

# True Metabolizable Energy for Seeds of Common Moist-Soil Plant Species

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**ABSTRACT** Understanding the true metabolizable energy (TME) value of food is important for constructing bioenergetic models. We estimated gross energy, nutrient composition, and TME values for the seeds of 3 native and 1 invasive exotic wetland plant that occur in the diet of waterfowl. True metabolizable energy values were  $0.50 \pm 0.080$  kcal/g for spike rush (*Eleocharis palustris*),  $0.65 \pm 0.080$  kcal/g for alkali bulrush (*Schoenoplectus maritimus*),  $1.31 \pm 0.090$  kcal/g for perennial pepperweed (*Lepidium latifolium*), and  $2.52 \pm 0.080$  kcal/g for lamb's quarters (*Chenopodium album*). The TME value for 3 of 4 species, including the invasive species, was low relative to the TME value of other seeds consumed by waterfowl. (JOURNAL OF WILDLIFE MANAGEMENT 71(6):1964–1967; 2007)

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Bioenergetic models are the primary tools used to estimate habitat needs for wintering waterfowl in North America (Central Valley Habitat Joint Venture 1990, Loesch et al. 1994, Esslinger and Wilson 2001). Using bioenergetic models to set habitat objectives requires knowledge of the types, abundance, and nutritional value (i.e., metabolizable energy) of individual foods (Miller and Newton 1999, Ballard et al. 2004). Estimates of metabolizable energy also provide a means of comparing habitat quality, assessing the effect of specific wetland management or restoration actions, and evaluating how invasive exotic plant species can affect wetland habitat quality for ducks. Despite the value of knowing a food's metabolizable energy (ME), we know the ME value for only 5 agricultural foods, 4 species of acorn, and the seeds of 16 moist-soil plants (Hoffman and Bookhout 1985, Petrie et al. 1998, Sherfy 1999, Checkett et al. 2002, Kaminski et al. 2003).

Several methods are available for directly estimating metabolizable energy using controlled feeding experiments; however, estimates of true metabolizable energy (TME) are most accurate (Sibbald 1976, Miller and Reinecke 1984). Unlike estimates of gross energy, TME estimates energy available to birds, and TME is preferable over estimates of apparent metabolizable energy because it accounts for fecal and urinary energy of nonfood origin (Sibbald 1976, Miller and Reinecke 1984). In this paper, we report the TME value for seeds of moist-soil plants commonly occurring in seasonal wetlands in the intermountain west.

## METHODS

We conducted feeding trials at Oregon State University in Corvallis, Oregon, USA, using game-farm male mallards (*Anas platyrhynchos*) >5 months of age. When not being

used in feeding trials, birds were confined in an unheated pen subject to natural temperature and photoperiod and provided with unlimited access to a commercial game bird ration (crude protein  $\geq 20\%$ , crude fat  $\geq 3.0\%$ , crude fiber  $\leq 5.0\%$ ), grit, and fresh water (Petrie et al. 1997). Husbandry practices were approved by Oregon State University's Institutional Animal Care and Use Committee (No. A3229–01).

We determined TME for the seeds of 3 native species (alkali bulrush [*Schoenoplectus maritimus*], lamb's quarters [*Chenopodium album*], common spike rush [*Eleocharis palustris*]), and perennial pepperweed (*Lepidium latifolium*), an invasive exotic. We selected the native species due to their common occurrence in wetlands in the intermountain west and presence in the diet of waterfowl (Pederson and Pederson 1983). Perennial pepperweed is eaten by mallard and pintail (*Anas acuta*; Pederson and Pederson 1983) and has invaded seasonal wetlands and riparian areas in the west where it often forms dense, monotypic stands that can effectively exclude native wetland plant species (Young et al. 1995). We obtained seeds from a commercial seed provider because, except for alkali bulrush, seeds were too small to collect a sufficient biomass from natural wetlands.

We conducted feeding trials mid-February to early June following general procedures outlined in Checkett et al. (2002). Prior to each feeding trial, we randomly selected 7 birds ( $n = 12$  possible treatment birds) to serve as treatment birds. To provide a measure of endogenous contributions to excreta energy (Sibbald 1976), we selected 3 additional birds to serve as controls (not fed). We used the same 3 control birds for all trials. At the beginning of each trial, we placed each bird ( $n = 10$ ) in a metabolic chamber ( $20 \times 20 \times 30$  cm), provided ad libitum water, and fasted them for 48 hours. After fasting, but prior to feeding, we weighed each bird ( $\pm 10$  g) then fed each treatment bird a known quantity of food (Sibbald 1976). For bulrush and spike rush we fed an amount equal to 1% of the bird's body mass; for

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perennial pepperweed and lamb's quarters we fed a reduced quantity (0.5%) because most birds regurgitated when fed 1%. Mean mass fed ( $\pm$ SE) was  $12.5 \pm 0.5$  g for common spike rush,  $12.1 \pm 0.5$  g for alkali bulrush,  $6.5 \pm 0.7$  g for lamb's quarters, and  $5.8 \pm 0.2$  g for perennial pepperweed. We fed treatment birds the same species of seed for each trial.

We precision-fed birds by inserting a tube ( $1.2 \times 40$  cm) into the esophagus and slowly pouring seed into the tube using a funnel and pushing seed down the tube using a wooden dowel. We collected, weighed, and subtracted seeds failing to enter the bird's esophagus (e.g., seeds clinging to the tube wall) from each bird's original dose (Sherfy et al. 2001, Kaminski et al. 2003). Although TME estimates are theoretically independent of food-intake level (Miller and Reinecke 1984), we removed any bird from a trial if it regurgitated any portion of the test food after feeding because the small seed size made it difficult to collect all the regurgitated seed. We conducted 2 trials for each food. For the second trial, only birds not successfully fed in the first trial were available for selection as treatment birds. Thus, no bird contributed  $>1$  TME estimate for any food.

We placed metal funnels under each metabolic chamber that directed fecal and urinary matter into a plastic bag (see picture in Checkett et al. 2002). We collected excreta from control and experimental cages 48 hours after feeding (Petrie et al. 1998, Checkett et al. 2002, Kaminski et al. 2003). We removed feathers and grit from each sample, oven-dried the remaining excreta to constant mass at  $60^\circ$  C, weighed the sample to the nearest 0.0001 g, and ground it with a mortar and pestle. We estimated gross energy ( $GE_F$ ; kcal/g) of whole seeds and excreta using a Parr adiabatic oxygen bomb calorimeter ( $\bar{x}$  of 2 1.0-g excreta samples for each trial bird or sample of whole seed). We calculated TME (kcal/g) as:

$$TME = [(GE_F \times W_F) - (EE_F - EE_C)]/W_F$$

where  $GE_F$  was the gross energy of the whole seed,  $W_F$  was the dry mass fed (g) to the treatment bird,  $EE_F$  was the energy voided as excreta by the experimental bird (kcal), and  $EE_C$  was the energy voided as excreta by control birds (kcal/g; Sibbald 1976). We used the average energy excreted by control birds as the estimate of  $EE_C$ . To account for potentially greater catabolism of body tissue by control birds and to avoid overestimating energy derived from nonfood origin, we corrected TME to zero nitrogen balance ( $TME_N$ ; Parsons et al. 1982, Sibbald and Morse 1982).

We determined the nutrient composition for all seeds using proximate analysis. We determined percent moisture by drying samples to a constant mass in a forced-air oven at  $100^\circ$  C and percent nitrogen using the Kjeldahl procedure (Association of Official Analytical Chemists 2000). We multiplied percent nitrogen by 6.25 to estimate crude protein. We estimated crude fat using ether extraction, acid detergent fiber, and neutral detergent fiber by the Ankom A200 (Ankom, Macedon, NY) filter bag technique, and ash content by heating in a cold furnace until  $625^\circ$  C after 15

hours (Association of Official Analytical Chemists 2002). We estimated crude fiber as  $ADF \times 0.80$  and calculated nitrogen free extract as  $(100\% - \%water - \%crude\ fiber - \%ash - \%fat - \%crude\ protein)$ . We expressed  $TME_N$  values as a percentage of gross energy  $[(TME_N/GE_F) \times 100\%]$  to estimate digestive efficiency (Petrie et al. 1998).

Because bird mass may influence TME results (Sherfy 1999), we first used single factor analysis of variance (ANOVA; Proc GLM) to compare body mass among months for birds used in feeding trials and for differences in mean treatment-bird mass among seed species. Mean body mass of mallards throughout the trial was  $1,193.9 \pm 14.1$  g. Body mass did not differ by date ( $F=0.78$ ,  $P=0.61$ ) or seed species ( $F_{3,22}=0.43$ ,  $P=0.73$ ), so we did not include mass as a covariate in subsequent TME analyses. We determined whether  $TME_N$  of the 4 foods differed by fitting a mixed-model ANOVA (Littell et al. 1996). Based on Shapiro-Wilk tests and Levene's test for homogeneity of variance,  $TME_N$  values for each seed species were normally distributed ( $W > 0.86$  and  $W < 0.96$ ,  $P > 0.23$ ) with equal variance ( $F_{3,22}=0.45$ ,  $P=0.72$ ). We treated seed species as a fixed effect, and included date of feeding trial and individual bird as random effects. To further examine differences in  $TME_N$  between seed species, we conducted pairwise multiple comparisons using a Tukey multiple-comparison test.

## RESULTS

The  $TME_N$  differed among seed species ( $F_{3,20}=80.5$ ,  $P < 0.001$ ; Table 1). Pairwise comparisons indicated mean  $TME_N$  differed for all pairs of seeds ( $P \leq 0.002$ ) except alkali bulrush and common spike rush ( $P=0.49$ ). True metabolizable energy was highest for lamb's quarters, which was 2.2 times higher than perennial pepperweed, 3.9 times higher than alkali bulrush, and 5.0 times higher than spike rush. Digestive efficiency ranged from lows of 12.0% and 13.0% for common spike rush and alkali bulrush, respectively, to 25.9% for perennial pepperweed and 57.6% for lamb's quarters. Perennial pepperweed seeds were high in protein and fat content, but intermediate in metabolizable energy value (Table 1). Common spike rush was highest in fiber and ash, whereas alkali bulrush was highest in carbohydrates (NFE).

## DISCUSSION

Mallards received the greatest nutritional value from lamb's quarters whose TME value (2.52 kcal/g) is similar to the mean reported for seeds of other moist-soil plants (2.47 kcal/g; Kaminski et al. 2003). Our TME estimate for spike rush (0.50 kcal/g) is the lowest value reported for any species of seed fed to waterfowl (list in Kaminski et al. 2003). True metabolizable energy of alkali bulrush is lower than for hard stem bulrush (*Schoenoplectus acutus*) fed to mallards (Hoffman and Bookout 1985), but similar to estimates for Olney's bulrush (*Schoenoplectus americanus*) and 3 square (*Schoenoplectus pungens*) reported for blue-winged teal (Sherfy 1999). Low metabolizable energy for species like bulrush and spike

**Table 1.** Gross energy (GE; kcal/g), least-squares predicted means of nitrogen-corrected true metabolizable energy (TME<sub>N</sub>; kcal/g), and nutrient composition (% dry mass basis) for the seeds of moist-soil plant species fed to adult, game-farm male mallards on campus at Oregon State University, Corvallis, Oregon, USA, February–June 2003.

Plant species <sup>a</sup>	n	GE <sub>F</sub>	TME <sub>N</sub>		Nutritional composition (%) <sup>a</sup>					
			$\bar{x}$	SE	Protein	Fat	Ash	NFE <sup>c</sup>	ADF	NDF
Alkali bulrush	7	4.42	0.65	0.080	7.6	4.0	2.7	66.3	24.3	39.2
Lamb's quarters	7	4.46	2.52	0.080	16.6	9.5	4.1	48.4	26.7	27.0
Pepperweed	5 <sup>b</sup>	5.32	1.31	0.090	26.6	20.3	4.9	36.4	14.9	38.6
Spike rush	7	3.93	0.50	0.080	7.5	5.5	12.5	46.5	34.8	47.9

<sup>a</sup> ADF = acid detergent fiber, NDF = neutral detergent fiber, nitrogen free extract (NFE) = 100% – (protein + fat + fiber + ash).

<sup>b</sup> Reduced sample size caused by regurgitation of food by fed birds.

rush has been attributed, in part, to seed coat hardness that can resist mechanical digestion (Hoffman and Bookhout 1985, Petrie et al. 1998); this hypothesis is consistent with our observation and the observations of others (Pederson and Pederson 1983) that large numbers of alkali bulrush seeds (up to 50%; B. D. Dugger, Oregon State University, unpublished data) pass through the digestive system intact. However, research is needed to test this seed-coat hardness hypothesis and other potential explanations.

Our TME estimate for alkali bulrush is lower than the apparent metabolizable energy value reported for alkali bulrush by Miller (1987; 3.24 kcal/g) or TME value reported in Ballard et al. (2004) for the genus *Schoenoplectus* (1.42 kcal/g). Those studies estimated ME using the regression relationship between TME and fiber content (Ballard et al. 2004) developed by Petrie et al. (1998) or on digestibility coefficients and metabolizable energy estimates of different nutrients from the literature (Miller 1987); neither study directly measured TME. The fiber content of *Schoenoplectus* exceeds the upper limits of fiber values used to generate the regression relationship, suggesting the relationship between fiber and TME may change at higher fiber levels. Differences in our estimates compared to those generated using regression or apparent metabolizable energy methods confirm that TME should be used when estimating the nutritional value of waterfowl foods. However, given the relative time and expense of conducting feeding trials and the large number of foods that could be sampled, the feasibility of estimating TME using some combination of a food's proximate components should be investigated.

Consistent with alkali bulrush's low TME value, northern pintails wintering in California's Central Valley (USA) tend to avoid this species relative to other seeds (Euliss and Harris 1987, Miller 1987). However, alkali bulrush is common in the spring diet of mallards and northern pintails feeding in seasonally flooded wetlands in the Klamath Basin, California (Pederson and Pederson 1983). Discrepancies between TME values and the occurrence of a specific food in a species' diet likely reflects the influence of other factors on the foraging equation like search and handling time (Euliss and Harris 1987, Barras et al. 1996), seasonal changes in relative food quality (e.g., due to decomposition, depletion, or change in TME; Checkett 2001), behavioral limitations (e.g., inability to discriminate among seed species while tactile foraging in benthic habitats), or

optimization for something other than total energy (e.g., Heitmeyer 1988). Unfortunately, the relative importance of these factors in determining food choice is little-understood for foraging ducks.

Invasive exotics present one of the greatest threats to the successful management and restoration of native wetland ecosystems (e.g., Levin et al. 2006). Perennial pepperweed is widespread in riparian and wetland habitats in the west where it displaces native plant species and forms dense monocultures (Young et al. 1998). Although it would be unwise to evaluate the overall influence of pepperweed on seasonal wetland function based solely on its foraging value to ducks, estimating TME does provide one measure of effect that is relevant to waterfowl managers. Pepperweed is reported in the diet of mallard, pintail, and green-winged teal, and one study classified pepperweed as a preferred food source for pintails (Pederson and Pederson 1983). Compared to many seeds commonly consumed by mallards, perennial pepperweed has lower energy content (1.31 vs.  $\bar{x}$  of 2.47 kcal/g reported in Kaminski et al. [2003]), but a relatively high level of protein (Checkett et al. 2002; Table 1). Given its intermediate TME value, the effect of pepperweed on foraging-habitat quality depends, in part, on the foraging value of the native plants being displaced.

Finally, we recommend that future TME studies adjust their study design to permit gathering information on seed survival (e.g., counting no. of seeds in addition to mass fed each bird). This would increase the scope and efficiency of future feeding experiments by helping understand the role waterfowl play as dispersers of native and exotic wetland plants (Powers et al. 1978, Figuerola and Green 2002, Mueller and van der Valk 2002).

## MANAGEMENT IMPLICATIONS

Our TME estimates are precise; thus, managers can use these estimates for assessment and planning purposes. Managers can use TME values with seed biomass estimates to calculate total energy production, a more accurate comparison of food production between habitats than relying solely on biomass comparisons. Our TME values can be used with information on diet to generate a composite TME value for a bird's diet, leading to a better understanding of energy intake and improving efforts to estimate a species' seasonal habitat needs (e.g., Miller and Newton 1999).

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