RESEARCH ARTICLE

WILDLIFE
SOCIETY BULLETIN
Open Access

True metabolizable energy of foods consumed by lesser scaup (*Aythya affinis*)

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Funding information
Illinois Department of Natural Resources, Grant/Award Number: W-200-R-1

Abstract

The energy derived from available foods is an important factor used in conservation planning for migratory species. Estimating true metabolizable energy (TME) of available foods has become a common method for resource managers to increase reliability in energetic carrying-capacity estimates. Lesser scaup (*Aythya affinis*; hereafter scaup), have experienced a population decline concurrent with suspected decreases in foraging habitat quality and quantity at spring stopover sites in the upper Midwest, USA. Unfortunately, few TME estimates are available for common diet items of scaup. We estimated nitrogen-adjusted TME (TME_N) of 5 common foods of scaup by conducting feeding trials on wild females and males. True metabolizable energy varied by food taxa, but not by pretrial body mass or sex. Mean TME_N (kcal/g[dry] ± SE) was greatest for wild millet (*Echinochloa crus-galli*; 2.20 ± 0.14), followed by chironomids (*Chironomus* spp.; 1.41 ± 0.49), amphipods (*Gammarus spp.*; 1.33 ± 0.23), planorbid snails (Planorbidae; 0.17 ± 0.07), and fingernail clams (Sphaeriidae; −0.79 ± 0.27). Our results, combined with scaup diet literature indicated that the management of spring staging areas for high-energy invertebrates (i.e., chironomids and amphipods) would provide improved opportunity for energy acquisition during migration. Further study could help determine if the acclimation of scaup

to particular diets, especially bivalves, increases their TME_N values.

Resource managers require estimates of energetic quality and diet composition from focal animals to parameterize bioenergetic models that can be used to guide habitat conservation and management at landscape scales (Williams et al. 2014, Livolsi et al. 2015). Additionally, managers use estimates of energy content of food items to inform actions that encourage or discourage proliferation of certain foods on the landscape (Hagy et al. 2021, 2022). Modern waterfowl management plans use a daily ration model to estimate the amount of food needed seasonally at each location to support the target number of migratory waterfowl (Gray et al. 2013, Hagy and Kaminski 2015, Gross et al. 2020b). Bioenergetic models have been used to identify wetlands that need additional protection, set goals for enhancement, and inform restoration activities (Williams et al. 2014, Gross et al. 2020a, Hagy et al. 2022).

Each of these bioenergetic models require information about biomass of available food, daily energy requirements of birds, and the amount of bioavailable energy per gram for each food type (Sibbald 1982, Gray et al. 2013, Williams et al. 2014). A measurement of bioavailable energy is critical because not all ingested food can be metabolized and converted to available energy (Miller and Reinecke 1984, Petrie et al. 1998). Accordingly, bioenergetic models use true metabolizable energy (TME) to provide an estimate of digestible energy (Miller and Reinecke 1984, Lancaster et al. 2019). Initially developed for evaluating domestic poultry feed quality, the TME assay is less sensitive to food intake than similar metabolizable energy estimates (i.e., apparent metabolizable energy [AME]; Sibbald 1976, Miller and Reinecke 1984).

Unfortunately, TME values are specific to the forager and forage taxa, and estimates have been limited to a few waterfowl species and food types, hampering precision of bioenergetic models for migratory waterfowl (Kaminski et al. 2003, Gross et al. 2020b). Among waterfowl, energy acquisition during spring is considered an important factor influencing populations, especially wetland-obligate-foraging ducks (Stafford et al. 2014, Janke et al. 2019). Fortunately, the focus on season-specific habitat conditions has resulted in the recent evaluation of a broad range of foods used by a variety of duck species (McClain 2017, McClain et al. 2019, Gross et al. 2020b). However, TME data for foods used by diving ducks remain limited (e.g., invertebrates; Anteau and Afton 2008, Clements et al. 2020) and existing research for other duck species suggests invertebrates have less bioavailable energy than seeds (Jorde and Owen 1988, Sherfy 1999, Ballard et al. 2004, Coluccy et al. 2015). Calculating energetic carrying capacity for diving ducks based on dabbling duck TME values or a standardized value may result in considerable bias or uncertainty in bioenergetic models (Livolsi et al. 2015, Gross et al. 2020b). It is therefore important to assess TME of each appropriate food for different waterfowl species, allowing for a more precise and accurate estimation of energetic carrying capacity when assessing habitat resources for diving ducks to better inform conservation measures (Livolsi et al. 2015, Marty 2017).

Lesser scaup (*Aythya affinis*; hereafter scaup) is a diving duck species that has experienced a population decline since the mid-1980's (Afton and Anderson 2001, Anteau et al. 2014). Degradation of mid-latitude spring migration stopover sites (i.e., wetlands in the upper Midwest) may have contributed to the initial decline and resulted in an interest in ensuring adequate food resources are still available at major stopover sites (Anteau and Afton 2004, 2009; Moore et al. 2010). Although diving ducks are included in conservation plans based on bioenergetic models (Soulliere et al. 2017), little information is available on metabolizable energy of foods for diving duck species (Richman and Lovvorn 2004, Lancaster et al. 2018). Considering the conservation status of scaup, their relative abundance within the diving duck guild across North America, and importance to recreationists, energy content of their key foods is an important information need (Osborn et al. 2016).

Our objectives were to estimate TME of 5 foods common in scaup diets, evaluate digestive efficiency of each food, and examine how TME for these foods compare to results from other duck species. We hypothesized that scaup TME

values would vary among food types similar to other duck species; additionally, we hypothesized that the soft-bodied invertebrates (i.e., amphipods, chironomids) would result in the highest digestive efficiency values (Anteau and Afton 2006).

STUDY AREA

We conducted trials at the Forbes Biological Station in Havana, Illinois, in April 2019 and at the Western Illinois University Kibbe Field Station in Warsaw, Illinois in March–April of 2020 and 2021. The Forbes Biological Station is located in the Illinois River Valley, while the Kibbe Field Station is located near navigational Pools 19 and 20 of the Mississippi River. Both areas are stopover locations for scaup within the Mississippi Flyway (Havera 1999).

METHODS

Pre-experimental fasting

True metabolizable energy feeding trials include a fasting period to remove any food within the birds' digestive system, followed by precision feeding of the test food and an excreta collection period the same length as the fast (Sibbald 1986). The excreta collected from fed birds is compared to excreta collected from fasted, unfed birds to determine TME_N (nitrogen-corrected TME), with total trial length potentially having a significant effect on TME_N values (Parsons et al. 1982, Gross et al. 2020b). A fasting period that is too short will not allow all pretrial food to be voided from the digestive tract in fed birds, and caloric input will be miscalculated (Parsons et al. 1981). Conversely, a prolonged period without food may accelerate tissue catabolism in control birds and lead to overestimated energy from non-food sources (Parsons et al. 1982). The ideal fasting time likely varies by species and pre-experimental fasting trials are an important consideration as TME_N trials grow to include waterfowl of varying sizes and diets (Gross et al. 2020b). Data from ongoing research related to best waterfowl husbandry practices and experimental TME approaches support shortened fasting periods to improve animal welfare and reduce bias associated with endogenous processes (Gross et al. 2020b, Beach et al. 2024). Given that our experimental design differed from previous TME_N studies and scaup had yet to be used in TME_N trials, we conducted a pre-experimental fasting assessment following Parsons et al. (1981) on October 25, 2018.

To quantify proper fasting duration prior to the TME_N trials, we used 16 scaup that were randomly selected from a group of wild birds captured the previous spring from the Emiquon Preserve in Fulton County, Illinois, USA. All scaup were female but their size range at the beginning of the trial was representative of both sexes (552–724 g). While there may be small differences in intestinal length or retention time between sexes, results from other TME studies indicate that sex is not a significant factor in evaluating metabolizable energy (Kaminski et al. 2003, McClain 2017, Gross et al. 2020b)

Two days before the fasting trial, we removed birds from their holding pen, trimmed the feathers in a 4-cm radius around the cloaca, and fit each bird with a backpack harness designed to catch excreta (Adeola et al. 1997, Lancaster et al. 2019). Following harness attachment, birds were returned to holding pens where they retained *ad libitum* access to water and food (Purina Game Bird Maintenance Chow; Purina Animal Nutrition, LLC, Arden Hills, MN, USA; 12.5% protein, 2.5% fat, 10% fiber). We began the fasting trial at 0800 by removing birds from the holding pen and immediately attaching a Whirl-Pak® (21 cm × 10 cm) bag to the harness to collect excreta (Lancaster et al. 2019). We placed each bird in a plastic metabolic isolette container (0.33 m × 0.23 m × 0.31 m or 0.31 m × 0.28 m × 0.31 m) with access to water *ad libitum* (Lancaster et al. 2019). The isolette was designed to capture excreta in the event of a bag leak or a harness failure. During the excreta collection period, isolettes were housed together in elevated outdoor pens (1.22 m × 6.1 m × 0.91 m or 0.76 m × 1.82 m × 0.5 m) subject to ambient lighting. We removed and replaced bags every 6 hours during the 48-hr trial (Parsons et al. 1981). Whirl-Pak® contents were rinsed, foreign materials were removed (i.e., feathers, grit), and the remaining excreta sample was dried in a forced-air drying oven at 60℃ to constant mass and was weighed (± 0.1 mg). We conducted a Kruskal-Wallis test in R (v. 4.0.3, R Core Team 2020) to determine whether the variation in mass among

collection periods was greater than the variation within time periods. Following a significant Kruskal-Wallis test (α ≤ 0.05), we used Dunn's test with a Bonferroni adjustment to make pairwise comparisons of excreta mass between collection periods to determine when excreta mass plateaued (Parsons et al. 1981).

Based on results from the first 6 hours of excreta collection and excretory rate data from Richman and Lovvorn's (2004) feeding trials, we determined a 24-hr fasting period would be sufficient for scaup to void previously ingested materials while reducing the likelihood of undesirable protein catabolism and inflated excreta nitrogen values. Since the birds would be captured during the day, a 24-hour fast also eliminated the need for nighttime feedings and avoided disruption of the birds' circadian rhythm.

Trial preparation

We identified 5 food items for TME estimation that appeared frequently or in high volumes in scaup diet studies (Rogers and Korschgen 1966, Gammonley and Heitmeyer 1990, Afton et al. 1991, Anteau and Afton 2008, Clements et al. 2020): wild millet (Echinochloa crus-galli), amphipods (Gammarus spp.), planorbid snails (Planorbidae), chironomids (Chironomus spp.), and fingernail clams (Sphaeriidae). Wild millet is consumed by scaup less frequently than the other foods (Moore et al. 1998) but was chosen for a comparison with dabbling duck studies. We obtained wild millet (River Refuge Seed, Brownsville, OR, USA), frozen chironomids (LiveAquaria®, Rhinelander, WI, USA), and frozen amphipods (Lincoln Bait, Staples, MN, USA) from commercial vendors due to the difficulty of collecting and isolating sufficient wild samples during the spring trial period (Sherfy 1999). Chironomids and amphipods were frozen in water with no added nutrients. We collected planorbid snails in February 2020 from Emiquon National Wildlife Refuge in Fulton County, Illinois, USA, and fingernail clams in June 2020 from Pool 13 of the Mississippi River in Carroll County, Illinois, USA. We froze (~ −18°C) all wet food items for storage and thawed them prior to feeding. We acknowledge that food sources and preservation method could affect TME, however all wet foods were preserved similarly and we assumed the relative effects would be consistent among food items. Moreover, the limited availability and time for collection and processing following ice-out in the Midwest and the trial period of food items precluded our ability to collect fresh specimens for the trials.

We used wild scaup, caught <24 hr before trial, to obtain TME estimates. Our design ensured scaup were in similar physiological condition as wild, free-living scaup (i.e., body mass, energy reserves, and gastrointestinal tracts were adapted to foods found along the migration corridor; Miller 1975, Kehoe and Ankney 1985, Beach et al. 2024). Concurrent research indicated that scaup held in longer-term captivity with access to ad libitum food tended to maintain much lower body masses than free-living birds (Beach et al. 2024), which also informed our decision to conduct feeding trials soon after capture to better represent metabolism and dietary adaptation of free-living birds (Gross et al. 2020b). However, this design decision required that we use a separate set of individuals (i.e., group-control method) for metabolic and endogenous waste correction instead of estimating these values from the same individuals later as each bird could only participate in one trial (Sherfy et al. 2005, Beach et al. 2024).

We captured scaup during spring migration on Pool 19 of the Mississippi River in Hancock County, Illinois, the Emiquon National Wildlife Refuge in Fulton County, Illinois, and the Chautauqua National Wildlife Refuge in Mason County, Illinois, using dive/swim-in traps baited with whole-kernel corn. Trapping occurred in March–April 2019–2021. Scaup were removed from swim-in traps, transported to holding pens, and immediately subjected to a fasting period to begin their trials.

Feeding trials

Following capture and transportation to the research site, we attached backpack harnesses using methods described above for fasting duration trials. We randomly selected 1/3rd of birds by sex to serve as unfed negative

controls for estimating and correcting metabolic and endogenous losses (Sibbald 1986). While in short-term captivity, scaup were housed in an elevated outdoor pen (1.5 m × 6 m) with *ad libitum* access to water.

Following a 24-hour fasting period, we weighed (± 1 g, Ohaus Corporation, Parsippany, NJ, USA) each bird and hand-fed an amount of the trial food item equal to ~1% of body mass (Lancaster et al. 2019). Wild millet, amphipods, chironomids, and in-shell fingernail clams were fed using an open-ended, 3-mL syringe to deposit contents into the esophagus (Adeola et al. 1997). The end of the syringe was covered with thin latex that was slit prior to feeding. The latex retained the food while the syringe was inverted but allowed ejection into the esophagus when the plunger was depressed. Millet seeds were weighed at atmospheric moisture but were saturated 15 minutes before feeding to prevent impaction. The remainder of wet food items were placed on paper towels to remove excess water before weighing (Jorde and Owen 1988). We fed the ducks planorbid snails in their shells by placing them at the back of the throat with gloved fingers (Richman and Lovvorn 2004, McClain 2017). All foods were fed in multiple portions with a small amount of water given between portions to prevent impaction. All feedings were timed with an average feeding time of 4.4 minutes.

Immediately after feeding and after 24-hr fasting for negative control birds, we attached a Whirl-Pak® (21 cm × 10 cm) to the harness (Lancaster et al. 2019) and placed each bird into an isolette (approximately 0.42 m × 0.36 m × 0.31 m) for a 24-hour excreta collection period. After completion of the 24-hour collection period, we removed the collection bag and rinsed any excreta adhering to the washer or connecting cap into the bag (Lancaster et al. 2019). Any leakage present in the isolette was also collected. Excreta samples were frozen for storage between collection and laboratory analysis. If regurgitated trial food was present in the isolette, we enumerated and adjusted fed mass. We removed the harnesses and returned birds to a group pen at a minimum density of 0.6 m^2 per bird with access to *ad libitum* water and food (Sportsman's Choice® Floating Pond and Catfish Food [32% protein, 4% fat, 7.5% fiber], Cargill Animal Nutrition, Minneapolis, MN, USA; Beach et al. 2024). We released the scaup back into the wild after the cloacal cap from the harness sloughed off naturally (1–5 days). The birds were released 1–5 km from the trap site to avoid recaptures. Recaptures were rare ($n = 2$) and were easily identified by their shaved feathers.

Sample processing

We thawed and cleaned each sample to remove feathers, grit ingested pretrial, and parasites (Kaminski et al. 2003). Shell fragments found in certain samples (i.e., control samples and birds fed wild millet, amphipod, chironomids, or fingernail clams) were removed as they were rare but obviously indigestible remnants of items ingested pretrial. Fingernail clam shells are fragile and did not remain intact though the digestive process. Any intact seeds were also removed from excreta samples (except for wild millet in samples from birds fed wild millet) as they would influence overall gross energy of the sample. Samples were placed in a forced-air drying oven at 60°C to remove water until they could be stirred without excreta adhering to the laboratory spatula (Kaminski et al. 2003, McClain 2017, Lancaster et al. 2019). Once dry, we powdered each sample with a mortar and pestle, weighed it (± 0.1 mg, Mettler Toledo, Columbus, OH, USA) and created 2 0.5 g pellets using a Parr pellet press. We combusted each pellet in a compensated jacket calorimeter and averaged estimates to obtain gross energy (Parr 6050, Parr Instrument Company, Moline, IL, USA). Representative samples of the dried food item that were not fed to the bird were also pelletized and processed through the calorimeter to obtain gross energy. Planorbid snails and fingernail clams were processed with their shells.

Percent dry matter, organic matter, nitrogen, crude protein, fat, and acid detergent and neutral detergent fibers were determined for each food item at the Animal Science Laboratory at the University of Illinois – Urbana Champaign using methods described in McClain (2017). Dry matter and nitrogen values were also determined for each excreta sample. We determined the wet to dry ratio for each food by weighing portions of each diet item in the condition it was fed, then drying them to constant mass at 60°C (Gross et al. 2020b). We calculated the ratio of wet to dry mass and used it to determine dry mass fed to each bird for TME calculation.

Data analysis

True metabolizable energy was determined using the equation of Sibbald and Morse (1982) following Gross et al. (2020b). The nitrogen content and group control samples were used in the application of a nitrogen correction factor (Sibbald and Morse 1982, Sibbald 1986). We used the gross energy of uric acid (8.2 kcal/g; Parsons et al. 1982) and proximate nitrogen values to correct for endogenous and urinary energy (Sibbald and Morse 1982). We determined digestive efficiency for each food using the ratio of TME to gross energy. We created a set of linear models in R to examine the effects of food type, pretrial mass of the bird, sex, and the interaction between food type and sex on TME_N (v. 4.0.3, R Core Team 2020). Models were ranked using Akaike's Information Criterion corrected for small sample sizes (AIC_C) in the *AICcmodavg* package (Mazerolle 2020). We examined residuals for normality, considered models ≤ 2 ΔAIC competitive, and calculated 85% confidence intervals for beta-coefficients in competitive models.

RESULTS

Pre-experimental fasting trial

Mass of excreta voided during the pre-experimental fasting trial (16 female) differed among 6-hr collection periods ($H_{7,117} = 41.775$, $P < 0.001$), with significantly more voided during the first 6-hr period than every collection period from 24–48 hours ($P ≤ 0.05$, Figure 1). Specifically, scaup excreted 2.3–4.4 times more dry matter from 0–6 hr following removal from ad libitum food access than any subsequent 6-hr period. Amounts excreted during the 6–12 hr collection period were also significantly more than the 30–36 hr collection period ($P ≤ 0.02$; Figure 1).
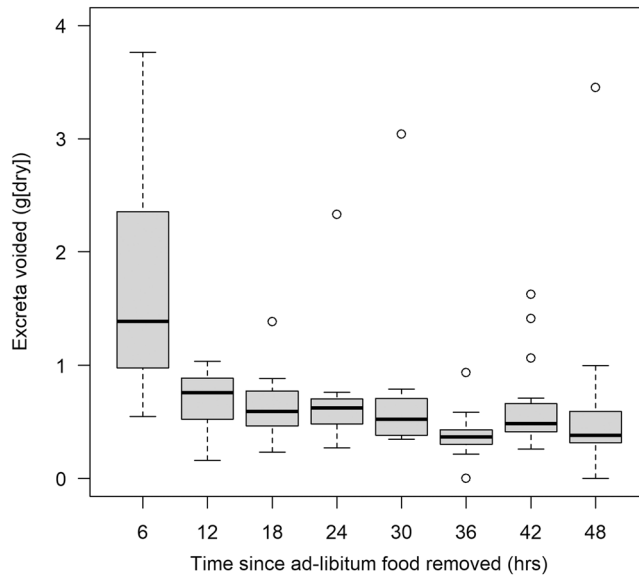

FIGURE 1   Median (bold horizontal line) mass (g[dry]) of excreta voided within 6-hour collection periods during a 48-hour, pre-experimental fast conducted with 16 female lesser scaup (*Aythya affinis*) at the Forbes Biological Station, Illinois, USA, in October 2018. Interquartile ranges (boxes), high and low values (whiskers), and outliers (points) are included.

TME trials

We processed 125 scaup (76 male, 49 female) through TME_N trials over the course of the study (89 fed birds and 36 control birds). Data from 2 individual feedings were censored due to harness failure and inability to adequately collect leakage from isolette. One bird was censored after producing an excessive amount (14 g[dry]) of excreta that was abnormal in color and twice the amount expected. We also censored 11 estimates (1 amphipod, 6 fingernail clam, and 4 planorbid snail) that resulted in TME_N estimates greater than the gross energy of the fed item.

Mean TME_N and gross energy varied among food types (Table 1). Mean TME_N (kcal/g[dry] ± SE) for wild millet (*Echinochloa crus-galli*; 2.2 ± 0.14) was greater than every invertebrate food, with chironomids (*Chironomus* spp.; 1.41 ± 0.49) and amphipods (*Gammarus spp.*; 1.33 ± 0.23) providing similar TME_N values to each other. On average, planorbid snails provided between 7.8 and 12.9 times less energy per gram than any of those 3 foods (Planorbidae; 0.17 ± 0.07), and fingernail clams were the only food item with a negative TME_N value (Sphaeriidae; −0.79 ± 0.27). The only competitive model for TME_N contained food type (Table 2). While an additional model containing both food type and pretrial mass also had a ΔAIC ≤ 2, the confidence interval for the model coefficient associated with mass crossed 0 and we excluded it from consideration.

DISCUSSION

While TME_N values from these foods did vary, neither of the soft-bodied invertebrates had the highest digestive efficiency. Regardless, these results provide TME estimates for scaup and for 2 foods (i.e., fingernail clams, planorbid snails) which have not been evaluated for any waterfowl species. Wild millet, chironomids, and amphipod TME values published in studies of dabbling ducks generally were greater than in our trials for scaup (Jorde and Owen 1988, Sherfy 1999,

TABLE 1 Energetic and nutritional composition in excreta samples and raw food items fed to lesser scaup (*Aythya affinis*) at the Forbes Biological Station and Kibbe Field Station, Illinois, USA, March–April 2019–2021.

Food		Excreta			Raw Food								
	n[a]	TME_N[b]	% DE[c]	% N[d]	GE[e]	DM[f]	OM[g]	N[h]	CP[i]	FAT[j]	NDF[k]	ADF[l]	WDC[m]
Amphipods	19	1.33 ± 0.23	40.05	14.98 ± 0.95	3.32	92.43	62.66	6.36	39.77	8.20	13.30	10.42	0.15
Chironomids	12	1.41 ± 0.49	33.13	21.75 ± 0.74	4.27	92.91	83.37	9.61	60.03	4.16	9.01	5.59	0.06
Fingernail clams	10	−0.79 ± 0.27	−301.97	12.14 ± 0.79	0.26	99.30	9.09	0.91	5.70	1.27	2.36	1.24	0.28
Planorbid snails	14	0.17 ± 0.07	30.82	12.50 ± 1.15	0.56	98.82	18.65	1.68	10.65	1.68	8.75	1.16	0.58
Wild millet	20	2.20 ± 0.14	50.38	7.84 ± 0.59	4.15	93.09	93.93	1.38	8.64	6.40	69.70	22.70	0.91

[a]Number of excreta samples.

[b]Mean true metabolizable energy (kcal/g [dry] ± SE).

[c]Digestive efficiency (%).

[d]Excreted nitrogen (%).

[e]Gross energy (kcal/g[dry]).

[f]Dry matter (%).

[g]Organic matter (%).

[h]Nitrogen (%).

[i]Crude protein (%).

[j]Soxhlet fat (%).

[k]Ash-corrected neutral detergent fiber (%).

[l]Ash-corrected acid detergent fiber (%).

[m]Per-gram wet-to-dry conversion factors.

TABLE 2 Ranked candidate models explaining true metabolizable energy (TME_N) for lesser scaup (*Aythya affinis*) from feeding trials conducted at the Forbes Biological Station and Kibbe Field Station, Illinois, USA, March–April 2019–2021 with beta estimates and confidence intervals for competitive models.

Model	K[a]	AIC_c[b]	ΔAIC_c[c]	$\omega i AIC_c$[d]	LL[e]	Variable	β-estimates	SE	Lower 85% CI	Upper 85% CI
Food	6	217.53	0.00	0.77	−102.16	Amphipods	1.33	0.22	1.01	1.65
						Chironomids	1.51	0.28	1.10	1.91
						Fingernail Clams	−0.79	0.29	−1.21	−0.37
						Planorbid Snails	0.17	0.26	−0.20	0.54
						Wild Millet	2.22	0.21	1.91	2.54
Food + sex	7	219.95	2.14	0.23	−102.15					
Food + sex + food × sex	11	227.25	9.75	0.01	−100.56					
Mass	3	265.00	47.46	0.00	−129.33					
Null	2	269.03	51.50	0.00	−132.43					
Sex	3	271.00	53.46	0.00	−132.33					

Abbreviation: CI, confidence interval.

[a]Number of model parameters.

[b]Akaike's Information Criterion for small sample sizes.

[c]Change in AIC_c value between models.

[d]Model weights.

[e]Log likelihood.

Checkett et al. 2002, Ballard et al. 2004). Checkett et al. (2002) reported a mean TME of 2.61 (± 0.12) kcal/g for wild millet in captive-reared mallards (*Anas platyrhynchos*) and Sherfy (1999) reported a mean TME of 2.65 (± 0.1) kcal/g for wild millet in captive-reared blue-winged teal (*Spatula discors*). These wild millet values were both greater than our TME_N values for wild millet, which is not surprising since mallard and blue-winged teal are generally granivorous (Havera 1999), while scaup have consistently demonstrated greater consumption of animal matter (Rogers and Korschgen 1966, Bartonek and Hickey 1969, Afton et al. 1991, Anteau and Afton 2006, Clements et al. 2020). For this reason, we expected scaup to assimilate more energy from invertebrates than dabbling ducks. Sherfy (1999) reported a TME value of 0.27 (± 0.05) kcal/g for chironomids fed to blue-winged teal, which was much less than our estimate for chironomids in scaup. Amphipod TME has been reported in 3 different studies (Jorde and Owen 1988, Sherfy 1999, Ballard et al. 2004). Sherfy (1999) fed amphipods to blue-winged teal and calculated a mean TME of 0.33 (± 0.52) kcal/g but had a small sample size (*n* = 6). Jorde and Owen (1988) and Ballard et al. (2004) reported amphipod TME greater than our results, with 2.18 (± 0.06) kcal/g for American black ducks (*Anas rubripes*) and 2.36 (± 0.06) kcal/g for captive-reared northern pintail (*Anas acuta*), respectively.

Digestive efficiency was within a consistent range for every trial with a positive TME_N and was greatest for wild millet even though excreta from birds fed wild millet also tended to contain intact seeds (~ 10–100 seeds). We expected scaup to have evolved gut physiology for consuming amphipods compared to other duck species given the documented importance of amphipods as an energy source for scaup (Anteau and Afton 2006, Anteau et al. 2014). Planorbid snails and fingernail clams were more difficult for scaup to digest, likely because processing shells required expending more energy (Richman and Lovvorn 2004). We assumed that our wild-caught scaup were conditioned to digest a variety of foods, but we were unable to account for their diet prior to capture beyond observing shell fragments and seed coatings from nontrial foods in their excreta.

Our finding that planorbid snails and fingernail clams provided the lowest TME value was consistent with our predictions. True metabolizeable energy has been estimated for several species of snails and clams, but none of the

genera used overlap those used in our trials (Jorde and Owen 1988, Sherfy 1999, Ballard et al. 2004, Coluccy et al. 2015). Sherfy (1999) reported a TME of −0.09 (± 0.04) kcal/g for gastropods in blue-winged teal. However, it is unclear what species of gastropods were fed in these trials making it difficult to compare with our planorbid snail values. While we did not expect our fingernail clam TME_N to be negative, the negative estimate was not improbable given their modest gross energy content and the effort required to digest (Gross et al. 2020b). Perhaps if gut morphology is adapted to bivalves specifically, large volumes of such prey must be profitable for free-living scaup considering several studies have documented scaup consuming bivalve prey nearly exclusively (Harmon 1962, Thompson 1973, Badzinski and Petrie 2006, Stroud et al. 2019). Further study could help determine if acclimation to particular diets, especially bivalves, increases their TME_N values for scaup.

We encountered several cases where nitrogen-adjusted energy of the control excreta exceeded the nitrogen-adjusted energy of fed individual's excreta (i.e., $EE_{CN} > EE_{FN}$; Sibbald and Morse 1982) resulting in unattainable TME_N estimates that exceeded gross energy of the diet. This occurrence has been reported by numerous studies of TME in waterfowl under varying fasting and excreta collection durations, therefore, we do not think this is an artifact of our 24-hr fasting and excreta collection period (McClain 2017, Lancaster et al. 2018, Gross et al. 2020b). Instead, we believe these improbable estimates stem from a directional effect (i.e., low energy) in the calculation of excreta energy from fed birds. We also observed greater nitrogen concentrations in the excreta of birds fed chironomids than other foods, something we had only expected in the trials with low energy foods as birds exhausted ingested energy and began protein catabolism. While the TME equation adjusts for nitrogen of the food and excreta, Gross et al. (2020b) suggested the use of a glucose supplement to prevent high nitrogen values due to protein catabolism during long periods without suitable nutrition. Future studies could examine the effectiveness of using glucose in trials where low-energy foods are being used to avoid excessive catabolism.

We would encourage resource managers to consider wet-to-dry conversion factors as well as handling time when considering the benefit of each food type for scaup. True metabolizable energy values are reported using dry grams, and the number of individual food items in 1 g[dry] varies greatly based on moisture content, particularly for invertebrates. For example, based on the size and type of food items used, we estimate 1 g[dry] of amphipods to be between 150 and 250 individuals and 1 g[dry] of planorbid snails to be between 2 and 10 individuals. We found that planorbid snails had a lower TME_N value than amphipods for scaup, but depending on location and availability amphipods may be more time-intensive to forage than planorbid snails.

Diet shifts from amphipods to mollusks or other benthic invertebrates have been observed in the upper Midwest, as have shifts to smaller prey as interspecific competition with fish limits the availability of larger prey items (Anteau and Afton 2006, 2008; Strand et al. 2008; Osborn et al. 2016). Consuming smaller prey increases the number of prey items needed to meet daily energetic requirements and will likely increase forage time and energy expenditure. Additionally, poorer nutrition may make scaup more susceptible to parasites (Beach 2021). A shift to different prey (i.e., gastropods) might be enough to meet energetic requirements if the new prey item occurs in high densities, but this shift comes at the cost of reducing lipid intake and stores which may affect survival during migration and subsequent recruitment (Anteau and Afton 2008, 2009). The Spring Condition Hypothesis suggests that scaup with reduced lipid reserves are less likely to recruit young (Afton and Anderson 2001, Anteau and Afton 2004). Although an abundance of a low-energy food (i.e., gastropods) may supplement energetic intake for scaup during spring migration, our results indicate that the management of spring staging areas for smaller, high-energy invertebrates (i.e., chironomids and amphipods) would provide greater opportunity for energy acquisition.

MANAGEMENT IMPLICATIONS

In future TME studies, short-term captivity could help remove additional intraspecific variation associated with the effects of long-term captivity while achieving best waterfowl husbandry practices. Additional research on how the stress of captivity might influence digestive efficiency may also lead to a better understanding of how collection

technique and calculation of control excreta energy influence TME. Our TME_N estimates will assist biologists in improving bioenergetic models for conservation planning to ensure food resources are available for diving ducks during migration. Our results can inform management decisions aimed at providing foods that convey more energy to scaup and perhaps other diving ducks. Within the Upper Mississippi River System, managing the flow of water and improving water clarity could benefit beds of aquatic vegetation that support amphipods, chironomids, and planorbid snails. Improved water clarity may also support the forage efficiency of scaup on nektonic foods (Tome and Wrubleski 1988), and water management for moist-soil plants could provide scaup with seed resources to supplement the animal matter in their diet (Moore et al. 2010, Larson 2021). This management would be important both in the spring to allow growth of aquatic vegetation, and in the fall to reduce the number of new seeds flushed from the seed bank.

DISCLAIMER

The findings and conclusions in this article are those of the author(s) and the U.S. Geological Survey, but do not necessarily represent the views of the U.S. Fish and Wildlife Service. Any use of trade, product, or firm names in this publication are for descriptive purposes only and does not imply endorsement by the U.S. government.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

Scaup were captured under IDNR Permits (W21.6179A, W21.6457A) and U.S. Fish and Wildlife Scientific Collection Permit (MB145466-0). Capture and handling methods were approved by Western Illinois University Institutional Animal Care and Use Committee (Protocol No. 002-20, No. 009-20), and the University of Illinois Institutional Animal Care and Use Committee (Protocol No. 18128).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Associate Editor: Adam Behney.