerol concentration from measured total triglyceride concentration (Smith and McWilliams 2010). Samples were diluted 3-fold with 0.9% NaCl before they were assayed.

Data Analysis

Linear mixed-effects (LME) models were used to investigate temporal changes in flower abundance and relative biomass of invertebrate prey in 2011 and 2013. Sampling location was included as a random effect to account for repeated sampling of the same site through time, with date added as a fixed-effect parameter within the model. Data on flower abundance in 2011, and invertebrate biomass in both years, were log-transformed to correct heteroscedasticity. Confidence intervals on predicted flower abundance and invertebrate biomass were estimated using the delta method (Seber 1982). Start of the seasonal transition in resource availability for our study area was determined by searching for the date that most strongly discriminated the 2 different rates of change in flower abundance during the season in 2011 (hereafter, termed the "food-resource pulse"). We used a change-point analysis to determine this date using the R package changepoint (Killick and Eckley 2014). The change-point analysis was performed on the predicted values for flower abundance based on the LME.

For each sparrow species, we quantified both within-species dietary breadth and between-species dietary-niche overlap using a standard ellipse area corrected for small sample size (SEA_c) (Jackson et al. 2011) in Stable Isotope Analysis in R (SIAR; Parnell et al. 2010). Stable isotope ellipses help elucidate foraging behavior of individual species within a community. Standard ellipse areas typically contain 40% of the prey-item data for an individual species. Ellipses are also unbiased with respect to sample size, and their estimation using Bayesian inference allows for comparison within or between sparrow species containing different sample sizes. We compared overlap (expressed in $‰^2$) in SEA_c within and between species from the periods before and after the food-resource pulse.

We used a one-way analysis of variance (ANOVA) to compare mean $\delta^{15}N$ values among invertebrate orders and

Downloaded From: https://complete.bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

grass seeds. Multiple comparisons among invertebrate orders and grass seeds were made using Holm pairwise comparisons, to maintain experiment-wise error rates at our selected alpha level. Clades of sparrow prey items that had statistically indistinguishable $\delta^{15}N$ values were lumped and treated as one group in all subsequent analyses, because stable isotope mixing models cannot estimate diet contributions of prey groups based on similar isotope values. We classified diet items only to the level of taxonomic order, as we were interested in comparing major patterns in sparrow dietary breadth and overlap before versus after a food pulse, rather than finely differentiating selected prey items from their relative availability. Using these ANOVA results, we then assessed temporal changes in invertebrate biomass within each of these taxonomic groups. The contribution of isotopically distinct dietary endpoints, as identified by the above ANOVA analysis, to the diets of sparrows was then investigated further using a concentration-dependent, six- (number of source contributions from 2011) or three-endpoint (number of source contributions from 2013), two-isotope Bayesian mixing model (SIAR) without informative priors to estimate relative contribution of foods from distinct invertebrate taxonomic orders to diets of Vesper and Brewer's sparrows before and after the food-resource pulse (Parnell et al. 2010). Isotopic endpoints in the mixing model included spiders (Araneae), ants (Hymenoptera), beetles, caterpillars (Lepidoptera), combined grasshoppers and leafhoppers (Hemiptera), and grass seeds in 2011. In contrast, in 2013 the model included (1) a combined ants, spiders, and beetles category, (2) a combined caterpillars, grasshoppers, and leafhoppers category, and (3) grass seeds. This model accounts for variation in isotopic values, carbon and nitrogen concentrations of prey sources, and a predictable shift in isotopic values of a sparrow's diet when assimilated to consumer tissues. A concentration-dependent model accounts for different ratios of carbon to nitrogen in grass seeds compared to insect prey, and is suitable for quantification of dietary contributions to omnivorous animals (Phillips and Koch 2002). Discrimination values were derived for bird plasma from controlled experiments (Pearson et al. 2003, Ogden et al. 2004) that fed birds a plant- or invertebrate-based diet, which included (mean ± 1 SD) 0.43 ± 0.21‰ for $\delta^{13}C$ and 3.0 ± 0.26‰ for $\delta^{15}N$ for invertebrates, and –0.9 ± 0.92‰ for $\delta^{13}C$ and 2.6 ± 0.07‰ for $\delta^{15}N$ for grass seeds.

Triglyceride concentrations of blood plasma were compared for Brewer's and Vesper sparrows before and after the food-resource pulse using a generalized linear model (with normally distributed errors) with a Gaussian link. All statistical analyses were conducted using R 3.2.2 (R Core Development Team 2015). Means are presented with ± 1 SE, unless stated otherwise. We determined significance with an alpha level of $P \leq 0.05$ for statistical tests.

RESULTS

Abundance of Flowers and Invertebrates

Log-transformed total abundance of flowers was positively predicted by date (LME: flower abundance = $e^{-29.813+0.219*\text{ordinal date}}$; $t_{11} = 9.750$, $P < 0.001$). Flower abundance at the beginning of the study (May 13) was 0, and it increased to a maximum count (1,415 ± 560) on June 23 (Figure 1A). The change-point model estimated the date at which flower abundance changed during the breeding season as being June 2 (ordinal date 153).

The average daily rate of increase of log-transformed total invertebrate biomass from pitfall traps was positively predicted by date in 2011 (LME: $b_{2011\ \text{Total Invertebrate}} = 0.08 \pm 0.02$ mg trap-day^{-1}, $t_{27} = 3.292$, $P = 0.003$), but not in 2013 (LME: $b_{2013\ \text{Total Invertebrate}} = -0.01 \pm 0.009$ mg trap-day^{-1}, $t_{40} = -1.090$, $P = 0.282$; Figures 1B and 1C). Spiders increased with date in 2011 ($b = 0.17 \pm 0.02$ mg trap-day^{-1}, $t_{26} = 7.377$, $P < 0.001$), as did ants ($b = 0.08 \pm 0.03$ mg trap-day^{-1}, $t_{26} = 3.163$, $P < 0.001$) and beetles ($b = 0.12 \pm 0.04$ mg trap-day^{-1}, $t_{26} = 3.25$, $P < 0.001$; Figures 1B and 1C). In contrast, caterpillars ($b = 0.06 \pm 0.03$ mg trap-day^{-1}, $t_{26} = 1.8311$, $P = 0.08$) and combined grasshoppers and leafhoppers ($b = 0.03 \pm 0.03$ mg trap-day^{-1}, $t_{26} = 0.926$, $P = 0.36$) in 2011 increased only slightly throughout the study. No change in log-transformed invertebrate biomass from any invertebrate group was strongly predicted by date in 2013 (all invertebrate groups: $t_{40} = -0.361$ to 0.531, all $P > 0.05$). Insect biomass at the beginning of the season in 2013 was 10.1 mg trap-day^{-1}, whereas in 2011 insect biomass did not reach this amount until toward the end of the season.

Diet Overlap between Sympatric Bird Species

In 2011, the dietary niche of Brewer's and Vesper sparrows overlapped to a larger extent before the resource pulse (1.67‰ overlap of ellipses) than after (0.20‰ overlap; Figures 2A and 2B). Additionally, after the food-resource pulse, Brewer's Sparrow diet breadth narrowed by 35.4% (from 3.65‰ to 2.36‰) while Vesper Sparrow diet breadth narrowed by 48.2% (2.55‰ to 1.23‰).

In 2013, dietary niche breadth of Brewer's Sparrows was wider before compared to after the food-resource pulse. The Brewer's Sparrow diet breadth narrowed by 34.8% (1.12‰ to 0.73‰) from before to after the resource pulse (Figure 2C).

Dietary Contributions to Sympatric Species

The $\delta^{15}N$ values of sparrow prey varied across 6 distinct prey groups in 2011 ($F = 131.9$, df = 6 and 104, $P < 0.001$) and 3 distinct prey groups in 2013 ($F = 31.0$, df = 5 and 97,

Downloaded From: https://complete.bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

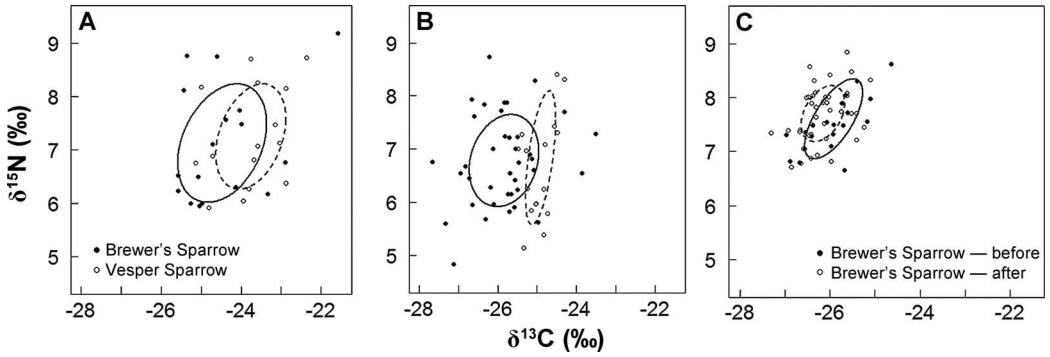


FIGURE 2. Stable isotope Bayesian ellipses depict diet breadth in, and overlap between, sympatric Brewer's (solid line and filled circles) and Vesper (dashed line and hollow circles) sparrows from before (**A**) and after (**B**) a dramatic increase in prey availability in 2011, and (**C**) diet breadth in Brewer's Sparrow from early (solid line and filled circles) and late (dashed line and hollow circles) in the summer, 2013.

$P < 0.001$; Table 1). All Holm pairwise comparisons tests of $\delta^{15}N$ values among sparrow prey categories showed significant differences between the 2 sparrow species ($P < 0.05$), except for grasshoppers and leafhoppers ($P = 0.99$; Table 1). In 2011, the 6 distinct prey groups included (1) spiders, (2) ants, (3) beetles, (4) caterpillars, (5) combined grasshoppers and leafhoppers, and (6) grass seeds. In 2013, Holm pairwise comparisons identified only 3 distinct groups based on $\delta^{15}N$ values, which included (1) combined beetles, ants, and spiders, (2) combined grasshoppers, leafhoppers, and caterpillars, and (3) grass seeds.

In 2011, results from isotopic mixing models suggested high dietary-niche overlap between sympatric sparrows before the food-resource pulse (Figure 3). During this time, spiders, ants, grasshoppers, leafhoppers, and caterpillars dominated the diets of both sparrow species. These prey items collectively contributed >80% of the total prey to diets of both sparrow species.

After the food-resource pulse in 2011, sparrow species exhibited both greater trophic segregation and narrowing of dietary niche breadth, as evidenced in the isotopic ellipses (Figure 2). Following the food-resource pulse, Brewer's Sparrows shifted their diet toward grass seeds and beetles (Figure 3), which comprised a majority (55%) of their diet. In contrast, Vesper Sparrows' diet consisted mainly (≥70%) of spiders, ants, and caterpillars, both before and after the food-resource-pulse (Figure 3).

Before the food-resource pulse in 2013, Brewer's Sparrows consumed mainly spiders, ants, and beetles (48%) and grass seeds (35%; Figure 3B). After the food-resource pulse, grass seeds constituted a slightly larger portion (44%) of Brewer's Sparrow diets, whereas the contribution of the 2 other prey-item groups remained relatively unchanged.

Energetic Consequences

Relative to concentrations before the food-resource pulse, triglyceride concentrations were 1.41× larger after the pulse for Brewer's Sparrows (Figure 4; GLM: $t_{46} = 2.58$, $P = 0.013$) and 1.78× larger for Vesper Sparrows ($t_{35} = 3.21$, $P = 0.003$; Figure 4). In contrast, Brewer's Sparrow triglyceride concentrations did not change across the season in 2013 ($t_{73} = -0.22$, $P = 0.67$). Brewer's Sparrow triglyceride concentrations were similar between years before the food-

TABLE 1. Carbon and nitrogen isotopic values (mean ± 1 SE) of sparrow prey (n = sample size) from 6 prey groups in 2011 and 3 prey groups in 2013. Groupings based on results from ANOVA and Holm pairwise comparisons. None of these samples are adjusted for isotopic discrimination. All samples were collected in the Centennial Sandhills, Centennial Valley, Montana, USA.

Organism	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Year
2011			
Spiders ($n = 8$)	−24.3 ± 0.5	6.5 ± 0.2	2011
Ants ($n = 25$)	−25.3 ± 0.1	5.4 ± 0.1	2011
Beetles ($n = 23$)	−26.2 ± 0.2	4.1 ± 0.3	2011
Caterpillars ($n = 7$)	−25.4 ± 0.3	2.8 ± 0.2	2011
Grasshoppers/Leafhoppers ($n = 24$)	−25.9 ± 0.3	1.4 ± 0.2	2011
Grass seeds ($n = 21$)	−25.9 ± 0.2	−0.4 ± 0.2	2011
2013			
Spiders/Ants/Beetles ($n = 56$)	−25.7 ± 0.1	5.5 ± 0.2	2013
Leafhoppers/Grasshoppers/Caterpillars ($n = 48$)	−26.6 ± 0.2	1.9 ± 0.2	2013
Grass seeds ($n = 29$)	−25.2 ± 0.2	1.1 ± 0.2	2013

Downloaded From: https://complete.bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

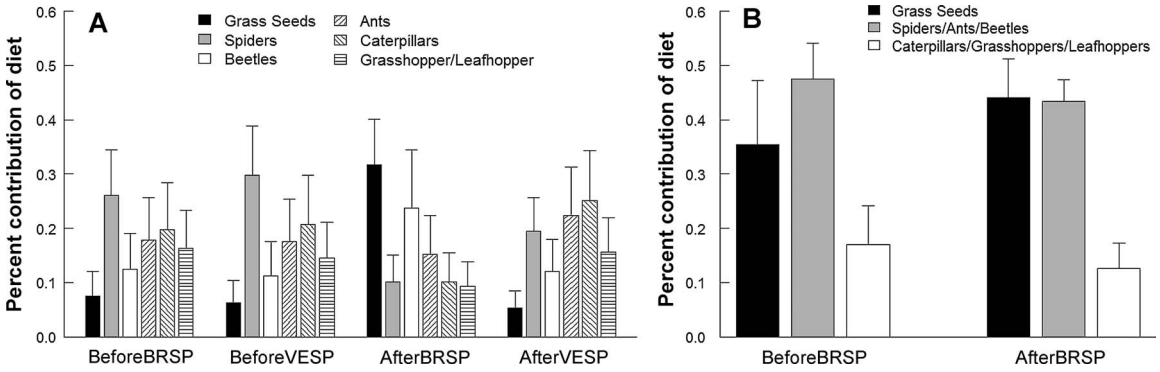


FIGURE 3. Contributions (mean percentage ± 1 SE) of prey from different trophic levels to the diets of Vesper (VESP) and Brewer's (BRSP) Sparrows before and after a food pulse in 2011 (**A**) and for Brewer's Sparrow in 2013 (**B**). Dietary estimates were derived from a concentration-dependent Bayesian isotope mixing model SIAR (following Parnell et al. 2010).

resource pulse ($t_{44} = -0.71$, $P = 0.48$), whereas triglyceride concentrations were higher after the food-resource pulse in 2011 compared with 2013 ($t_{93} = -4.78$, $P = <0.001$).

DISCUSSION

The tracking of food resources by birds across seasons influences their energetic condition and eventually their survivorship and fecundity. In our system, we observed a dramatic seasonal pulse in resource availability, and this produced a sharp post-pulse decline in both the dietary breadth and overlap of 2 sympatric sparrow species in one year (2011), along with more gradual declines in diet breadth of Brewer's Sparrows in the second year (2013). When diet of sparrows became more specialized, amidst greater availability of food items, their energetic condition improved in 2011. This was not observed in 2013, a year without a marked change in availability of food resources, when energetic condition of Brewer's Sparrows remained stable throughout the (2013) study period. Stable isotope mixing models revealed that the seasonal declines in diet breadth and overlap between sparrow species were associated with changes in the dominant prey consumed.

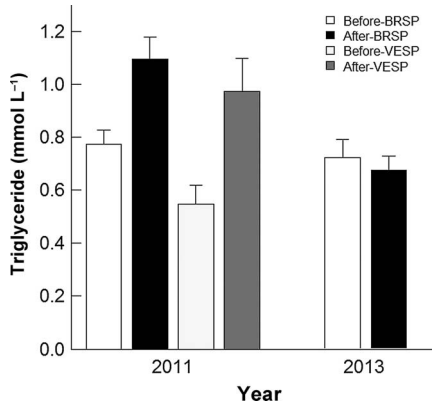


FIGURE 4. Model-predicted mean (± 1 SE) plasma-triglyceride concentration in blood of Brewer's and Vesper sparrows before and after a dramatic increase in food availability in 2011 and of Brewer's Sparrows in 2013.

Abundance and Phenology of Flowers and Invertebrates

The timing of life-cycle events of invertebrates in montane sagebrush ecosystems has been shown to be strongly influenced by temperature and precipitation (Hodkinson 2005, Bates et al. 2006, Lowe et al. 2010). At our study site, we found that abundance of invertebrates increased exponentially throughout the breeding season in 2011, but declined during 2013 after a brief, early-season peak. This difference between years in intra-annual trend in invertebrate abundance is consistent with between-year differences in accumulated winter and spring precipitation. Namely, accumulated precipitation was 2.11 times higher in 2011 than in 2013 (Appendix Figure 6). Wenninger and Inouye (2008) experimentally demonstrated direct effects of water availability on insect abundance and distribution in a sagebrush ecosystem in Idaho that is slightly drier than our system. Additionally, the date of snowmelt in high elevations strongly influences the start of the growing season, as well as the timing of flower (Inouye 2008) and insect emergence (Hodkinson 2005). The disappearance of snowpack at our study sites occurred approximately 3 weeks later in 2011 than in 2013 (K.A.C. personal observation), which could partially explain the delayed increase in food-resource abundance in 2011. Effects of earlier snowmelt on food-resource abundance is particularly insightful, in light of widespread advancement of timing in spring snowmelt in the Intermountain West during the 20th century (Mote 2003, Mote et al. 2005), predictions for even earlier snowmelt in the future (Leung et al. 2005), and predicted changes in precipitation (Hamlet et al. 2005). Although it is difficult to distinguish their individual contributions on number of distinct prey classes between the 2 years (6 in 2011 vs. 3 in 2013), these

Downloaded From: https://complete.bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

interannual differences in physical conditions (e.g., much-higher precipitation in 2011 than 2013 in a water-limited ecosystem, disappearance of snowpack in 2013 earlier than when most of our sampling occurred) may each have played some role in determining numbers of prey classes.

Feeding Niches of Sparrows: How Diet Breadth and Overlap Change with Resource Availability

OFT and competition theory have differing predictions about diet breadth and degree of niche overlap of sympatric species in prey-limited and prey-rich periods. We therefore were able to distinguish which of these 2 theories potentially influence the coexistence of sagebrush birds through niche partitioning at our study sites. In competition theory, one challenge is that for 2 species to be truly syntopic (i.e. strongly competing), a resource (e.g., prey) must be strongly limiting for interspecific competition to be reduced by greater niche segregation. One prediction of OFT is that a consumer's diet breadth should decrease during times of high resource availability to maximize returns per unit of energy expenditure, resulting in increased resource specialization (MacArthur and Pianka 1966, Perry and Pianka 1997, Correa and Winemiller 2014). We predicted that an increase in food resources during summer in high-elevation sagebrush communities would result in reduced diet breadth and dietary niche overlap for 2 sympatric sparrow species, Vesper and Brewer's sparrows. Consistent with this prediction, diet breadth and overlap of both sparrow species in our study decreased markedly across the food-resource pulse in 2011. Specifically, Brewer's Sparrow diets shifted to more seed- and beetle-based resources after flower availability increased dramatically, whereas Vesper Sparrow diets shifted to contain higher proportions of spiders, ants, and caterpillars. Brewer's Sparrows exhibited the same narrowing of their diet breadth across the season in 2013. Given the taxonomically coarse filter to which our isotopic analyses were constrained, we were still able to detect general reductions in dietary breadth in both sparrow species across a food-resource pulse. Krebs et al. (1977) similarly showed support for optimal foraging in Great Tits (*Parus major*), which also reduced dietary breadth during periods of high resource availability in experimental feeding trials. However, the observed dietary shifts in our sparrow species are not only influenced by prey quantity, but are likely also affected by prey quality, foraging and processing efficiency, and bird abundance (Weimerskirch et al. 2003, Owen et al. 2005, Cerasale and Guglielmo 2010).

In sagebrush communities of the northern Great Basin, Rotenberry (1980a) and Rotenberry and Wiens (1998) showed that erratic interannual precipitation influenced annual variation in net primary productivity (NPP). Accordingly, Brewer's Sparrows tracked the changes in vegetation structure and composition that accompany changes in NPP, and the associated changes in food resources, and correspondingly adjusted their foraging-patch selection from year to year (Rotenberry and Wiens 1998). We found substantial year-to-year differences in the magnitude of this seasonal change in diet breadth. Specifically, grass seeds contributed more to the early-summer diet of Brewer's Sparrow during the dry year (2013), whereas spiders, ants, grasshoppers, leafhoppers, and caterpillars contributed more to their early-summer diets during the wet year (2011). Such interannual variability in winter and spring accumulated precipitation clearly affects the extent and timing of the resource pulse in high-elevation sagebrush ecosystems (Rotenberry and Wiens 1998, Beaulieu and Sockman 2012), and this in turn influences the foraging behavior of avian consumers such as Brewer's and Vesper sparrows.

Energetic Consequences of Seasonal Changes in Feeding Niche

We predicted that energetic condition of both sparrow species would increase with corresponding decreases in dietary breadth and overlap. Changes in food resources available to sparrows during the breeding season corresponded with increased plasma triglyceride concentrations in 2011, but not in 2013. This inconsistent response in energetic condition is corroborated by studies on seabirds that showed that changes in plasma triglycerides were associated with a corresponding diet shift during the breeding season in one year, but not in the next year (e.g., Franci et al. 2015). Additionally, breeding Southwestern Willow Flycatchers (*Empidonax traillii extimus*) that reduced their diet breadth and specialized on less-abundant but higher-quality prey items improved their energetic condition (Owen et al. 2005). Based on our admittedly short-term dataset, it appears that this dietary niche pattern carries little energetic penalty and thus may have little ecological relevance other than to indicate that when resources are abundant, the different sparrow species reduce their dietary breadths to specialize on consuming different prey items, potentially reflecting different optima. For example, comparison of portions left of the change-point arrow in Figures 1B and 1C showed that total prey abundance before the food pulse was markedly higher in 2013 than in 2011, and correspondingly, dietary-niche breadth was much smaller in 2013 than in 2011. Clearly, other factors such as bird abundance, prey quality, and foraging efficiency can influence changes in foraging patterns that lead to changes in energetic condition in some years but not others (Owen et al. 2005, Cerasale and Guglielmo 2010, MacDade et al. 2011, Franci et al. 2015). Further work on sagebrush bird communities is needed to assess whether other niche dimensions besides prey choice show similar intra-annual

Downloaded From: https://complete.bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

and interannual changes, and their consequences for the ecology, conservation, and management of this bird community.

ACKNOWLEDGMENTS

We thank S. Ismar, J. Rotenberry, and an anonymous reviewer, as well as S. B. Correa and E. R. Pianka for critical reviews of earlier drafts of the manuscript. G. Pasini, E. Trusz, J. Saba, and S. Essig provided field assistance. B. West and staff of Red Rock Lakes National Wildlife Refuge provided logistical support. W. F. Cross provided lab access. R. Levine and J. A. Dullum assisted with database design. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The authors declare no conflict of interest.

Funding statement: This research was funded by the Wildlife Health Lab of the U.S. Fish and Wildlife Service, and the Montana Association of Conservation Districts.

Ethics statement: This research was conducted in compliance with federal (06266), state (2011-53), and animal care and use (017-12MAWEST-042412) permits.

Author contributions: K.C., M.A., and E.B. conceived the idea, design, and experiment. K.C., M.A., S.S., N.K., E.K. and S.M. performed the experiments. K.C. with inputs from co-authors and others analyzed the data. K.C., M.A., E.B., and S.M. with inputs from co-authors wrote the paper.

LITERATURE CITED

Arizmendi-Mejía, R., T. Militão, G. Viscor, and J. González-Solís (2013). Pre-breeding ecophysiology of a long-distance migratory seabird. Journal of Experimental Marine Biology and Ecology 443:162–168.

Bates, J. D., T. Svejcar, R. F. Miller, and R. A. Angell (2006). The effects of precipitation timing on sagebrush steppe vegetation. Journal of Arid Environments 64:670–697.

Beaulieu, M., and K. W. Sockman (2012). One meadow for two sparrows: Resource partitioning in a high elevation habitat. Oecologia 170:529–540.

Best, L. B. (1972). First year effects of sagebrush control on two sparrows. Journal of Wildlife Management 36:534–544.

Bradley, B. A. (2010). Assessing ecosystem threats from global and regional change: Hierarchical modeling of risk to sagebrush ecosystems from climate change, land use and invasive species in Nevada, USA. Ecography 33:198–208.

Cerasale, D. J., and C. G. Guglielmo (2010). An integrative assessment of the effects of tamarisk on stopover ecology of a long-distance migrant along the San Pedro River, Arizona. The Auk 127:636–646.

Chalfoun, A. D., and T. E. Martin (2007). Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. Journal of Applied Ecology 44:983–992.

Correa, S. B., and K. O. Winemiller (2014). Niche partitioning among frugivorous fishes in response to fluctuating resources in the Amazonian floodplain forests. Ecology 95:210–224.

Franci, C. D., F. Vézina, F. Grégoire, J. F. Rail, and J. Verreault (2015). Nutritional stress in Northern Gannets during an unprecedented low reproductive success year: Can extreme sea surface temperature event and dietary change be the cause? Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 181:1–8.

Hamlet, A. F., P. W. Mote, M. P. Clark, and D. P. Lettenmaier (2005). Effects of temperature and precipitation variability on snowpack trends in the western United States. Journal of Climate 18:4545–4561.

Haney, J. C. (1999). Numerical response of birds to an irruption of elm spanworm (*Ennomos subsignarius*; Geometridae: Lepidoptera) in old-growth forest of the Appalachian Plateau, USA. Forest Ecology and Management 120:203–217.

Hodkinson, I. D. (2005). Terrestrial insects along elevation gradients: Species and community responses to altitude. Biology Review 80:489–513.

Holt, R. D. (1977). Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12:197–229.

Holt, R. D. (1984). Spatial heterogeneity, indirect interaction, and the coexistence of prey species. American Naturalist 124:377–406.

Hutchinson, G. E. (1959). Homage to Santa Rosalia, or why are there so many kinds of animals? American Naturalist 93:145–159.

Inouye, D. W. (2008). Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. Ecology 89:353–362.

Jackson, A. L., R. Inger, A. C. Parnell, and S. Bearhop (2011). Comparing isotopic niche widths among and within communities: SIBER – stable isotope Bayesian ellipses in R. Journal of Animal Ecology 80:595–602.

Jenni-Eiermann, S., and L. Jenni (1994). Plasma metabolite levels predict individual body-mass changes in a small long-distance migrant, the Garden Warbler. The Auk 111:888–899.

Jenni-Eiermann, S., and L. Jenni (1997). Diurnal variation of metabolic responses to short-term fasting in passerine birds during the post-breeding, molting and migratory period. The Condor 99:113–122.

Jones, S. L., and J. E. Cornely (2002). Vesper Sparrow (*Pooecetes gramineus*). In The Birds of North America, no. 624 (A. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. doi:10.2173/bna.624

Killick, R., and I. A. Eckley (2014). changepoint: An R package for changepoint analysis. Journal of Statistical Software 58:1–19.

Knick, S. T., and J. T. Rotenberry (2002). Effects of habitat fragmentation on passerine birds breeding in intermountain shrubsteppe. In Effects of Habitat Fragmentation on Birds in Western Landscapes: Contrasts with Paradigms from the Eastern U.S. (T. L. George and D. S. Dobkin, Editors). Studies in Avian Biology 25:130–140.

Krab, E. J., R. S. Van Logtestijn, J. H. Cornelissen, and M. P. Berg (2012). Reservations about preservations: Storage methods affect δ13C signatures differently even in closely related soil fauna. Methods in Ecology and Evolution 3:138–144.

Krebs, J. R., J. T. Erichsen, M. I. Webber, and E. L. Charnov (1977). Optimal prey selection in the Great Tit (*Parus major*). Animal Behaviour 25:30–38.

Leung, L. Y. R., Y. Qian, X. Bian, W. M. Washington, J. Han, and J. Roads (2005). Mid-century ensemble regional climate change scenarios for the western United States. Climate Change 62:75–113.

Downloaded From: https://complete.bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Lowe, C. C., S. M. Birch, S. P. Cook, and F. Merickel (2010). Comparison of trap types for surveying insect communities in Idaho sagebrush steppe ecosystems. Pan-Pacific Entomologist 86:47–56.

Luck, G. W. (2003). Differences in the reproductive success and survival of the Rufous Treecreeper (*Climacteris rufa*) between a fragmented and unfragmented landscape. Biological Conservation 109:1–14.

Ma, Z. J., X. J. Gan, C. Y. Choi, and B. Li (2014). Effects of invasive cordgrass on presence of marsh grassbird in an area where it is not native. Conservation Biology 28:150–158.

MacArthur, R. H. (1958). Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599–619.

MacArthur, R. H., and E. R. Pianka (1966). On optimal use of a patchy environment. American Naturalist 100:603–609.

MacDade, L. S., P. G. Rodewald, and K. A. Hatch (2011). Contribution of emergent aquatic insects to refueling in spring migrant songbirds. The Auk 128:127–137.

Martin, T. E. (1988). On the advantage of being different: Nest predation and the coexistence of bird species. Proceedings of the National Academy of Sciences USA 85:2196–2199.

McShea, W. J. (2000). The influence of acorn crops on annual variation in rodent and bird populations. Ecology 81:228–238.

Morbey, Y. E., and R. C. Ydenberg (2001). Protandrous arrival timing to breeding sites: A review. Ecology Letters 4:663–673.

Mote, P. W. (2003). Trends in snow water equivalent in the Pacific Northwest and their climatic causes. Geophysical Research Letters 30:1601. doi:10.1029/2003GL017258

Mote, P. W., A. F. Hamlet, M. P. Clark, and D. P. Lettenmaier (2005). Declining mountain snowpack in western North America. Bulletin of the American Meteorological Society 86:39–49.

Noss, R. F., and R. L. Peters (1995). Endangered Ecosystems of the United States: A Status Report and Plan for Action. Defenders of Wildlife, Washington, D.C., USA.

Ogden, L. J. E., K. A. Hobson, and D. B. Lank (2004). Blood isotopic ($\delta^{13}C$ and $\delta^{15}N$) turnover and diet-tissue fractionation factors in captive Dunlin (*Calidris alpina pacifica*). The Auk 121:170–177.

Owen, J. C., M. K. Sogge, and M. D. Kern (2005). Habitat and sex differences in physiological condition of breeding Southwestern Willow Flycatchers (*Empidonax traillii extimus*). The Auk 122:1261–1270.

Parnell, A. C., R. Inger, S. Bearhop, and A. L. Jackson (2010). Source partitioning using stable isotopes: Coping with too much variation. PLOS One 5(3):e9672. doi:10.1371/journal.pone.0009672

Pearson, S. F., D. J. Levey, C. H. Greenberg, and C. M. del Rio (2003). Effects of elemental composition on the incorporation of dietary nitrogen and carbon isotopic signatures in an omnivorous songbird. Oecologia 135:516–523.

Perry, G., and E. Pianka (1997). Animal foraging: Past, present and future. Trends in Ecology and Evolution 12:360–364.

Phillips, D. L., and P. L. Koch (2002). Incorporating concentration dependence in stable isotope mixing models. Oecologia 130:114–125.

Pyke, G. H. (1984). Optimal foraging theory: A critical review. Annual Review of Ecology and Systematics 15:523–575.

R Core Development Team. (2015). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Rotenberry, J. T. (1980a). Bioenergetics and diet in a simple community of shrubsteppe birds. Oecologia 46:7–12.

Rotenberry, J. T. (1980b). Dietary relationships among shrubsteppe passerine birds: Competition or opportunism in a variable environment? Ecological Monographs 50:93–110.

Rotenberry, J. T., M. A. Patten, and K. L. Preston (1999). Brewer's Sparrow (*Spizella breweri*). In The Birds of North America, no. 390 (A. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. doi:10.2173/bna.390

Rotenberry, J. T., and J. A. Wiens (1989). Reproductive biology of shrubsteppe passerine birds: Geographical and temporal variation in clutch size, brood size, and fledging success. The Condor 91:1–14.

Rotenberry, J. T., and J. A. Wiens (1991). Weather and reproductive variation in shrubsteppe sparrows: A hierarchical analysis. Ecology 72:1325–1335.

Rotenberry, J. T., and J. A. Wiens (1998). Foraging patch selection by shrubsteppe sparrows. Ecology 79:1160–1173.

Sauer, J. R., J. E. Hines, G. Gough, I. Thomas, and B. G. Peterjohn (2000). The North American Breeding Bird Survey results and analysis. Version 98.1. Patuxent Wildlife Research Center, Laurel, MD, USA. http://www.mbr-pwrc.usgs.gov/bbs/

Seber, G. A. F. (1982). The Estimation of Animal Abundance and Related Parameters, 2nd edition. Macmillan, New York, NY, USA.

Smith, R. J., and F. R. Moore (2005). Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. Behavioral Ecology and Sociobiology 57:231–239.

Smith, S. B., and S. R. McWilliams (2010). Patterns of fuel use and storage in migrating passerines in relation to fruit resources at autumn stopover sites. The Auk 1:108–118.

Sogge, M. K., C. Owen, E. H. Paxton, S. M. Langridge, and T. J. Koronkiewicz (2001). A targeted mist net capture technique for the Willow Flycatcher. Western Birds 32:167–172.

Stutchbury, B. J. M., E. A. Gow, T. Done, M. MacPherson, J. W. Fox, and V. Afanasyev (2011). Effects of post-breeding molt and energetic condition on timing of songbird migration into the tropics. Proceedings of the Royal Society of London, Series B 278:131–137.

Warne, R. W., A. D. Pershall, and B. O. Wolf (2010). Linking precipitation and C_3–C_4 plant production to resource dynamics in higher-trophic-level consumers. Ecology 91:1628–1638.

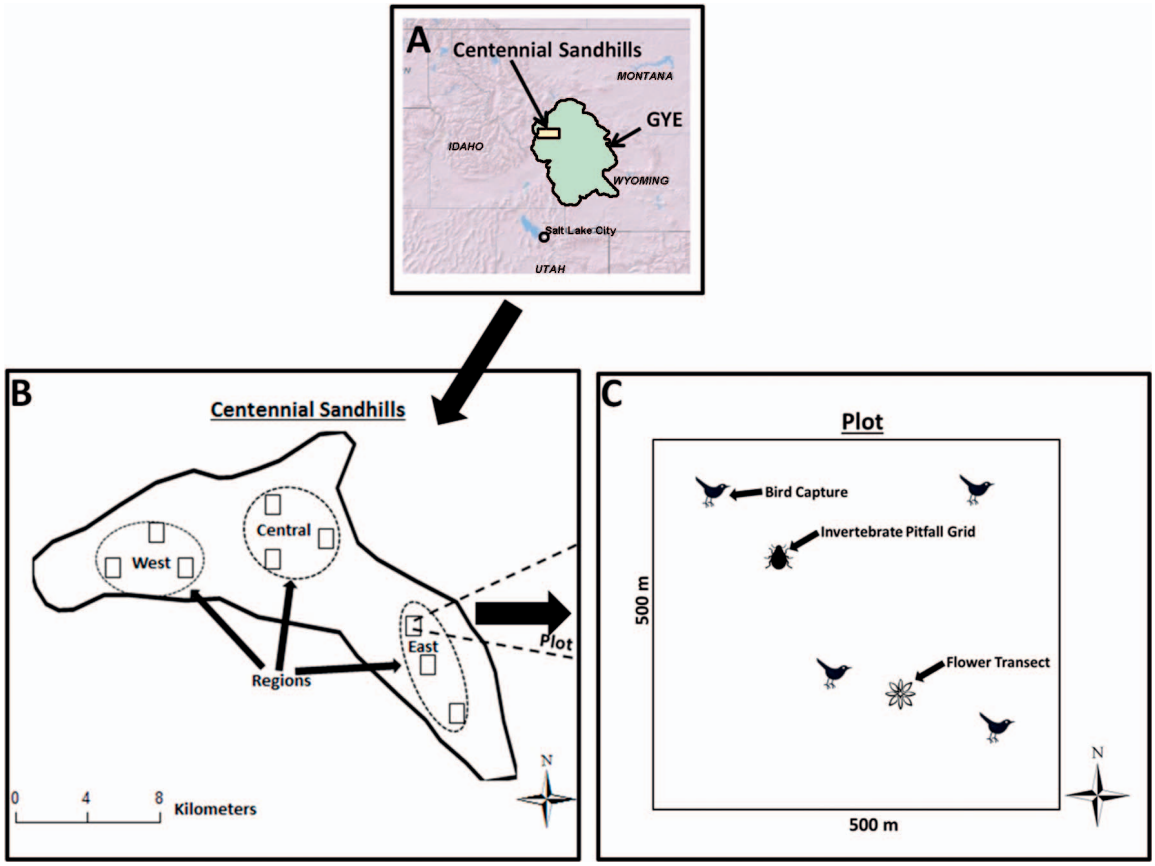
Weimerskirch, H., A. Ancel, M. Caloin, A. Zahariev, J. Spagiari, M. Kersten, and O. Chastel (2003). Foraging efficiency and adjustment of energy expenditure in a pelagic seabird provisioning its chick. Journal of Animal Ecology 72:500–508.

Wenninger, E. J., and R. S. Inouye (2008). Insect community response to plant diversity and productivity in a sagebrush-steppe ecosystem. Journal of Arid Environments 72:24–33.

Wood, E. M., and A. M. Pidgeon (2015). Extreme variations in spring temperature affect ecosystem regulating services provided by birds during migration. Ecosphere 6:art216. http://onlinelibrary.wiley.com/doi/10.1890/ES15-00397.1/pdf

Yang, L. H., J. L. Bastow, K. O. Sence, and A. N. Wright (2008). What can we learn from resource pulses? Ecology 89:621–634.

Downloaded From: https://complete.bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use



APPENDIX FIGURE 5. Depiction of our sampling strategy. **(A)** Location of Centennial Sandhills within the western edge of Greater Yellowstone Ecosystems (GYE), our sampling regions within the Sandhills **(B)**, and sampling locations within each plot **(C)**. As described in the text, we sampled flowers, insects, and birds within plots.

APPENDIX

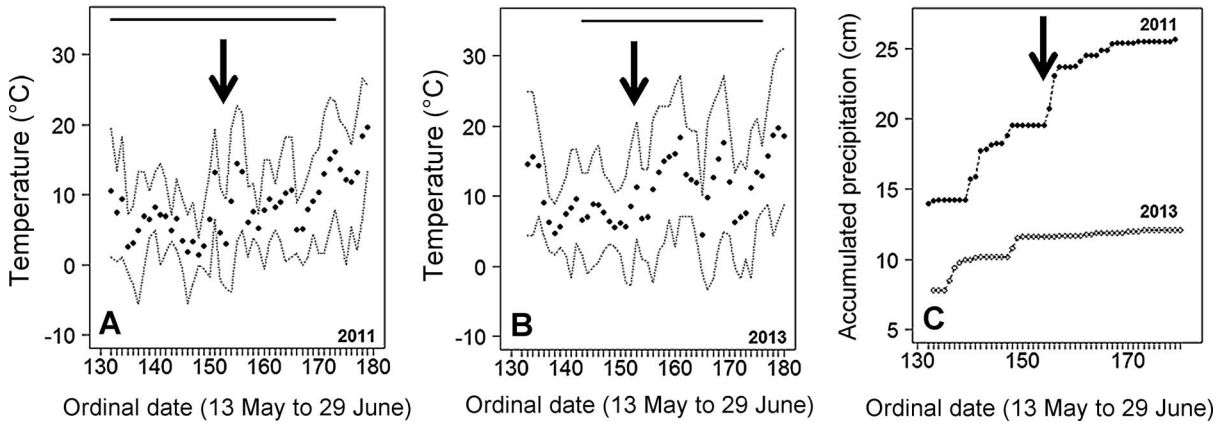
Air Temperature and Precipitation

Methods. To assess the transition from spring to summer, we examined hourly air temperatures and precipitation data from a RAWS weather station in the Centennial Sandhills (http://raws.wrh.noaa.gov/cgi-bin/roman/meso_base.cgi?stn=RRDM8&time=GMT). The weather station is located 2 km west of the study area, at an elevation of 2,027 m. We quantified between-winter differences in accumulated precipitation from October 1 to May 13 during both winters of study (i.e. 2010 to 2011 and 2012 to 2013).

Results. During both years, air temperature increased considerably following the onset of flower emergence (Figures 1A and 1B). Overwinter accumulated precipitation from October 1 to May 13 was 2 times greater during the winter of 2010 to 2011 than during the winter of 2012 to 2013.

In 2011, total accumulated precipitation at the start of the study was stable in periods before the pulse (May 13–21) and after the pulse (June 19–29), with a total of <1 cm of precipitation falling during these periods. However, 45% of the study duration's total accumulated precipitation fell during the middle portion (May 20 to June 4, 2011) of the study timeframe. In contrast, precipitation during the study was 75% lower in 2013 than in 2011. Most of this fell during the before-pulse period (3.8 cm of accumulated precipitation from May 16 to 29), and only 0.4 cm additional precipitation accumulated after the pulse (Appendix Figure 6).

Downloaded From: https://complete.bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use



APPENDIX FIGURE 6. Temporal changes in ambient temperature (**A**, **B**) and accumulated daily precipitation (**C**) before and after the phenological pulse on ordinal date 157 (June 6), Centennial Sandhills, Montana, USA, during 2011 (**A**) and 2013 (**B**). Temperature data (**A**, **B**) show mean daily values (dots) as well as the recorded range of maximum and minimum daily values (dotted lines). Thick lines at the top of (**A**) and (**B**) represent the period during which birds were captured and sampled in the field. Day 133 (May 13) corresponds to the first capture date in 2011, while day 143 (May 23) was the first capture date in 2013. Arrow denotes the point of inflection of the curve as determined by a change-point analysis (Killick and Eckley 2014). This point demarcated the before-pulse from the after-pulse periods.

Downloaded From: https://complete.bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use