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Extreme climatic variability during migration invokes physiological and dietary plasticity among spring migrating ducks

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Keywords

Spatula discors, *Aythya affinis*, Blue-winged Teal, diets, environmental stochasticity, Lesser Scaup, lipid metabolites, nutrient reserves, South Dakota, spring migration

Disciplines

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Extreme climatic variability during migration invokes physiological and dietary plasticity among spring migrating ducks

Adam K. Janke, Michael J. Anteau, and Joshua D. Stafford

Abstract: Environmental stochasticity encountered during migration can have negative consequences for individuals and population demographics through direct reductions in survival or cross-seasonal impacts. We took advantage of substantial interannual variation in spring migration conditions over a 4 year field study to examine physiological and dietary variation among two species of migrant ducks. We collected female Lesser Scaup (*Aythya affinis* (Eyton, 1838)) and Blue-winged Teal (*Spatula discors* (Linnaeus, 1766)) during spring migration and measured lipid and protein reserves, an index of recent lipid metabolism based on concentrations of lipid metabolites in plasma, and diets. We documented systematic interannual variation among these metrics in both species, contrasting primarily the warmest, earliest spring and the coldest, latest spring. Lesser Scaup had reduced lipid and protein reserves and consumed less energy-rich prey during the coldest and latest spring but showed no interannual variation in the index of lipid metabolism. Blue-winged Teal similarly had reduced protein reserves in the cold, late spring but maintained constant lipid reserves among years, likely facilitated by increased consumption of energy-rich seeds reflected in diets and lipid metabolism. Our results reveal impacts of environmental stochasticity on migrants and suggest that recruitment may be impacted by variable conditions encountered during migration during extreme weather events.

Key words: *Spatula discors*, *Aythya affinis*, Blue-winged Teal, diets, environmental stochasticity, Lesser Scaup, lipid metabolites, nutrient reserves, South Dakota, spring migration.

Résumé : La stochasticité environnementale durant la migration peut avoir des conséquences négatives pour les individus et la démographie de populations par l'entremise de réductions directes de la survie ou d'impacts inter-saisonniers. Nous mettons à profit l'importante variation interannuelle des conditions de la migration printanière pendant une étude de terrain de quatre ans pour examiner les variations physiologiques et du régime alimentaire chez deux espèces de canards migrateurs. Nous avons prélevé des petits fuligules (*Aythya affinis* (Eyton, 1838)) et sarcelles à ailes bleues (*Spatula discors* (Linnaeus, 1766)) femelles durant les migrations printanières et mesuré leurs réserves de lipides et de protéines, un indice du métabolisme des lipides récent basé sur les concentrations de métabolites lipidiques dans le plasma et leurs régimes alimentaires. Nous documentons des variations interannuelles systématiques de ces paramètres chez les deux espèces, distinguant principalement le printemps le plus précoce et le plus chaud du printemps le plus tardif et le plus froid. Les petits fuligules présentaient des réserves de lipides et de protéines réduites et consommaient des proies moins riches en énergie durant le printemps plus tardif et plus froid, mais leur indice de métabolisme lipidique ne montre aucune variation interannuelle. Les sarcelles à ailes bleues présentaient aussi des réserves réduites en protéines durant le printemps tardif et froid, mais conservaient des réserves de lipides constantes d'une année à l'autre, un phénomène probablement facilité par une consommation accrue de graines très énergétiques qui se reflète dans les régimes alimentaires et le métabolisme des lipides. Nos résultats révèlent des effets de la stochasticité environnementale sur les migrants et donnent à penser que le recrutement pourrait être influencé par les conditions variables rencontrées durant la migration pendant des événements météorologiques extrêmes. [Traduit par la Rédaction]

Mots-clés : *Spatula discors*, *Aythya affinis*, sarcelle à ailes bleues, régimes alimentaires, stochasticité environnementale, petit fuligule, métabolites lipidiques, réserves de nutriments, Dakota du Sud, migration printanière.

Introduction

Variability in habitat and climatic conditions encountered during migration can structure population dynamics among migrant animals across a wide range of taxa and ecosystems (e.g., Alisauskas 2002; Briedis et al. 2017; Agrawal and Inamine 2018; Middleton et al. 2018). Migrant species have evolved a diversity of

life history strategies that minimize exposure to seasonality, but time constraints for critical life history events often force migrants into volatile climates that can affect population dynamics through increased mortality or impaired physiological condition and subsequent carryover effects (Alerstam et al. 2003; Drent et al. 2006; Newton 2006, 2007; Briedis et al. 2017). Further, climate

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variability and phenological mismatches related to climate change increasingly expose migrants to unfavorable conditions throughout migration and have potential to yield long-term impacts on population productivity or sustainability (Miller-Rushing et al. 2010; Bailey and van de Pol 2016; Lennox et al. 2016). Understanding factors affecting condition of migrants preceding and during critical life history phases within the annual cycle can inform conservation of these populations (Cooke et al. 2012).

Among migratory birds, early breeding is adaptive (Blums et al. 2005; Drent et al. 2006); therefore, individuals transitioning to the breeding season often push the limits of their ecological tolerances to arrive in breeding areas early. Speed and success of migration is driven by a combination of intrinsic (i.e., physiological) and extrinsic (i.e., environmental) factors that determine the ability of a migrant to complete flights and arrive in suitable condition to survive and breed (Schmaljohann and Eikenaar 2017). Environmental stochasticity is one important extrinsic driver of migratory success because it can result in direct inhibition of movements to the breeding grounds (Richardson 1978) or have indirect impacts on migration success by altering foraging conditions (Lindstrom and Alerstam 1992; Bauer et al. 2008) or nutrient budgets (Drent et al. 2007). Delays driven by environmental stochasticity can result in later nest initiation dates and reduce fitness (Skinner et al. 1998; Krapu et al. 2000; Alisauskas 2002; Devries et al. 2008; Briedis et al. 2017).

The primary intrinsic factor controlling progression of migration in many birds is the accrual and use of nutrient reserves (namely lipids) to fuel migration (Jenni and Jenni-Eiermann 1998) and for allocation to reproduction after arrival (Drent et al. 2006). Impediments to nutrient accumulation or maintenance during stopover can slow migration (Lindstrom and Alerstam 1992; Drent et al. 2003; Smith and McWilliams 2014). Faster migration and earlier arrival confers energetic advantages for birds limited by nutrient acquisition prior to breeding (i.e., capital breeders sensu Drent and Daan 1980) because it allows time to acquire nutrients for use in clutch formation (Klaassen et al. 2006) or territory establishment and maintenance (Krapu 1981; Smith and Moore 2005). Thus, nutrient reserve balances during the transition to breeding areas among many birds, and particularly waterfowl (Ankney et al. 1991), are strong predictors of onset of reproduction and ultimately productivity (Esler and Grand 1994; Ebbinge and Spaans 1995; Alisauskas 2002; Devries et al. 2008). Therefore, understanding factors affecting nutrient reserve dynamics among migrants across a range of environmental conditions experienced during migration could help explain observed dynamics in population productivity (e.g., Alisauskas et al. 2014; Arnold et al. 2016) and offer insights into the potential consequences of changing migration conditions predicted under future climate scenarios (Marra et al. 2005; Bailey and van de Pol 2016).

Here, we report on the results of a four-year field study on spring-migrating Lesser Scaup (*Aythya affinis* (Eyton, 1838)) and Blue-winged Teal (*Spatula discors* (Linnaeus, 1766)) during which environmental conditions related to spring warmup spanned the entire range of seasonal warming patterns documented on the study area over the preceding 30 years. The seasonal variation that we observed, coupled with our study design focusing on wetland-obligate foragers with seasonally variable diets (Anteau and Afton 2006; Hitchcock 2009), variable wetland habitat preferences (Baldassarre 2014), and contrasting migration timing strategies (i.e., Blue-winged Teal are late migrants, while Lesser Scaup are early migrants: Austin 2002; Austin et al. 2002), provided a unique glimpse into the consequences of environmental stochasticity during avian migration. We hypothesized that the highly variable conditions that prevailed during spring in our study area would result in variation in key metrics of migrant physiology. We measured these physiological and dietary responses of migrants with two classes of metrics: (1) relatively static indicators of migrant condition based on whole-body protein and lipid reserve indices

and (2) dynamic indicators of behavior and physiological condition based on concentration of lipid metabolites circulating in plasma and recent food consumption patterns. Combining static indicators with more responsive indicators of condition and behavior (Jenni-Eiermann and Jenni 1998) allowed us to ask whether physiology of migrants varied throughout migration and whether migrants, on average, were able to actively overcome impairments in condition with increased refueling or dietary lipid intake. Relating variability in these metrics among years and between these two species offered insights into how dietary and physiological plasticity varied with environmental conditions and suggested possible consequences of environmental stochasticity encountered during migration.

Materials and methods

Study area

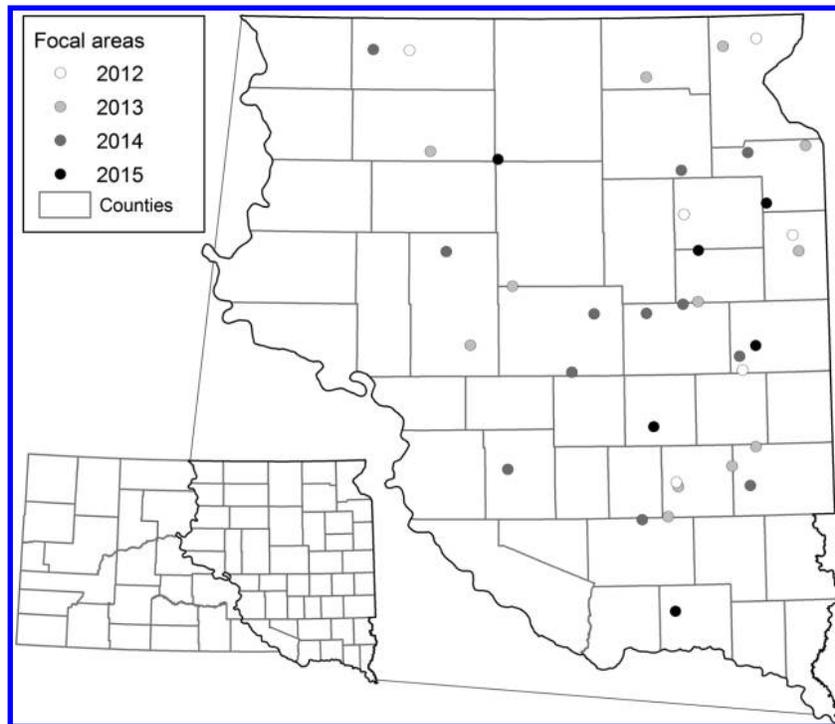
We conducted our study in the Prairie Pothole Region of eastern South Dakota, which included most of the land east the Missouri River in the state (Fig. 1). The region was described in detail by Johnson and Higgins (1997), who reported that wetlands comprised 9.8% of the land area in eastern South Dakota. Upland land uses were a mix of row crop agriculture (primarily corn and soybeans) and grasslands (Naugle et al. 2001). The region was mostly privately owned with scattered small (generally <260 ha) parcels of public ownership that were managed for waterfowl and other wildlife. We conducted our research on wetlands within circular study areas ($n = 6$ during 2012 and 2015 and $n = 12$ during 2013 and 2014) within an 8 km radius (2012) or 4 km radius (2013–2015). Study areas during 2012 were larger because we worked exclusively on publicly owned wetlands whereas during the remaining 3 years of the study, we worked on a mix of privately and publicly owned wetlands. Locations of the study areas changed annually but were always distributed throughout the region (Fig. 1) and across a gradient of upland cropping intensity and thus annually provided a representative sample of wetlands and migrants (Janke 2016).

Field collections

We used shotguns to collect females of each species on our study areas; collected females yielded three important sources of data: diet, nutrient reserves, and metabolism. While live capture methods would have yielded metabolism information, they are only logistically feasible with the use of bait (e.g., Dieter et al. 2009), which would constrain and bias dietary and physiological metrics that were the focus of this study. We collected all birds with nontoxic shot (Environ-Metal, Inc., Sweet Home, Oregon) from shore or small boats and without the aid of decoys to avoid potential biases (Pace and Afton 1999). We drew a 0.5–1 mL sample of whole blood via cardiac puncture immediately after collection with a 16–21 gauge heparinized needle and 3 mL heparinized syringe. We transferred whole blood from the syringe to a heparinized 1.5 mL microcentrifuge tube and stored the sample in a cooler away from direct contact with ice until centrifuging. We then slowly injected a small volume (3–5 mL) of 10% buffered formaldehyde solution into the upper gastrointestinal (GI) tract to stop postmortem digestion and placed a small rubber band around the bill to retain upper GI contents. We uniquely labeled each bird and blood sample and placed the bird in a freezer bag and stored it at -20°C until processing. We centrifuged blood samples in the field for 5–10 min and transferred plasma to a 1.5 mL microcentrifuge tube and froze it at -20°C . Plasma samples were transferred to a -80°C freezer within 1 month of collecting and stored until processing within 8 months.

To ensure that we collected across the entire region in each year, we attempted to collect approximately 10 individuals of each species on each study area, although in some instances, Lesser Scaup were not abundant enough on a site to meet this criterion.

Fig. 1. Location of study areas used to study spring-migrating Lesser Scaup (*Aythya affinis*) and Blue-winged Teal (*Spatula discors*) in eastern South Dakota during spring migration (March–May) of 2012–2015.



We began collections on a site once surface water was approximately $\geq 60\%$ ice-free to ensure that all wetlands in the region were available for foraging as part of a concurrent study. This could occasionally have precluded sampling the vanguard of the migration among Lesser Scaup because they often arrived while some larger wetlands and lakes were still ice-covered. However, we attempted to time our collections to coincide with peak migration in each year, which consistently occurred after the ice-out criterion was met. Thus, any bias associated with missing early migrants should be small and consistent among years. All collections were done ≥ 6 h after sunrise to allow individuals to forage in the study area before being collected. We targeted foraging individuals but opportunistically collected nonforaging birds if they were encountered. In all cases, we noted whether the individual was observed foraging or with foraging conspecifics. This research was conducted in compliance with the Guidelines to the Use of Wild Birds in Research and approved by the Institutional Animal Care and Use Committee at South Dakota State University (12-013A). Collections were authorized by the US Fish and Wildlife Service under Scientific Collecting Permit MB068976 and South Dakota Department of Game, Fish and Parks under Scientific Collector's Permits No. 25.

Laboratory analyses

Necropsies

We conducted detailed necropsies on all individuals following Janke et al. (2015) and Afton and Ankeny (1991). We measured the wet mass of each thawed bird (± 1 g) and recorded the following morphometrics (± 1 mm): total length from tip of the bill to the end of the longest retrix, length of the longest retrix, wing chord length, keel length, and tarsus length. We excised one breast muscle, including the supracoracoideus and pectoralis, and one leg and thigh muscle, removed all visible fat and bones, and recorded the wet mass of the muscle tissue. We removed all visible fat deposits in the abdominal cavity, including discrete omental fat deposits and all fat associated with the heart, gizzard, and intestines, and recorded its total wet mass (hereafter abdominal

fat). We recorded the wet mass of the heart. We removed the gizzard and recorded the wet mass with all contents and then rinsed it to remove contents and recorded the wet mass. We repeated the same procedure with intestinal contents and mass to account for the mass of ingesta in the lower GI tract. Finally, we rinsed and froze contents of the esophagus and proventriculus to evaluate diets.

We attempted to time collections to coincide with peak migration but we may have incidentally collected individuals that had transitioned into breeding because our study areas were in the breeding range of both species. Our strategy to gauge migration progression and commence collections immediately after ice melt ensured that most collections occurred before transition into breeding, particularly after the pilot year in 2012. During 2012, however, we attempted to collect more individuals on each site and continued collections into the early breeding season, particularly for Blue-winged Teal (Janke et al. 2015). We collected ducks over 45 days in 2012 whereas we never exceeded 33 days for Lesser Scaup or 26 days for Blue-winged Teal in the other 3 years. Therefore, to maintain consistency among years, we excluded all birds collected after 30 April in 2012 to avoid including birds that were transitioning into breeding status (see Janke et al. 2015) and to focus inferences on peak migration timing in that year. We further restricted our analyses to migrants by excluding individuals that had commenced rapid follicle growth, which we defined among Blue-winged Teal as having mean size of the three largest ovarian follicles > 5 mm (Janke et al. 2015). No evidence of rapid follicle growth was noted among Lesser Scaup during necropsies.

Proximate analysis

We used proximate analysis to quantitatively determine whole-body lipids for a systematic subsample of individuals of each species to build a predictive relationship between abdominal fat and whole-body lipids (Devink et al. 2008). We used a systematic random sample to select 15 individuals of each species across the range of abdominal fat measurements recorded in the necropsy and included the individual with the largest and smallest abdom-

inal fat measurements (total $n = 17$ individuals/species). We homogenized ingesta-free individuals with all organs, fat, and feathers in a Hobart industrial meat grinder (model 4146; Hobart Corporation, Troy, Ohio) and further homogenized the wet sample with a food processor (model QB900; SharkNinja Operating LLC, Newton, Massachusetts). We then took an approximately 100 g subsample of the wet homogenate and dried it to a constant mass at 80 °C for 24–36 h. We reweighed the dried sample to calculate sample dry mass and further homogenized the sample with a high-speed rotor mill (Retsch Ultra Centrifugal Mill ZM 200; Retsch GmbH, Haan, Germany) so it could pass through a 2 mm sieve. We submitted an approximately 10 g subsample of the homogenate to SGS Laboratories in Brookings, South Dakota, to perform petroleum ether lipid extraction in a modified Soxhlet apparatus. We determined the mass of lipids in the sample by multiplying the proportion of lipids in the subsample by the sample dry mass (Afton and Ankney 1991).

We used simple linear regression to predict total somatic lipids (grams) in the sample from the mass of abdominal fat (grams) recorded during necropsy. We square-root transformed abdominal fat to improve model fit (Devink et al. 2008) and evaluated if ingesta-free mass (mass of ingesta from gizzard and intestines subtracted from wet mass) improved model fit. We excluded one sample with the highest abdominal fat mass among the Blue-winged Teal because it was a substantial outlier. The final model predicted this individual to have 57.8 g of lipids, but the laboratory procedures determined it to have 17.8 g. We had noted the presence of irregular structures of abdominal fat during the necropsy of this bird and therefore feel that this exclusion was justified. Ingesta-free mass improved model fit for Blue-winged Teal ($P = 0.003$), but not for Lesser Scaup ($P = 0.712$), so we included it in the former model but not in the latter. The final equations to predict somatic lipid reserves of each species are

$$\text{Blue-winged Teal somatic lipids (g)} = -55.89 + 15.04 \times \sqrt{\text{ABF}} + 0.17 \times \text{IFM}$$

$$\text{Lesser Scaup somatic lipids (g)} = -27.24 + 35.98 \times \sqrt{\text{ABF}}$$

where ABF is abdominal fat in grams and IFM is ingesta-free mass in grams. Both equations had strong model fit (Blue-winged Teal adjusted $r^2 = 0.955$, Lesser Scaup adjusted $r^2 = 0.931$) and were used to predict somatic lipids for the remaining individuals in our sample.

Diet processing

We thawed diets and sorted and identified food items into the following categories: we identified invertebrates into families, except we identified Amphipoda to genus and non-Amphipoda crustaceans to order (i.e., Copepoda, Ostracoda, or Cladocera) and fish to species and distinguished between agricultural (i.e., corn) and nonagricultural (natural) seeds. We dried contents in each category to a constant mass in a 60 °C oven and recorded dry mass (± 0.0001 g).

Metabolite assays

We measured concentrations of key lipid metabolites in the plasma to index the recent trajectory of lipid reserves of each individual. Metabolites respond relatively quickly (i.e., hours to 1 day) to changes in metabolic states of individuals (Jenni-Eiermann and Jenni 1998; Guglielmo et al. 2005) and therefore allowed us to evaluate if, on average, birds migrating through the study area in each year were accumulating or catabolizing lipids at different rates. We focused on two key lipid metabolites, triglycerides and β -hydroxybutyrate, which each reflect contrasting trajectories of either lipid accumulation (triglycerides) or catabolism (β -hydroxybutyrate). We measured concentrations in plasma samples in a micro-

plate spectrophotometer using commercially available reagents and standards typical in other lipid metabolite studies (e.g., Guglielmo et al. 2005; Anteau and Afton 2008c; Janke 2016).

Statistical analyses

Weather and spring chronology

We calculated a seasonal climate index for each study year to describe the progression of spring temperatures relative to observations over the preceding 30 years. The climate index was the cumulative mean daily temperature for all days during 1 March through 20 May each year. This index served as a proxy for the progression of spring thaw, which has been shown to influence timing and migration ecology of Lesser Scaup (Austin et al. 2002; Finger et al. 2016), other waterfowl (Murphy-Klassen et al. 2005), and other migratory birds (Marra et al. 2005; Swanson and Palmer 2009). We calculated the index for each year during 1985 through 2015 by extracting daily temperatures at our 30 study areas from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) daily mean temperature raster data sets available for the continental United States (PRISM Climate Group, Oregon State University). The sites at which we extracted temperature values were evenly distributed throughout the study area, and therefore, their average provided a suitable approximation of temperatures observed across the region in each year (Fig. 1). We also evaluated daily temperatures during collection dates from our study to describe the environmental conditions during our field work. We compared mean temperatures over the span of collection dates in each year with an analysis of variance (ANOVA). This test allowed us to ask if observed variation in diets or physiology among years was most likely associated with variation in temperatures directly experienced during the collection periods or associated with the trajectory of spring warming. Significant interannual variation in temperatures during collection windows would suggest that any physiological or dietary differences could be associated with direct experience with temperatures during collections (e.g., colder temperatures associated with physiological changes: Swanson and Thomas 2007) whereas no evidence for interannual variation in temperatures during collections would suggest that any observed physiological or dietary variation was associated with the progression of spring conditions.

Physiological condition

We tested for differences in somatic lipid and protein reserves among the 4 years for each species. We used predicted total somatic lipid mass from the proximate analysis equations to test differences in lipid reserves. We calculated an index of protein reserves by summing two times wet mass of breast and leg muscles and wet mass of the heart. Muscle mass and heart mass were correlated in both species (Lesser Scaup $r = 0.73$, Blue-winged Teal $r = 0.43$). Breast and leg muscles represent important protein pools in waterfowl (Alisauskas et al. 1990; Janke et al. 2015) and heart mass is indicative of improved overall physiological condition in migrants (Driedzic et al. 1993). We calculated an index of body size by using the first axis from a principal components analysis that combined four correlated morphometrics: body length (total length minus rectrix length), wing length, keel length, and tarsus length (Afton and Ankney 1991). The first principal component for Lesser Scaup loaded all terms from 0.18 to 0.69 and explained 34.4% of the variation in the four morphometrics. The first principle component for Blue-winged Teal loaded all terms from 0.47 to 0.54 and explained 41.6% of the variation in the four morphometrics. We then used analysis of covariance (ANCOVA) with this covariate to test for annual differences in nutrient reserves of each species, controlling for structural size variation among individuals (Afton and Ankney 1991). The principal components analysis axis was significant ($P < 0.001$) in all analyses except for the Lesser Scaup fat analysis ($P = 0.050$) but was left in the analysis for consistency.

We used the linear regression model that predicted mass change from concentrations of triglycerides and β -hydroxybutyrate from the capture–recapture study done by Anteau and Afton (2008c) as a composite refueling index for each individual. This refueling index approach allowed us to combine information contained each metabolite concentration into a single metric that accounts for latent correlation structure between the two metabolites and expresses values in an index of lipid refueling performance (Janke 2016). Higher values of the index indicated relatively improved lipid accumulation (Anteau and Afton 2008c). Higher mean values in years would thus indicate that birds collected in that year were, on average, accumulating more lipids than birds in years with lower mean scores. We used ANOVA to test for variation in mean refueling indices among years for each species. Before compositing the indices, we conducted exploratory analyses on the individual metabolite concentration to ensure that there was no bias associated with collection timing within the day, latitude of collection, or pair or foraging status of the individual noted at the time of collection. We did not find any biases in these metrics, so we continued with raw metabolite concentrations, excluding highly hemolyzed samples (plasma hemoglobin concentration >1 g/dL; Janke 2016).

We tested for potential biases of only sampling on publicly owned lands in the first year of the study (2012) by testing for additive impacts of land ownership (public versus private) with each individual response variable described above in the three subsequent years of the study when we collected on private and public lands. The land ownership term was insignificant in all models ($P \geq 0.208$), so we assumed that there was no bias among study years and reported results from models without the land ownership term.

Finally, we were interested in direct comparisons of physiological condition among years between the two species to compare potentially contrasting nutrient strategies or physiological impairments among years. To facilitate direct comparisons between the two species, we calculated the ratio of lipids to ingesta-free body mass in each year and tested for differences between species and years with an ANCOVA. This ANCOVA used principal component 1 as a covariate, which was interacted with species to mimic the species-specific models used above. Significant species-specific effects in the ratio would indicate that the two species contrasted in the ratio of lipid reserves to whole-body mass among years, perhaps indicating different responses to interannual variation in migration conditions.

Diets

We excluded all diet samples with <2 mg (dry mass) of food in the upper GI and considered those samples empty to avoid averaging aggregate percentages across small samples. We conducted three statistical tests on diet data for each year. First, we used a χ^2 test to evaluate if there was a difference in the number of individuals collected in each year that had <2 mg of food in their upper GI as an index of feeding success or frequency for each species among years (Anteau and Afton 2008a). Second, we used ANOVA to test for differences among years in the proportion of the diet samples composed of animal material (fish and invertebrates) to evaluate annual variation in the relative contribution of animal- or plant-based foods (seeds and vegetation) to diets of each species. Finally, we used multivariate analysis of variance (MANOVA) to test for annual variation in the composition of key taxonomic groups of food items in the diets. We categorized food items into seven categories based on previous research that demonstrated the relative importance of key food items for Lesser Scaup and Blue-winged Teal (e.g., Dirschl 1969; Swanson et al. 1974; Anteau and Afton 2008a; Hitchcock 2009; Tidwell et al. 2013). We focused on three specific categories of invertebrates that both species consume in the Northern Plains or during migration, Amphipoda, Chironomidae, and Mollusca (including Sphaeriidae and gastro-

ods), and grouped remaining invertebrate taxa into another invertebrates category. We examined seed consumption separately from other vegetation (algae, tubers, leaves, etc.) to evaluate relative seed consumption among years, which is variable between both species (e.g., Hitchcock 2009). We used MANOVA to test for annual variation in the proportion of diets comprising the four main diet items in our analysis: Amphipoda, Chironomidae, Mollusca, and seeds. In excluding other invertebrates, vegetation, and fish, we focused our evaluation on the key diet items in the study and also reduced dependency among the proportions in the analysis. We used a randomization procedure to guard against violations of the multivariate normality assumption of MANOVA by randomly reordering the year factor in the data frame and calculating Wilks' Λ for 10 000 simulations (Chippis and Garvey 2007). We then compared our test statistic with the distribution of the randomization procedure test statistics to evaluate whether it was in the 5th percentile or lower, indicating significance at $\alpha = 0.05$. We used a Tukey honestly significant difference test to make post hoc multiple comparisons of all ANCOVAs and ANOVAs and assessed significance at $\alpha = 0.05$.

Results

Long-term average cumulative mean temperature on 20 May was 5.5 °C (95% CI = 4.8 – 6.2 °C) over the 30 year time series. Cumulative mean temperatures on 20 May during our study ranged from 1.4 to 10.1 °C and included the coldest (2013) and warmest (2012) seasons in the 30 year time series (Fig. 2; Table 1). The other 2 years in the study fell near the 25th (2014) and 75th (2015) percentiles of the cumulative mean temperature observations in the last 30 years (Fig. 2). Thus, the 4 years of our study spanned the range of spring temperatures observed in the study area over the preceding 30 years.

We included 232 Lesser Scaup and 322 Blue-winged Teal in the nutrient reserve analyses (Table 1). Collection dates among years varied in association with the climate index: for example, 75% of the Lesser Scaup collected during the two warmest years (2012 and 2015) were collected before all but one individual in the coldest spring (2013) was collected (Table 1). Although there was substantial interannual variation in cumulative mean temperatures during the study (Fig. 2; Table 1), temperatures during collections did not differ significantly for Blue-winged Teal ($F_{[3,90]} = 0.515$, $P = 0.673$) or Lesser Scaup ($F_{[3,108]} = 1.091$, $P = 0.356$) (Fig. 3), suggesting that any observed physiological or dietary variation was likely attributable to seasonal variation rather than to temperatures directly experienced by birds at the time of collections.

Mean whole-body mass of Lesser Scaup was 700.8 g (SD = 74.3), varied annually ($P < 0.001$), and was positively correlated with lipid mass ($r = 0.647$) and the protein index ($r = 0.792$). Mean whole-body mass of Blue-winged Teal was 344.5 g (SD = 34.5), varied annually ($P = 0.004$), and was positively correlated with lipid mass ($r = 0.824$) and the protein index ($r = 0.872$). The index of protein reserves of Lesser Scaup varied significantly among years ($F_{[3,227]} = 11.692$, $P < 0.001$) (Fig. 4) and a multiple comparisons test revealed that the mean protein reserve index was lower in 2013 but not different among other years (Fig. 4). Blue-winged Teal protein masses followed the same results, illustrating significant interannual variation ($F_{[3,317]} = 9.306$, $P < 0.001$) (Fig. 4), with the only paired significant differences being a lower mean during 2013 (Fig. 4). There was significant interannual variation in lipid masses of Lesser Scaup among years ($F_{[3,227]} = 11.3195$, $P < 0.001$) and the multiple comparisons test revealed variable differences among years (Fig. 4). The ANCOVA indicated significant annual variation in lipid masses of Blue-winged Teal ($F_{[3,317]} = 3.226$, $P = 0.0228$), but the multiple comparisons test revealed no significant differences among paired years (Fig. 4).

We included 181 Lesser Scaup in the metabolite assays after excluding highly hemolyzed samples (range = 28 – 75 samples in-

Fig. 2. Cumulative spring temperatures in eastern South Dakota over 4 years (2012–2015, lines) during which we collected spring migrating female Lesser Scaup (*Aythya affinis*) and Blue-winged Teal (*Spatula discors*). Cumulative spring temperatures were a rolling average of all daily mean temperatures recorded from the observation date to 1 March in that year. Long-term interquartile range (IQR) (dark shaded region) and long-term mean (light shaded region) were based on daily observations of the cumulative spring temperatures recorded over 30 years.

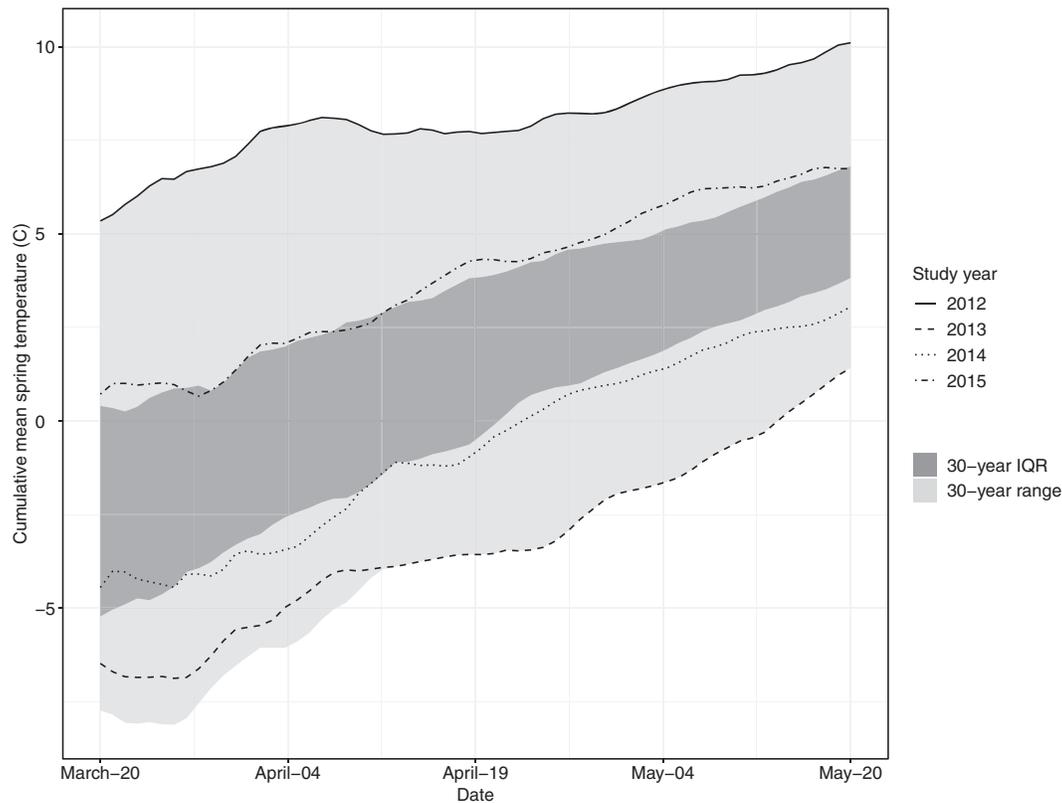


Table 1. Mean state-wide average temperature, sample size, and collection dates of female Lesser Scaup (*Aythya affinis*) and Blue-winged Teal (*Spatula discors*) collected during spring migration in eastern South Dakota during March–May of 2012–2015.

Year	Mean temperature (°C) ^a	n	Collection dates			
			First	25th percentile	75th percentile	Last
Lesser Scaup						
2012	10.1	61	5 April	12 April	22 April	29 April
2013	1.4	38	23 April ^b	24 April	8 May	16 May
2014	3.0	88	11 April	23 April	29 April	13 May
2015	6.7	45	23 March	3 April	15 April	21 April
Blue-winged Teal						
2012	10.1	60	1 April	9 April	24 April	30 April
2013	1.4	102	29 April	3 May	13 May	16 May
2014	3.0	101	21 April	24 April	5 May	12 May
2015	6.7	59	7 April	15 April	22 April	30 April

^aMean daily temperature from 1 March to 20 May.

^bOne individual was collected on 8 April prior to the onset of a severe storm that refroze wetlands and delayed additional collections and migration until 23 April.

cluded annually). There was no significant variation in the refueling index among years for Lesser Scaup ($F_{[3,176]} = 1.763$, $P = 0.156$) (Fig. 4). We included 285 Blue-winged Teal samples in the metabolites analysis (range = 48–94 samples/year). There was significant annual variation in the refueling index ($F_{[3,227]} = 11.463$, $P < 0.001$), and the multiple comparisons test revealed variable differences among years (Fig. 4).

Analysis of the ratio of lipids to ingesta-free body mass revealed significant differences among years ($F_{[3,544]} = 6.347$, $P < 0.001$), species ($F_{[1,544]} = 152.331$, $P < 0.001$), and their interaction ($F_{[3,544]} = 10.497$, $P < 0.001$). The multiple comparisons procedure revealed that Lesser Scaup had significantly greater ratios than Blue-winged Teal during 2012, 2014, and 2015 (mean difference \pm SE = 5.2 ± 0.7 , 4.7 ± 0.5 , and 4.4 ± 0.7 , respectively; $P < 0.001$) but did not significantly differ during 2013 (0.3 ± 0.8 , $P = 0.684$) (Fig. 5).

We recovered usable diet samples from 228 Lesser Scaup, of which 29 (12.7%) had < 2 mg of food. There was no annual variation in the proportion of diet samples containing ≥ 2 mg of food ($\chi^2 = 5.352$, $P = 0.148$) and there was also no annual variation in the proportion of the diet comprising animal material ($F_{[3,195]} = 1.057$, $P = 0.368$) (Fig. 6). There was evidence for significant annual variation in the composition of diets (Wilks' $\Lambda = 0.8954$, 4.6th percentile of simulations, $P = 0.045$) (Fig. 7). Post hoc ANOVA of individual diet items included in the MANOVA indicated that only Mollusca varied significantly among years ($P = 0.013$). We recovered usable diet samples from 314 Blue-winged Teal and found that 95 individuals (30.2%) had < 2 mg of food. There was no annual variation in the proportion of diet samples containing ≥ 2 mg of food ($\chi^2 = 0.625$, $P = 0.8907$); however, there was significant variation in the proportion of the diet comprising animal material among years ($F_{[3,215]} = 13.232$, $P < 0.001$) (Fig. 6). There was also significant inter-annual variation in the composition of Blue-winged Teal diets (Wilks' $\Lambda = 0.754$, < 1 st percentile of simulations, $P < 0.001$) (Fig. 6). The post hoc ANOVA indicated that Chironomidae ($P < 0.001$) and seeds ($P < 0.001$) varied significantly among years.

Discussion

We observed notable interannual variation in the physiology and diets of two sympatric wetland-obligate foraging ducks during

Fig. 3. Boxplot of the range of daily temperature values observed in eastern South Dakota across the range of collection dates for spring-migrating Lesser Scaup (*Aythya affinis*) and Blue-winged Teal (*Spatula discors*) during March–May of 2012–2015. The relative constancy of the boxplots for each species illustrates that although spring temperatures leading up to collection periods for each species were highly variable, temperatures during peak migration were similar among years.

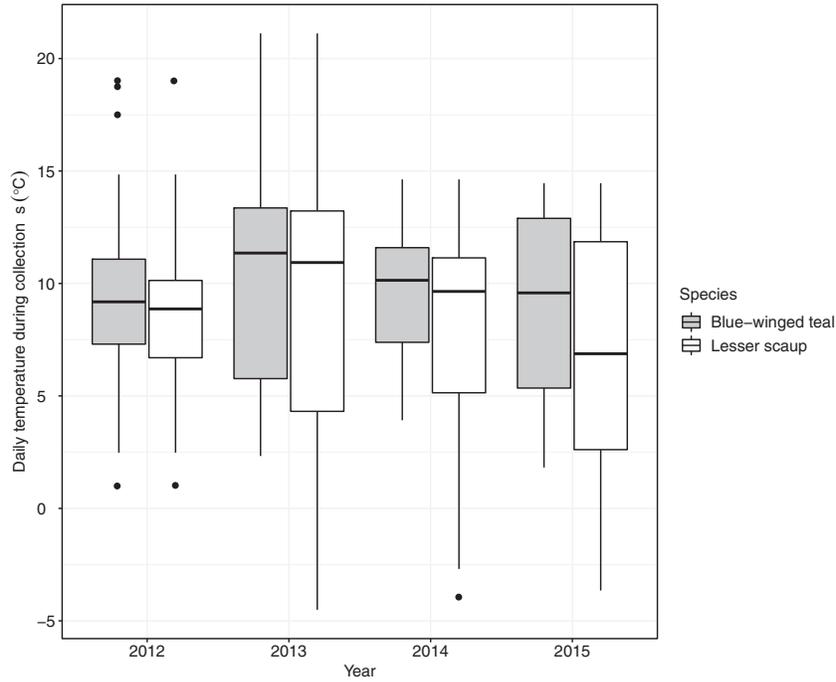


Fig. 4. Annual variation in key physiological metrics measured in migrating female Lesser Scaup (*Aythya affinis*) and Blue-winged Teal (*Spatula discors*) collected throughout eastern South Dakota during spring migration (March–May) of 2012–2015. Unique letters on figures indicate significant differences among years within the species based on a Tukey–Kramer post hoc multiple comparisons test ($\alpha = 0.05$). Means for protein and lipid mass are least-squared means after controlling for variation in body size.

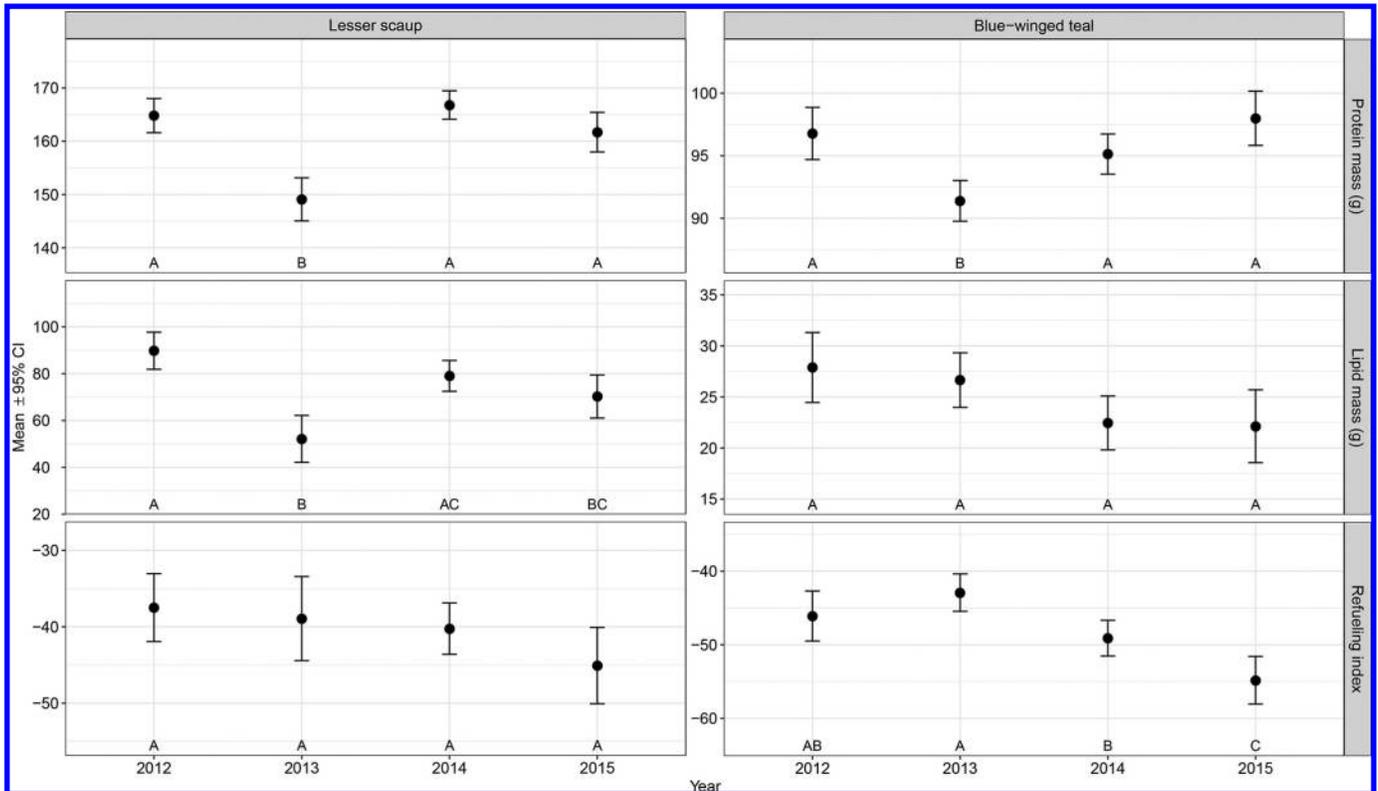


Fig. 5. Annual variation in the ratio of lipid mass to ingesta-free body mass of migrating female Lesser Scaup (*Aythya affinis*) and Blue-winged Teal (*Spatula discors*) collected throughout eastern South Dakota during spring migration (March–May) of 2012–2015. Asterisks indicate significant species differences within each year based on a Tukey–Kramer post hoc multiple comparisons test ($\alpha = 0.05$).

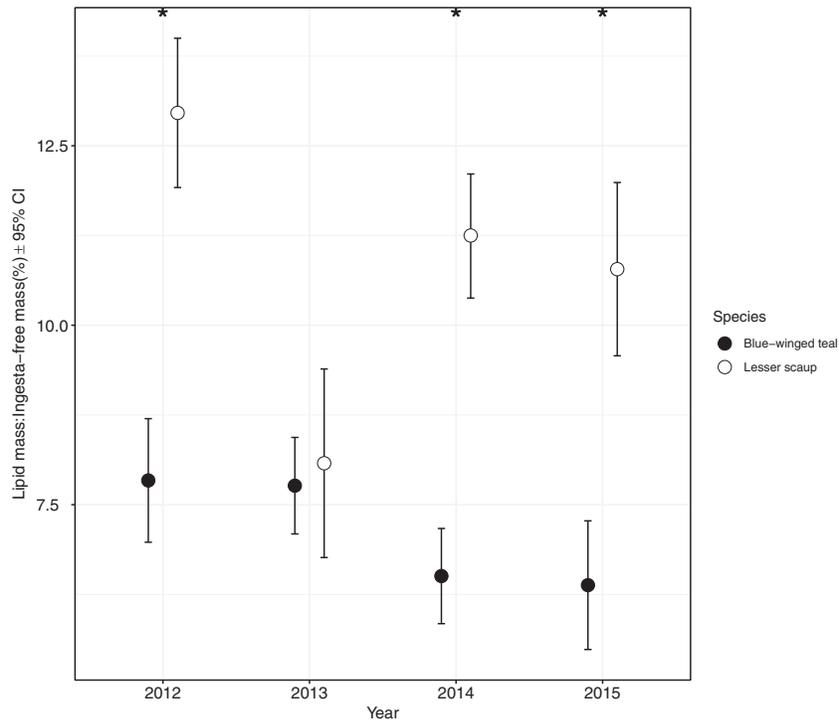
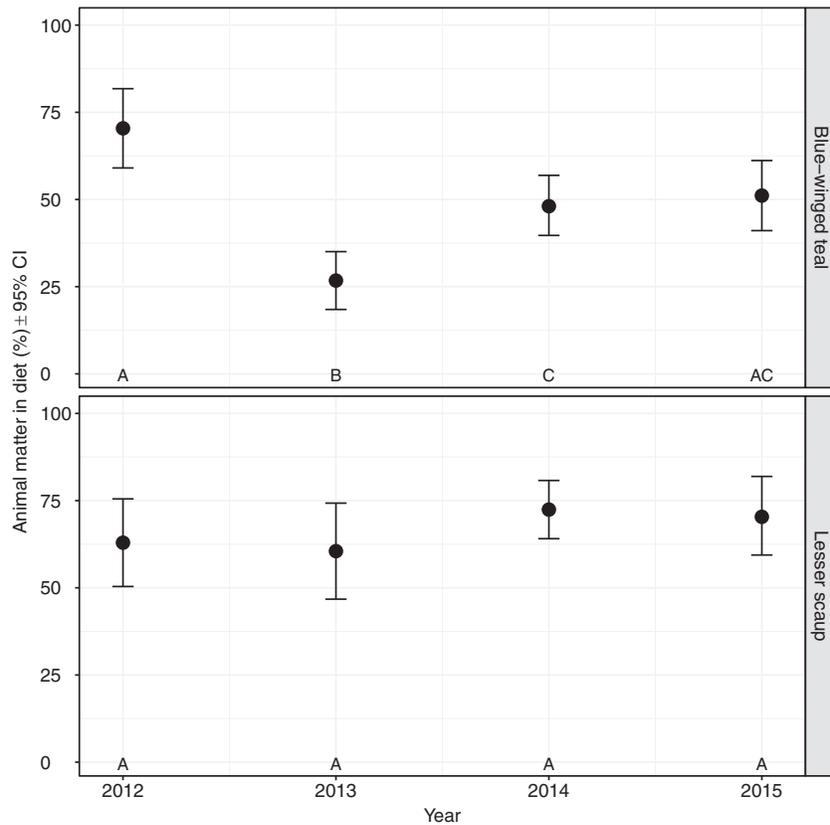
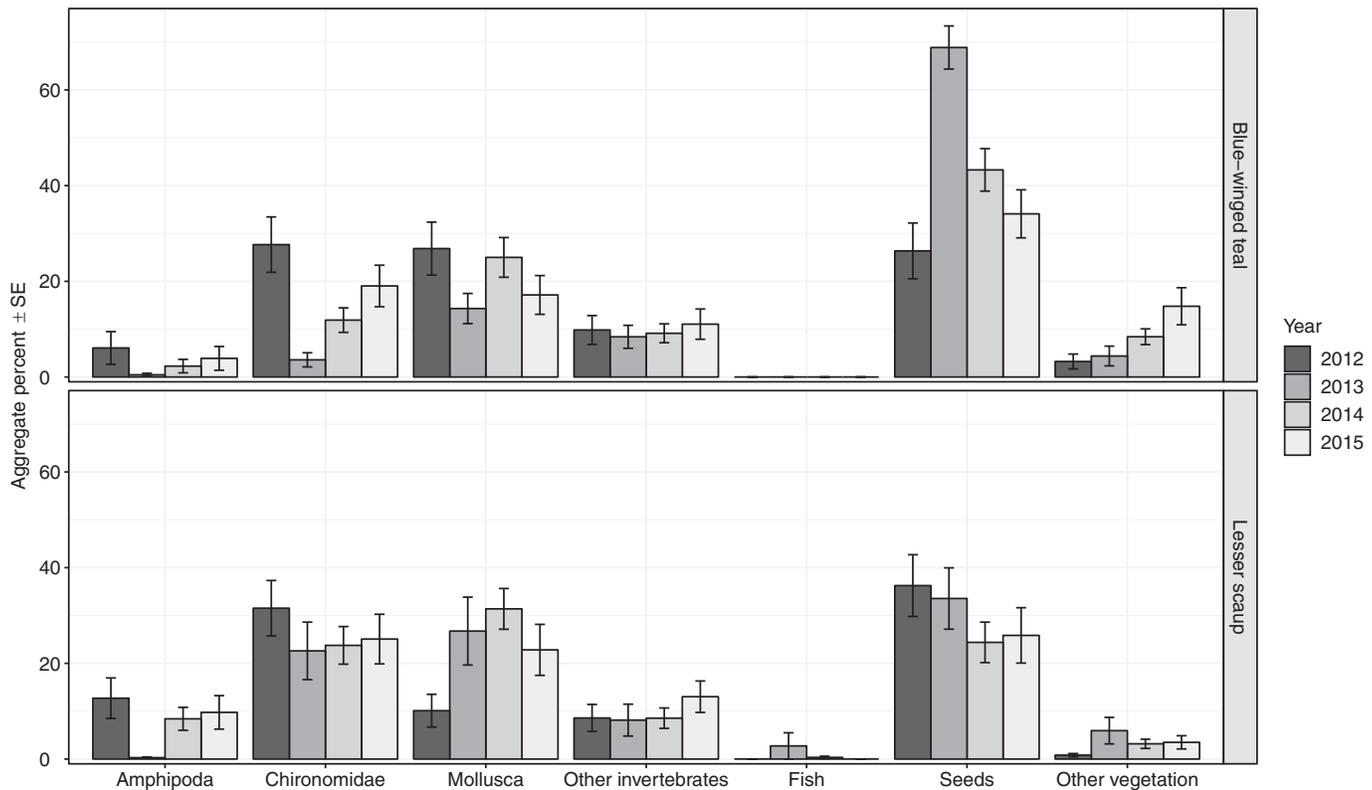


Fig. 6. Annual variation in the proportion of food material in the upper gastrointestinal tract that was animal matter in migrating female Lesser Scaup (*Aythya affinis*) and Blue-winged Teal (*Spatula discors*) collected throughout eastern South Dakota during spring migration (March–May) of 2012–2015. Unique letters on figures indicate significant differences among years within the species based on a Tukey–Kramer post hoc multiple comparisons test ($\alpha = 0.05$).



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Fig. 7. Annual variation in the aggregate percentages of different food items in the upper gastrointestinal tract of migrating female Lesser Scaup (*Aythya affinis*) and Blue-winged Teal (*Spatula discors*) collected throughout eastern South Dakota during spring migration (March–May) of 2012–2015.



four sequential and highly variable spring migration periods. The similar temperatures that we observed during collections in each year, despite the month-wide span of collection dates among years, suggest that variation in physiology and diet was related to factors other than the direct effect of ambient temperature experienced by ducks at the time of collections. Rather, it appeared that variation in diets and key physiological metrics of these migrants changed in association with weather variability that annually influenced timing of migration or the phenology of wetland foraging habitats. Such interannual variation has implications for understanding factors affecting successful migration and corresponding carryover effects related to climatic variability or extremes encountered during migration (Sedinger and Alisauskas 2014; Bailey and van de Pol 2016).

The warm spring of 2012 and cold spring of 2013 provided a contrast and allowed for comparison of environmental extremes during spring migration. Among the metrics that demonstrated annual variation, 2012 and 2013 always differed. In contrast, patterns across the more moderate years of 2014 and 2015 were less discernable, which is consistent with previous research on spring migrant physiology that reported similarly low interannual variation (Strand 2005; Anteau and Afton 2009; Tidwell 2010). The tendency for low interannual variation in migrant physiology during moderate years may be due to confounding factors that combine to influence migrant condition. To this end, many studies have reported variable nutrient reserves within and among wintering areas (e.g., Baldassarre et al. 1986; Miller 1986; Whyte et al. 1986; Thompson and Baldassarre 1990; Lovvorn 1994) and some studies have linked condition of birds on wintering areas to population parameters measured on breeding areas in subsequent seasons, suggesting that intervening migration conditions were on average inconsequential in those studies (Heitmeyer and Fredrickson 1981; Raveling and Heitmeyer 1989; Tamisier et al.

1995; Guillemain et al. 2008). Therefore, observed variation in our study in concordance with climatic conditions encountered during migration arguably portends a range of responses among spring-migrating Lesser Scaup and Blue-winged Teal to annual climatic variation that would be otherwise difficult to detect in moderate years and among migrants mixing from distant and diverse wintering areas.

Mean lipid mass of Lesser Scaup during the cold spring (2013: 52.2 g, SE = 5.1 g) was markedly lower than in the other 3 years (mean range = 70.2–89.8 g) and was almost unprecedented in the literature, particularly among migration studies. Only one lipid reserve estimate, among >30 estimates that we found in the literature for Lesser Scaup, was lower than our mean value from 2013: that study (Austin and Fredrickson 1987) was conducted on post-breeding Lesser Scaup undergoing remigial molt in late summer. Gammonley and Heitmeyer (1990) reported a comparably low (53 g) mean lipid mass for females collected during spring migration in California but their sample size was small ($n = 5$) and variable (SE = 27 g). DeVink et al. (2008) reported that lipid masses among females arriving in Boreal breeding habitats at the end of spring migration averaged 61.7 g (SE = 2.8). Anteau and Afton (2009) collected migrating female Lesser Scaup throughout the upper Midwest over 3 years and never reported a least-squared mean lipid mass <70 g. Fewer studies reported lipid masses of Blue-winged Teal, but our values (mean range = 22.1–27.9 g) were functionally identical to those reported recently for migrants in Nebraska (26 g; Tidwell 2010). Therefore, lipid reserves of Blue-winged Teal appeared to be typical for migrants among all 4 years of our study whereas Lesser Scaup lipid reserves appeared to be sensitive to annual variation in climatic conditions and notably low during the coldest and latest spring.

Patterns apparent in protein reserves, a relatively static indicator of condition, and in the more sensitive metrics of refueling

and foraging behavior, the lipid metabolite refueling index and upper GI tract contents, help to paint a clearer picture of the physiological conditions and strategies that these species employed as they encountered variable environmental conditions during our study. Among Blue-winged Teal, we noted a decline in protein reserves during the coldest spring (2013) coincident with maintenance of similar lipid reserves in that year. The consequence of reduced protein reserves for migrating birds is likely minimal because protein does not constitute an important fuel source (Jenni and Jenni-Eiermann 1998) and can be easily recouped by Blue-winged Teal on their breeding grounds with invertebrate-rich diets (Ankney et al. 1991). Further, during the same period, Blue-winged Teal appeared to increase intake of energy-rich foods (seeds) and had the highest refueling index score, suggesting an increased emphasis in that year on lipid intake. Such a diet shift could explain the maintenance of lipids in that year and the concomitant decline in protein because high intake of invertebrate-rich diets has been associated with increases in protein masses in ducks (Alisauskas et al. 1990; Barzen and Serie 1990; Alisauskas and Ankney 1994). This adaptive dietary intake to focus on maintaining the same relative reserve of lipids seems consistent with an “income migrant” strategy (sensu Arzel et al. 2007) where migrants adjust foraging to meet demands encountered en route rather than relying on stores built up at previous stopovers or wintering areas.

Lesser Scaup followed a pattern similar to that of Blue-winged Teal with protein reserves, but all other metrics notably contrasted between the two species. During the cold, late year (2013), lipid reserves of Lesser Scaup were lowest, but they seemed to maintain the same lipid accumulation or catabolism pattern as in previous years (based on the refueling index) while shifting dietary intake away from energy-rich foods, like Amphipoda (12.7% in 2012 and 0.3% in 2013; Jorde and Owen 1988; Sherfy 1999), towards energy-deficient foods like mollusks (10.1% in 2012, 26.7% in 2013; Jorde and Owen 1988; Sherfy 1999; Ballard et al. 2004). The significance of this energy-deficient diet when lipid reserves were low is unclear. One hypothesis could be that increased protein intake was related to repair of muscle damage sustained during flight or starvation related to unexpected extreme weather (Suter and Van Eerden 1992; Guglielmo et al. 2001). Another, arguably more plausible, hypothesis is that dietary shifts without concomitant increases in refueling performance suggest that lipid-rich prey were unavailable in sufficient quantities. This interpretation would be consistent with a large body of work that suggested foraging conditions for Lesser Scaup have become degraded in a way that inhibits lipid accumulation or maintenance during migration (Anteau and Afton 2008a, 2008b, 2009, 2011). Consistently impaired foraging conditions encountered during migration would be consistent with the static refueling index that we observed in each year. However, this explanation fails to explain the shift away from relative energy-rich prey items during the cold, late year.

The ratios of lipid mass to ingesta-free mass were the most straightforward quantitative way to compare the physiology of the two sympatric species. Results from that analysis revealed a similar pattern in the average and warm years, with Lesser Scaup females consistently carrying more relative mass of lipids than the smaller-bodied Blue-winged Teal. However, in the coldest year, Blue-winged Teal appeared to maintain a similar ratio, while Lesser Scaup regressed to a relative mass statistically similar to that of Blue-winged Teal. This result, combined with other metrics, lends further support to the conclusion that Lesser Scaup were burdened with increased energetic demands that they were not able to overcome by the time the late migration progressed in our study area in 2013. These results suggest that Lesser Scaup may conform more to a “capital migrant” strategy (sensu Arzel et al. 2007), relying more on carrying a larger balance of lipid reserves acquired during winter (Anteau and Afton 2004; Herring

and Collazo 2006) and opportunistically during migration (Esler et al. 2001; Anteau and Afton 2009) but less prone to recovering from losses associated with energetically demanding environmental or migration conditions. It is also plausible that forgoing lipid accumulation altogether was a strategy in and of itself among migrating Lesser Scaup during the coldest and latest year to try to minimize possible trade-offs with wing loading or navigation associated with high lipid burdens (Lima 1986), although migrants would still have to meet minimum lipid balances necessary to complete migration and breeding, which tend to limit clutch size and reproduction in Lesser Scaup (Afton and Ankney 1991) and other ducks (Ankney et al. 1991).

Differences in the timing and tempo of migration between the two species could also help interpret patterns of nutrient reserve variation. Species that time migration to arrive later in the season have less interannual variation in arrival dates (Murphy-Klassen et al. 2005), likely because they have less exposure to environmental stochasticity during transition from winter to spring. Blue-winged Teal are generally the last duck to commence spring migration (Baldassarre 2014) and therefore have a strategy that makes it less likely that they will have to overcome energetic burdens associated with late-winter conditions. In contrast, Lesser Scaup arrive at midlatitude stopovers earlier and therefore experience greater risk of exposure to environmental stochasticity. Field observations during the coldest spring (2013) supported this pattern; we observed substantial numbers of migrating scaup prior to the onset of a cold-weather system during mid-April whereas we did not observe any Blue-winged Teal until after the system had entirely subsided in late April and early May. Further, the metabolite index did not suggest that Lesser Scaup were actively catabolizing fat more during the year in which they had the lowest lipid reserves, suggesting that deficits in lipid reserves relative to other years occurred, at a minimum, days prior to collections during migration in our study area. Plausible explanations for reduced lipid reserves among Lesser Scaup exposed to environmental stochasticity in the late, cold season could include unanticipated energetic demands (e.g., increased costs of thermogenesis associated with cold temperatures: Suter and Van Eerden 1992; Lovvorn 1994), decreased food availability because of ice cover (Lovvorn 1989), or potential energetic costs of reverse migration (Richardson 1978) related to the onset of that unexpected winter storm at the start of their typical migration period through the study area.

Regardless of the mechanisms driving annual variation in nutrient dynamics of migrating ducks, our work demonstrates the potential impacts of environmental stochasticity on nutrient budgets and energy expenditure immediately preceding the breeding period. In addition to those energetic burdens, migrants in late years are additionally constrained for reproduction because of time schedules for arriving, initiating clutch formation, and raising young to fledge at northern latitudes (Gurney et al. 2011). Thus, late-winter conditions during traditional migration time periods may lead to delays in arrival for both species. In Lesser Scaup specifically, adverse winter conditions may result in energetic burdens that are difficult for females to overcome, especially if stopover conditions are not conducive to lipid accrual, as appeared to be the case in our study area and elsewhere (Anteau and Afton 2009). Such burdens could lead to recruitment failures in years with strong environmental stochasticity during migration (Briedis et al. 2017). Collectively, our results raise a number of important questions for understanding how migrants are influenced by environmental heterogeneity encountered during migration, which could have important implications for conservation and management of migrants, as environmental heterogeneity is predicted to increase throughout the 21st century.

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