CHAPTER 1

METABOLIZABLE ENERGY OF MOIST-SOIL PLANT SEEDS AND INVERTEBRATES

INTRODUCTION

Waterfowl Nutrition

Diets of wintering waterfowl are diverse and include aquatic invertebrates, moist-soil plant seeds, and agricultural grains (Afton et al. 1991, Delnicki and Reinecke 1986, Euliss and Harris 1987, Chabreck et al. 1989, Combs and Fredrickson 1996). Research in waterfowl nutrition has recognized variability in value among foods (Jorde and Owen 1988, Hoffman and Bookhout 1985, Petrie et al. 1998), whereas studies of waterfowl food habits (e.g., Miller 1987, Thompson et al. 1992, Combs and Fredrickson 1996) and foraging ecology (e.g., Euliss and Harris 1987, Euliss et al. 1991) have focused primarily on differences in abundance among foods. Winter diet restriction in waterfowl can affect timing of molt (Richardson and Kaminski 1992), body mass, mortality and pair formation (Demarest et al. 1997), and nest initiation date (Dubovsky and Kaminski 1994). Studies also have shown that food quality can affect egg production (Krapu 1979) and timing of remigial molt (Richardson and Kaminski 1992). Canvasbacks (*Athya valisineria*) quickly regain lost body mass when fed a nutritionally balanced diet following short-term food deprivation, but continue to lose mass when fed unbalanced diets (Jorde et al. 1995). Thus, diet quality is important not only in maintaining condition of wintering birds, but in mitigating physiological effects of short-term food deprivation. Given the maintenance and anabolic costs of migrating and wintering birds, wetland management techniques that promote the production of nutritionally balanced foods should be encouraged.

Despite recognizing the potential demographic consequences of nutritional status, few studies have described nutritional value of waterfowl foods. Laboratory analyses (gross energy and proximate analysis) have been completed for seeds of moist soil plants of Missouri (Fredrickson and Taylor 1982), Ohio (Hoffman and Bookhout 1985), and Louisiana (Junca et al. 1962, Bardwell et al. 1963). Other studies have focused primarily on nutritional value of plant foods on the breeding grounds (Thomas and Prevett 1980, Sedinger 1984). Because the importance of invertebrates to waterfowl is primarily recognized in reference to protein requirements of the breeding season (Krapu and Swanson 1975), most studies have focused on caloric and protein content of these foods in marshes of the Midwest and Canadian prairies (Wissing and Hasler 1968, 1971, Sugden 1973*a*, 1973*b*, Driver et al. 1974, Sedinger 1984). Pertinent physiological data relative to condition (Ringleman and Szymczak 1985, Hepp et al. 1986) and feeding ecology (Jorde et al. 1983, Delnicki and Reinecke 1986, Miller 1987) of wintering birds is available, but there are few corresponding nutritional data to assist managers in evaluating the contribution of winter foods to condition of birds. Knowledge of the nutritional quality of waterfowl foods is an important management concern (Jorde et al. 1995).

Metabolizable energy data have been published for invertebrate (Sugden 1973*b*, Jorde and Owen 1988) and plant foods (Hoffman and Bookhout 1985, Miller 1987, Petrie et al. 1998). As the latter studies have focused primarily on agricultural foods, few metabolizable energy data are available for moist-soil plant seeds. Disproportionate waterfowl use of moist-soil habitats relative to natural marshes has been attributed to higher food production in managed wetlands (Haukos and Smith 1993, Gordon et al. 1998). Freshwater wetlands generally provide abundant and diverse macroinvertebrate and seed resources for wintering birds (Tietje and Teer 1988), whereas available foods in agricultural habitats are typically dominated by a single plant species. Variance in nutritional value among moist-soil species may therefore be an important proximate factor contributing to within-wetland patterns of habitat selection by waterfowl. Further, the accuracy of carrying capacity estimations for moist-soil habitats (Prince 1979, Reinecke et al. 1989) will be improved where empirical data are available for dominant plant species.

Methods of Estimating Dietary Quality

Excretory energy (EE) represents the fraction of dietary energy that is voided by an animal, and is thus unavailable for maintenance and growth. Dietary energy that is not voided is defined as metabolizable energy (ME), representing the portion of intake energy that is available to the animal (Robbins 1983). Metabolizable energy may be estimated either as apparent (AME) or true (TME). Apparent metabolizable energy (AME) is defined as intake energy minus excretory (fecal and urinary) energy losses (Sibbald 1980). However, excretory energy losses may be partitioned into dietary and endogenous fractions (Sibbald 1980). Thus, apparent estimates introduce a penalty for endogenous losses, defined as the excretory energy of non-dietary origin (Sibbald 1976, Miller and Reinecke 1984). True metabolizable energy may be obtained by correcting the estimate for the fraction of excretory energy that originates from nondietary sources. Because measures of AME do not account for the endogenous fraction, AME underestimates the true metabolizable energy (TME) of a given diet (Sibbald 1976, Miller and Reinecke 1984). Sibbald (1975) supported the view that endogenous excretory energy is independent of intake level, causing AME values to vary with intake. TME is generally viewed as a more accurate and appropriate expression of metabolizable energy in poultry nutrition (Sibbald 1980).

True metabolizable energy may be estimated by conducting a series of total-collection feeding trials at varying intake rates. Measurement of intake energy (IE) and excretory energy (EE) at each intake level provide several estimates of AME. Linear regression can then be used to describe the relationship between AME and IE. The slope of the resulting regression equation estimates the difference between gross energy and TME, and the intercept estimates endogenous losses (i.e., excretory energy at zero intake). The cumbersome nature of this experimental approach led Sibbald (1975, 1976) to propose a new feeding trial method designed to provide rapid and accurate estimates of TME.

The method described by Sibbald (1975, 1976) requires a single feeding trial lasting 48-72 hr to estimate true metabolizable energy. Test birds are starved for approximately 24 hr, and then force-fed a known quantity of the test diet. Each bird is placed in a separate holding cage with a clean excreta collection tray beneath the cage. A separate group of control birds also is isolated in similar cages, but these birds are not provided with food. After 24 hr, excreta are quantitatively collected, frozen, freeze-dried, and weighed. Gross energy concentration of the excreta is determined by bomb calorimetry. The product of excreta mass and excreta gross energy concentration is the excretory energy for each bird. Excretory energy of control birds estimates endogenous losses, whereas excretory energy of fed birds is used to estimate AME.

TME is calculated by pairing control and fed birds on the basis of weight, and subtracting the endogenous loss estimate of the control bird from the excretory energy of the fed bird.

Several advantages to this method have been described in the literature:

1. Use of the endogenous loss correction removes the penalty on ME, and provides a more accurate estimate of ME (Sibbald 1976, Miller and Reinecke 1984). Because among-bird variation in endogenous losses is removed, TME data are generally more reproducible than AME data (Sibbald 1980).
2. This method eliminates the need to employ the multiple-trial regression approach, substantially reducing time and labor requirements.
3. AME is uncorrected for endogenous losses, and thus varies with intake level (Sibbald 1975, 1976, 1980, Miller and Reinecke 1984). Because TME accounts for excretory energy of non-dietary origin, these values are independent of intake level. Sibbald (1975) observed a linear relationship between intake energy and excretory energy using the TME approach, confirming that TME is independent of intake. In contrast, the AME approach produces a curvilinear relationship between intake and excretory energy. This curve asymptotically approaches the TME value at high levels of intake (Sibbald 1975).
4. Assuming no synergistic effects, TME values of diet components should be additive. Sibbald (1977) conducted TME assays of corn, wheat, soybean meal, fish meal, and 10 diets composed of varying levels of these 4 components. TME of the composite diets was calculated both according to relative abundance and TME of the components, and by a TME assay of the composite diet. The lack of statistical difference between the 2 estimates confirms that TME values of diet components are additive. In contrast, Sibbald (1980) reports that similar investigations have shown that AME values are not additive.
5. Sibbald (1980) reports substantial variation in AME values among domestic poultry species, but less inter-species variation in TME values. The difference is believed to occur because the ratio of endogenous losses to intake energy varies with species (Sibbald 1980). Therefore, TME data should have broader applicability than AME data.

6. Sibbald (1976) recommends force feeding a food amount of approximately 1% of the body weight of the bird. In contrast, the AME approach requires that the test diet be available in *ad libitum* quantities for at least 1 week. Feed availability is probably a minimal concern in poultry nutrition research, but the TME method is gaining favor among wildlife nutritionists due to the low diet requirement. Collection of sufficient quantities of native plants for AME trials often is not feasible.

Nutritional Value of Invertebrate and Plant Foods

Management of moist-soil impoundments for migratory birds should maximize production of nutritionally beneficial foods (Fredrickson and Taylor 1982). Given the significance of winter food quality to waterfowl condition, survival, and reproduction (Alisauskas and Ankney 1992), nutritional analysis of important winter waterfowl foods is warranted. Comparatively little information is available regarding the nutritional needs of spring migrating shorebirds, but it holds that a nutritionally balanced diet would be advantageous and could ultimately affect survival, condition and reproduction in these species.

Hoffman and Bookhout (1985) reported TME values for seeds of 5 common fall waterfowl food plants in northern Ohio. Their analysis indicated substantial variation within (up to 600%) and between (up to 350%) plant species, and did not include several plant species that are important to wintering waterfowl in the mid-Atlantic region, such as switchgrass (*Panicum virgatum*), dotted smartweed (*Polygonum pennsylvanicum*), big cordgrass (*Spartina cynosuroides*), spikerushes (*Eleocharis spp.*) and bulrushes (*Scirpus spp.*) (Bellrose 1980, Hindman and Stotts 1989).

Sugden (1973b) reported AME values for 18 plant and 3 invertebrate foods consumed by blue-winged teal (*Anas discors*). Despite high gross energy of the test diets, he observed consistently low AME values, including negative AMEs for three foods. Miller (1984) found that AME of common barnyardgrass (*Echinochloa crusgalli*) seeds did not differ among northern pintails (*A. acuta*), gadwalls (*A. strepera*) and northern shovelers (*A. clypeata*). Neither author provided estimates of TME for test diets. Given that AME measures vary with intake levels and do not account for endogenous sources of excretory energy, TME is a more reliable standard for evaluation of diet quality (Sibbald 1980, Miller and Reinecke 1984).

Prince (1979) and Reinecke et al. (1989) proposed the calculation of duck use-days as a desirable means for evaluating waterfowl habitat management. Data requirements for these calculations include estimates of food production, food quality, and the daily energy requirements of target species. Reinecke et al. (1989) illustrated the application of this approach using an assumed mean metabolizable energy for moist-soil seeds of 2.5 kcal / g. Investigations of seed metabolizable energy have shown considerable variation among species (Hoffman and Bookhout 1985 [range 1.08 - 3.00 kcal / g], Petrie et al. 1998 [range 1.59 - 3.90 kcal / g]). Foraging habitats used by wintering waterfowl may vary markedly in diversity of food production, including both homogeneous (e.g., agricultural fields) and heterogeneous (e.g., moist-soil impoundments) plant communities. Where available foods are dominated by a few species of particularly high (e.g., agricultural grains) or low (e.g., moist-soil plants) metabolizable energy, assuming a common metabolizable energy for all species may lead to error in duck use-day estimates. Accuracy of duck use-day estimates will be improved where estimates of metabolizable energy are available for all plant species of interest.

OBJECTIVES

The goal of this study was to evaluate true metabolizable energy content of waterfowl and shorebird foods that commonly occur in Atlantic coastal moist-soil impoundments. Both plant and invertebrate foods were investigated.

METHODS

Experimental Birds and Husbandry Methods

Thirty-six hatch-year blue-winged teal (18M, 18F) were obtained from Delta Waterfowl and Wetlands Research Station in October 1996. Field crews at Delta recovered eggs from abandoned nests in agricultural fields during spring 1996. Eggs were incubated and hatched in the aviary at Delta. Birds were transported by commercial airline to Charlotte, North Carolina, and by passenger vehicle to Blacksburg, Virginia. Pens at the Center Woods Wildlife Research Facility were used to house birds and conduct metabolizable energy trials. Birds were randomly assigned to one of four 1.8 m x 2.7 m x 1.8 m outdoor pens. The pens were constructed of lumber framing covered with vinyl-coated 1.3 cm x 2.5 cm mesh hardware cloth, and were elevated so that pen floors were >30cm above ground level. Thus, birds did not have free access to natural sources of grit. Birds were provided water in 1 1.1 m-radius plastic wading pool, 1 55 cm x 60 cm x 3 cm aluminum pan and 3 ceramic bowls per pen. Wading pools were filled to a sufficient depth to allow swimming by birds, and were cleaned weekly. A stock tank de-icer (Farm Innovators Ice Chaser #H-418, 1250 watts) was placed in each pool during winter months to prevent water from freezing. Aluminum pans and ceramic bowls were emptied and cleaned daily.

Preliminary Grit Experiment

Prior to initiation of feeding trials, all birds were used in a preliminary study to evaluate the influence of grit and hard seed consumption on metabolizable energy of seed diets (Appendix D). One of 4 pre-trial diets was assigned to each of 4 pens, and birds were assigned randomly to pens within sexes. The basal diet fed to all birds was a pelleted, non-medicated chicken starter (minimum crude protein 20.6%, minimum crude fat 3.0%, maximum crude fiber 7.0%; Big Spring Mills, Elliston, VA). The experimental diets were generated by varying availability of granite grit and milo: 1) chicken starter only; 2) chicken starter + milo; 3) chicken starter + grit; and, 4) chicken starter + milo + grit. Passage rate of grit for waterfowl has not been determined, although Robel and Bisset (1979) found that grit remained in bobwhite (*Colinus virginianus*) crops for at least 9 months after it was removed from the diet. Therefore, ME determinations in feeding trials subsequent to the grit study could have been confounded if: 1) grit remained in the gizzards of some birds; and, 2) presence of grit influenced digestive efficiency (Petrie et al. 1997). To remove this potential source of bias, all birds were provided with both grit and milo after completion of the grit study, regardless of the treatment group to which they had been assigned. Despite the manipulation of diets for the grit study, subsequent TME feeding trials were conducted under the assumption that digestive efficiency did not differ among bird pens.

Experimental Approach

Birds were maintained on a mixed diet of chicken starter and milo (2:1 v/v). Each pen was provided daily with *ad libitum* quantities of this diet in ceramic bowls. Wet or powdery feed was removed from feed bowls daily. Granite grit (approximately 10g) was sprinkled over the surface of the feed daily, and also was provided separately in a fourth bowl. This allowed birds free access to grit and provided for incidental consumption during feeding. Incidental observations suggested that birds consumed grit, although grit use was not directly measured. There also was little anecdotal evidence that birds avoided milo. To the contrary, the surface layer of feed often contained little milo after 24hr, suggesting that birds may have selected for milo.

A series of feeding trials was conducted during spring 1998 that were designed to control 2 primary factors. First, it was desirable to control for variation among individuals in endogenous losses. Rather than selecting separate test and control groups of birds, each bird served as its own control (Kaminski and Essig 1992). Thus, endogenous losses were measured for each bird during the first trial. From an experimental standpoint, it would have been preferable to intersperse measurements of endogenous losses among feeding trials. However, some mortality of birds was anticipated based on previous experience with the TME Method. The chosen approach ensured that TME could be calculated for any birds that died, because endogenous loss data were available for all birds. Apart from endogenous loss measurements, the trials were designed so that time and experimental diet were minimally confounded.

True metabolizable energy was determined for 13 species of moist-soil plant seeds, 1 agricultural seed, and 5 aquatic invertebrate taxa. Data for 2 seed diets (milo and millet) were obtained from GRITMILO birds in the preliminary grit study (Appendix D). These data were collected under identical conditions used to evaluate TME of the remaining seed diets. Four invertebrate taxa were collected from moist-soil impoundments at Back Bay National Wildlife Refuge during April 1998 (Table 1.1). Because it was desirable to conduct feeding trials with these taxa immediately after collection, 1 feeding trial was devoted exclusively to fresh invertebrate taxa. Invertebrates were dried 24hr at 60 ºC prior to feeding trials. Fresh invertebrate taxa were randomly assigned to birds prior to this trial.

For the remaining taxa, the initial goal was to complete feeding trials on 6 birds for each of the 12 foods. These foods consisted of 11 seed taxa that were either obtained from a commercial source or collected from the impoundments at Back Bay NWR, and 1 invertebrate taxon (Amphipods) that was obtained from a commercial source (Table 1.1). At the beginning of this portion of the study, 24 birds remained alive. The diets were systematically assigned to trials and randomly assigned to birds within trials, with the constraint that no bird would receive the same diet twice. Due to bird mortality and problems with force-feeding of some diets, the desired feeding trial schedule could not be strictly followed. At the completion of each trial, an assessment was made of the remaining diets to be studied, and diets were assigned to birds for the next trial in a manner that ensured interspersion of diets among trials.

Sibbald (1975) recommended feeding an amount of the test diet equal to 1% of the animal's body weight. Bird weights were recorded at the beginning and end of each trial (see below); most birds lost weight during trials and regained weight between trials. Body weight for each bird was approximated by adding an estimate of between-trial weight gain (generally around 20g) to the weight of the bird at the end of the previous feeding trial. Foods that could only be obtained in small quantities (i.e., aquatic invertebrates) and foods for which 1% of body weight represented a food volume for which crop compaction was a concern were fed at approximately 0.5% of body weight. Although TME is independent of the amount of test diet (Sibbald 1975), an attempt was made to maintain consistent diet mass relative to body size among birds.

Feeding Trial Methods

Each feeding trial was conducted over a 3-day period. Birds were randomly assigned to 1 of 24 46 cm x 46 cm x 60 cm cages. The cages were constructed of vinyl-coated chicken wire and hardware cloth. Pens immediately adjacent to the permanent bird holding pens were used for feeding trials. On the first trial day, birds were removed from holding pens, placed in individual cages, and provided with water. Cages were supported by 2 lengths of 0.5 cm diameter reinforcing bars, beneath which a clean aluminum pan was placed. On the second trial day, birds were weighed and force-fed a known quantity of the test diet. Force-feeding was accomplished by inserting a 0.5 cm diameter thin-walled plastic tube into the bird's esophagus. The test diet was introduced to the tube by a plastic funnel and pushed through the tube with a wooden dowel rod. The dowel was marked equivalent to the length of the tube so that the distal end could be

Table 1.1. Sources of foods, sample sizes, and dates for true metabolizable energy feeding trials.

		Sample Size per Feeding Trial							
Food Item	**Source**	**14 July - 3 Sept 1997**[a]	**1 Oct - 5 Nov 1997**[a]	**11 - 13 Feb 1998**	**25 - 27 Feb 1998**	**11 - 13 March 1998**	**25 - 27 March 1998**	**15 - 17 April 1998**	**28 - 30 April 1998**
Invertebrates									
Amphipoda	Miami Aqua-Culture Inc.				1	3	1	1	
Chironomidae	Collected at Back Bay NWR								3
Corixidae	Collected at Back Bay NWR								1
Gastropoda	Collected at Back Bay NWR								5
Isopoda	Collected at Back Bay NWR								1
Seeds									
Bidens cernua	Southern Tier Consulting				1		2		
Cyperus esculentus	Collected at Back Bay NWR			1	2			2	
Echinochloa crusgalli	Southern Tier Consulting		5						
Eleocharis obtusa	Southern Tier Consulting						4	1	
Fimbristylis annua	Collected at Back Bay NWR				2			3	
Juncus canadensis	Southern Tier Consulting				2		2	1	
Milo	Kester's Wild Game Food Nursery	6							
Panicum dichotomiflorum	Southern Tier Consulting					3	1	2	
Panicum virgatum	Southern Tier Consulting				2	3	1		
Scirpus americanus	Collected at Back Bay NWR			1	2	3			
Scirpus pungens	Southern Tier Consulting			1	1	3	1		
Spartina patens	Collected at Back Bay NWR				2		2	1	
Zizania aquatica	Southern Tier Consulting			1	2	3			

[a] Several feeding trials were conducted over this range of dates (see Appendix D).

prevented from protruding into the bird’s esophagus. The distal end of the dowel was sanded to minimize the potential for injury to birds.

The amount of effort required to force-feed birds varied with diets. Large, hard-coated seeds could be fed quickly, whereas smaller seeds required more effort because they tended to adhere to the tube. An attempt was made to minimize variation in feeding time among diets. Feeding generally required <5 minutes per bird. Water was used sparingly to wash residual feed into the esophagus. The esophagus was gently massaged after feeding to ensure that food reached the crop. Immediately after feeding, the bird was returned to its cage and the collection pan was thoroughly cleaned. A wooden barrier was inserted between cages to prevent cross-contamination of excreta.

Excreta collection occurred on the third day of the trial. Birds were removed from the cages 24hr after feeding, weighed, and returned to the holding pens. Excreta were scraped from pans using flexible putty knives and placed in 150-ml plastic containers. Small amounts of water were used to loosen dried excreta from the pans.

Birds frequently regurgitated a portion of the test diet. Other investigators who have encountered this phenomenon have omitted these birds from data analysis (Petrie et al. 1997, 1998, D. Jorde, Patuxent Wildlife Research Center, personal communication, R. Hoffman, Ducks Unlimited Inc., personal communication). Due to the frequency of regurgitation in this study, omission of these birds would have resulted in extremely low sample sizes within diets. An advantage to the TME method is that TME should be independent of intake (Sibbald 1975), theoretically allowing intake level to be adjusted for unconsumed (i.e., regurgitated) food. Therefore, regurgitated feed was collected separately from excreta and air-dried >24hr. Mass of regurgitated feed was subtracted from Initial Feed Mass, and TME was calculated based on the resulting Net Food Intake. This approach assumes: 1) collection and weighing of regurgitated feed without error; and, 2) no physiological consequences of regurgitation that would alter digestive efficiency.

Laboratory Analysis

After collection from pans, excreta samples were stored in a freezer >24hr, freeze-dried for >36hr, manually ground, and weighed. Gross energy was analyzed using a Parr model 1241 adiabatic bomb calorimeter. This instrument is intended for analysis of samples that are approximately 1g and that produce a heat rise of about 2-3 °C upon combustion. Samples that weighed ≤1g thus would not allow for analysis of duplicates. Excreta from control birds that weighed approximately 0.5g were common. To enable analysis of small samples on the available calorimeter, duplicate subsamples of approximately 0.2g were taken from each sample and pelletized. Each subsample was ignited in the bomb with a 0.8g pellet of benzoic acid (Fisher Scientific #A68-30). This method produced a total heat rise of approximately 2 °C, and allowed calculation of gross energy for the excreta subsample by subtracting heat attributable to benzoic acid combustion.

Gross energy of seed foods also was determined using the Parr model 1241 calorimeter. Due to the effort required for collection of invertebrate foods, adequate sample mass for use of this calorimeter could not be obtained. Thus, gross energy of invertebrate foods was determined using a Phillipson Micro-Bomb calorimeter. Proximate analysis for seed diets was conducted by the Forage Testing Laboratory at Virginia Tech. Low sample volume precluded proximate analysis for invertebrate foods.

Data Analysis

True metabolizable energy was calculated after Sibbald (1986) as

$$\mathrm{TME} = [\,(\mathrm{GE}_f \times \mathrm{W}_f) - (\mathrm{EE}_f - \mathrm{EE}_c)\,] / \mathrm{W}_f,$$

where:

TME = True metabolizable energy (kcal / g)

GE_f = Gross energy of the test diet (kcal / g)

W_f = Net Food Intake (g)

EE_f = Excretory Energy of fed bird (kcal)

EE_c = Excretory Energy of unfed bird (kcal).

For each observation, Net Food Intake was calculated by subtracting Regurgitated Food Mass from Initial Food Mass. Percent Regurgitation was calculated as: [Regurgitated Food Mass / Initial Food Mass] x 100. Relative Food Intake was calculated as: [Net Food Intake / Bird Mass] *100. Excretory Energy was calculated by multiplying excreta mass by the mean of duplicate gross energy determinations for each sample. Metabolizable energy coefficients (MEC) were calculated as [TME / GE_f] x 100.

Variation in TME among observations was investigated by linear regression of TME on Bird Mass and Percent Regurgitation. The results of this study were evaluated relative to predicted relationships from Sibbald (1975) by linear regression of TME on Net Food Intake and Relative Food Intake, and of Excreta Mass and Excreta Energy on Net Food Intake. Analysis of variance was used to evaluate variation among foods in Net Food Intake, Relative Intake, Excreta Mass, Excreta Energy Density and Percent Regurgitation. Following significant main effects in ANOVA, Tukey's test was used to evaluate differences between means for individual diets. Arithmetic means of TME were calculated for each experimental food, and are presented ± 1 SE.

TME was <0 for 24 of 84 observations (29%). Negative TME values should not occur because excretory energy for a fed bird should always exceed excretory energy for a fasted bird, especially for foods of extremely low nutritional value. Though energetic costs of assimilation might exceed energy gain from a given diet, such losses would occur at the cellular level and would thus not be reflected in excretory energy. Consequently, negative TME values likely reflect variation related to experimental or analytical methods. As no overt changes in methodology were employed during this study, there was no defensible decision point for deletion of observations. Retention of all observed values was desirable in seeking to increase power of regression models aimed at explaining variation among observations. However, precision tended to be higher for foods with high TME, suggesting that diet composition could explain some of the observed variability.

Variation in TME among seed diets was investigated using stepwise linear regression, with TME as the dependent variable and each component of the proximate analysis as an independent variable. TME values near or <0 tended to occur for foods that appeared to have high fiber content, suggesting that proximate composition could be used to generate predicted TME values. Thus, the regression analysis was conducted on 2 datasets. First, the mean TME for each diet was calculated using all observations (the “full dataset”), and these means were used as dependent variables in the regression analysis. A second regression analysis was conducted using only those species for which the coefficient of variation (CV; %) for the mean TME was <20% (the “reduced dataset”; Table 1.2). This CV value is near the maximum variation observed by Petrie et al. (1998). For the reduced dataset, all observations were retained to generate means for the selected species, while the remaining species (CV > 20%) were deleted. Both resulting regression equations were used to generate predicted TME values for all seed diets.

Approvals and Permits

This study was approved by the Virginia Tech Animal Care Committee under Proposal #96-051-F&W. Holding of birds in captivity was authorized by the U.S. Fish and Wildlife Service under Scientific Collecting Permit #PRT-820445 and the Virginia Department of Game and Inland Fisheries under Scientific Collecting Permit #SCP96133. Import and export authorizations were provided by Manitoba Department of Natural Resources Permit to Export Wild Animals #XP-03322, Canadian Wildlife Service Scientific Permit to Possess and Transfer Migratory Birds #WS-M51, and U.S. Fish and Wildlife Service Migratory Bird Import/Export Permit #PRT-820538.

RESULTS

There was substantial variation in TME within and among diets. The highest TMEs were recorded for wild rice (*Zizania aquatica*; 3.47 kcal/g) and milo (3.38 kcal/g). At least one negative TME occurred for 10 species; mean TME did not differ from 0 for any of these ($P > 0.05$). Mean TME was <0 for snails and spikerush seeds (Table 1.2). Coefficient of variation was <20% for 5 seed foods, but was >100% for 7 plant and 1 invertebrate food. Mean TME was > 2.0 kcal / g for the 5 seed species that exhibited lowest variability (Table 1.2). Metabolizability coefficients (MEC) were similarly variable; negative mean TMEs produced negative MECs for 2 species (Table 1.2). Gross energy ranged from 3.50 - 4.83 kcal / g for seeds and 1.01 - 4.22 kcal / g for invertebrates.

Table 1.2. Proximate composition, true metabolizable energy (kcal / g), and metabolizable energy coefficient (%) for invertebrate and moist-soil seed diets fed to blue-winged teal.

							True Metabolizable Energy						
Species	**GE**[a]	**DM**[b]	**CP**[c]	**ADF**[d]	**NDF**[e]	**EE**[f]	**Mean**	**n**[g]	**SE**	**Min**	**Max**	**CV**	**MEC**
Invertebrates													
Amphipoda	3.52						0.33	6	0.52	-0.81	2.60	380.1	9.6
Chironomidae	3.79						0.27	3	0.05	0.18	0.35	30.2	38.9
Corixidae	4.22						0.48	1	--	0.48	0.48	--	99.2
Gastropoda	1.01						-0.09	5	0.04	-0.19	0.01	-95.7	-78.7
Isopoda	2.56						0.08	1	--	0.08	0.08	--	24.5
Seeds													
Bidens cernua	4.83	0.90	17.66	38.09	45.89	8.39	0.55	3	1.98	-1.96	4.46	629.0	11.3
Cyperus esculentus	4.51	0.91	8.88	38.99	55.07	4.82	1.96	5	0.50	-0.69	3.53	57.7	43.5
Echinochloa crusgalli	4.18	0.90	10.28	24.97	33.49	3.26	2.65	4	0.10	2.38	2.82	7.5	63.2
Eleocharis obtusa	3.50	0.92	6.36	53.74	65.28	1.64	-0.18	5	0.50	-1.49	1.54	-622.8	-5.1
Fimbristylis annua	4.35	0.92	6.27	50.08	68.74	4.05	0.49	5	0.65	-1.00	2.27	294.7	11.4
Juncus canadensis	4.79	0.91	15.78	50.52	89.88	0.00	1.21	5	0.70	-0.47	3.24	128.8	25.2
Milo	3.84	0.89	7.78	5.76	10.78	3.19	3.36	6	0.24	2.59	3.89	12.8	77.5
Panicum dichotomiflorum	4.13	0.88	11.23	19.72	23.22	5.24	2.54	6	0.15	2.13	2.92	14.1	61.6
Panicum virgatum	4.30	0.90	15.28	28.76	33.92	5.20	2.05	6	0.13	1.65	2.57	15.3	47.6
Scirpus americanus	4.59	0.92	6.30	31.28	49.57	2.55	0.64	6	0.49	-0.93	2.65	189.4	13.9
Scirpus pungens	4.61	0.91	6.96	43.28	53.19	4.31	0.50	6	0.25	-0.51	1.07	122.4	10.8
Spartina patens	4.36	0.94	6.56	51.76	75.57	--[h]	0.05	5	0.56	-1.38	1.95	2505.3	1.1
Zizania aquatica	4.02	0.90	12.50	2.79	4.75	0.68	3.47	6	0.12	3.07	3.92	8.3	86.3

[a] Gross energy (kcal / g)

[b] Dry matter (%)

[c] Crude protein (%)

[d] Acid detergent fiber (%)

[e] Neutral detergent fiber (%)

[f] Ether extract (%)

[g] Number of independent observations for TME feeding trials.

[h] Insufficient sample for analysis.

Net Food Intake and Relative Food Intake explained 39% and 32% of the variation in TME, respectively ($P < 0.0001$; Fig. 1.1, 1.2). Wild rice was fed at the highest levels of any food (Table 1.3), and also had the highest TME of all foods studied (Table 1.2). Similarly, the lowest TMEs occurred in species with the lowest Net and Relative Intake levels (e.g., *Bidens cernua*, *Fimbristylis annua*, *Spartina patens*; Table 1.3). TME increased linearly with Bird Mass, but Bird Mass explained only 6% of the variation in TME (Fig. 1.3).

There was a weak negative relationship between Percent Regurgitation and Initial Food Mass, but the resulting regression equation explained only 4% of the variation in Percent Regurgitation (Fig. 1.4). The relationship appeared to be driven by low Percent Regurgitation for invertebrate foods, which were fed at high (wet) masses. When data were analyzed separately for seed and invertebrate foods, neither regression equation was significant ($F < 1.32$, $P > 0.255$). TME was weakly but significantly dependent on Percent Regurgitation; foods that were regurgitated at lower rates tended to have higher TMEs (Table 1.3, Fig. 1.5). All foods with $n>1$ were regurgitated by at least one bird. Nine of the 13 moist-soil seeds were regurgitated by all birds to which they were fed (Table 1.3). Regurgitation occurred in 65 of 84 observations (77.3%). The overall mean percentage of the test diet regurgitated was 18.4 ± 2.0%. However, mean percentage of the test diet regurgitated was higher for moist-soil seeds (20.5 ± 2.3) than for invertebrates (9.5 ± 2.6; $t = 3.13$, $P = 0.0032$).

Total gross energy excretion tended to increase with increasing Net Food Intake (Fig. 1.6). The resulting regression equation explained only 4% of the variation in energy excretion, and predicted energy excretion of 5.81 kcal for a starved bird (Fig. 1.6). There also was a weak positive relationship between Net Food Intake and Excreta Mass that explained little variation (4%) in Excreta Mass (Fig. 1.7).

Crude protein (range 6.2 - 17.6 %), ether extract (range 0 - 8.4 %) and gross energy (range 3.5 - 4.8 kcal / g) of seed diets were within, but at the lower end of the range of values reported by Petrie et al. (1998) (Table 1.2). Stepwise regression analysis revealed significant relationships between TME and acid detergent fiber (ADF) for both the full and reduced datasets:

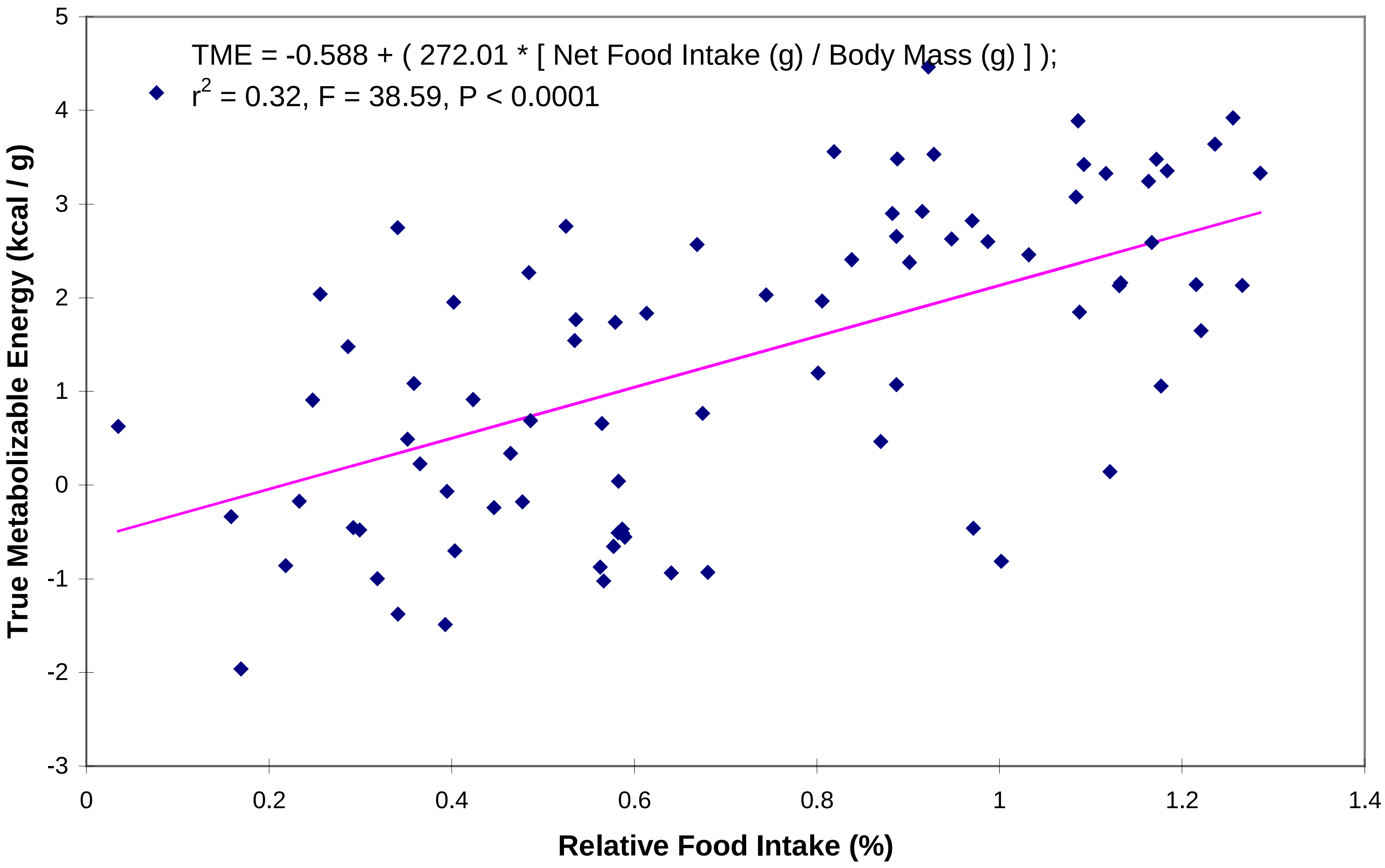

Figure 1.2 Relationship of true metabolizable energy (TME; kcal / g) to relative food intake (5; [Net Food Intake / Bird Mass] * 100) for moist-soil plant seeds and aquatic invertebrates fed to blue-winged teal.

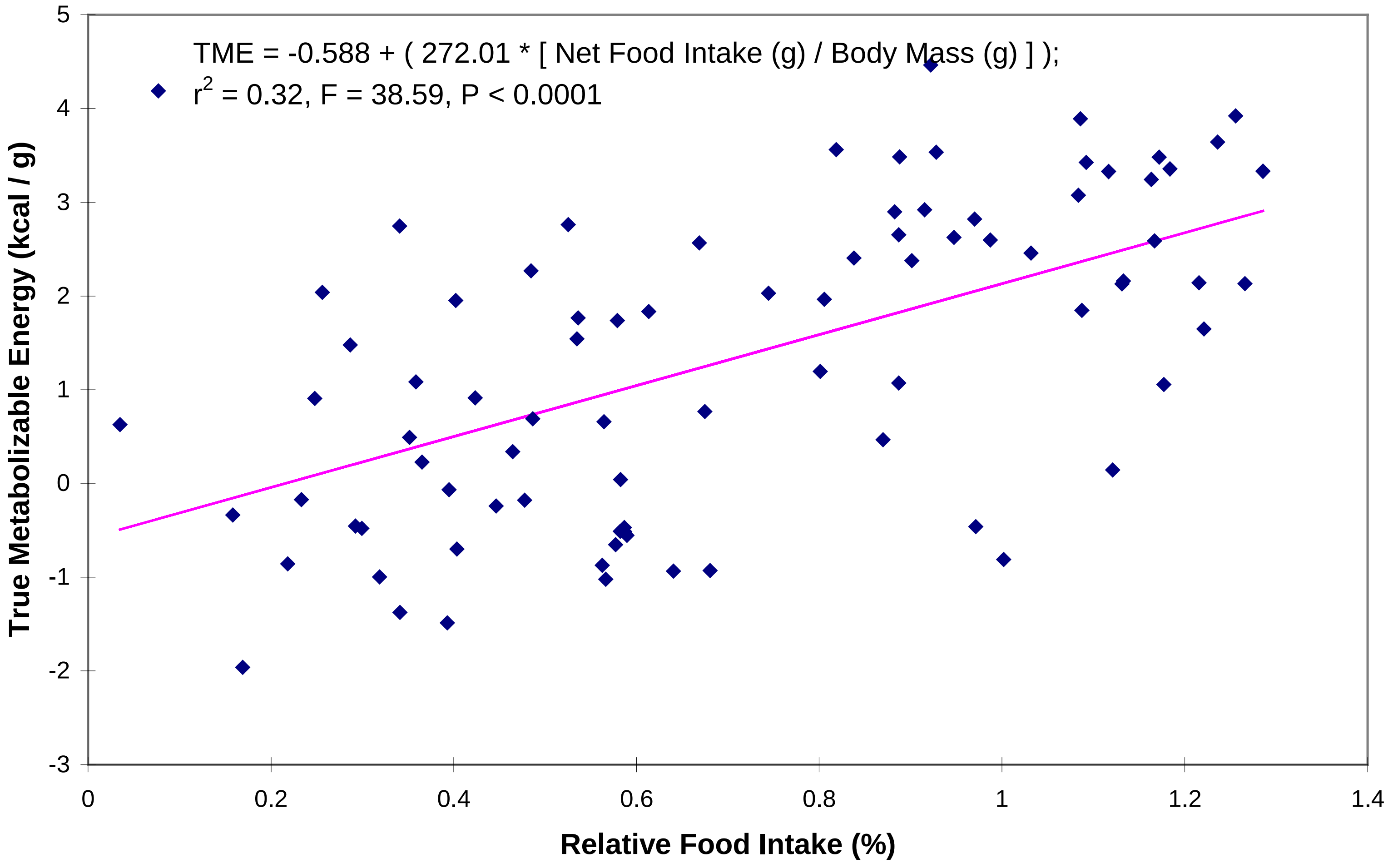

Figure 1.2 Relationship of true metabolizable energy (TME; kcal / g) to relative food intake (5; [Net Food Intake / Bird Mass] * 100) for moist-soil plant seeds and aquatic invertebrates fed to blue-winged teal.

Table 1.3. Mean Net Intake (g), Relative Intake (% of body mass), Excreta Mass (g), Excreta Energy Density (kcal / g), and Percent Regurgitation (% of Initial Food Mass) for aquatic invertebrates and moist-soil plant seeds fed to blue-winged teal.

	Net Intake (g)[a]		Relative Intake (%)[b]		Excreta Mass (g)		Excreta Energy Density (kcal / g)		Percent Regurgitation[c]			
Species	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**n**	**n_r[d]**
Invertebrates												
Amphipoda	AE[e] 2.3	0.3	BCD 0.7	0.1	AED 2.3	0.4	AC 3.58	0.18	AC 16.5	5.1	6	5
Chironomidae	BDE 0.9	<0.1	BE 0.3	<0.1	BE 1.0	0.1	AD 3.33	0.08	AC 3.4	2.6	3	2
Corixidae	BDEFG 0.3	--	BDE 0.1	--	BCD 1.1	--	AD 3.33	--	AC 0.1	--	1	1
Gastropoda	AE 2.0	0.1	BCD 0.6	<0.1	BCD 2.0	0.2	BD 2.52	0.11	BC 8.7	3.6	5	3
Isopoda	BDEJ 0.1	--	BE <0.1	--	BD 0.6	--	AD 3.22	--	AC 0.0	--	1	0
Seeds												
Bidens cernua	BCEH 1.6	1.0	BDE 0.4	0.2	BCD 1.6	0.2	AD 3.03	0.14	AC 27.8	14.4	3	3
Cyperus esculentus	AE 2.5	0.4	BCD 0.7	0.1	ADEF 2.1	0.2	AC 3.62	0.26	AC 21.1	5.6	5	5
Echinochloa crusgalli	ACF 3.1	0.3	ADE 0.8	0.1	BCD 1.9	0.1	AD 3.22	0.26	AC 22.8	6.7	4	4
Eleocharis obtusa	BDEH 1.4	0.1	BDE 0.4	<0.1	ADEF 2.1	0.1	AD 3.37	0.21	AC 16.5	7.2	5	5
Fimbristylis annua	BDE 1.3	0.2	BE 0.3	0.1	BD 1.6	0.1	AC 3.77	0.17	AC 30.6	5.8	5	5
Juncus canadensis	AE 2.0	0.4	BCD 0.7	0.1	AD 2.6	0.2	AC 3.58	0.23	AC 21.7	6.4	5	5
Milo	AC 3.2	0.2	AC 1.0	0.1	BF 0.9	0.2	AC 3.53	0.15	BC 7.9	5.3	6	2
Panicum dichotomiflorum	ACGJ 3.0	0.4	AD 0.9	0.1	BCD 1.9	0.2	AC 3.86	0.10	AC 13.7	11.7	6	4
Panicum virgatum	ACG 3.1	0.3	AC 1.0	0.1	AD 2.5	0.2	AC 3.71	0.06	BC 10.1	7.0	6	2
Scirpus americanus	AE 2.2	0.4	BCD 0.6	0.1	AC 3.0	0.3	AC 3.52	0.18	A 44.3	7.1	6	6
Scirpus pungens	ADH 2.6	0.3	AD 0.9	0.1	A 3.3	0.3	A 3.89	0.15	AC 27.1	6.0	6	6
Spartina patens	BE 1.0	0.1	B 0.3	<0.1	BCD 2.0	0.2	AD 3.33	0.16	AC 28.1	9.9	5	5
Zizania aquatica	A 3.5	0.1	A 1.2	<0.1	BD 1.4	0.1	BCD 3.08	0.09	BC 2.3	2.2	6	2
F[f]	6.40		8.64		6.59		3.82		2.43			
r^2	0.62		0.69		0.63		0.50		0.38			
P	<0.0001		<0.0001		<0.0001		<0.001		0.0053			

---

[a] Net Intake = Initial Food Mass - Regurgitated Food Mass.

[b] Relative Intake = (Net Food Intake / Body Mass) * 100.

Table 1.3, cont'd.

[c] Percent Regurgitation = 100 * [Σ (Regurgitated Feed Mass / Initial Food Mass)] / n.

[d] n_r = Number of birds within diets that regurgitated during feeding trials.

[e] Means within columns with similar letters do not differ ($P > 0.05$; Tukey's test).

[f] df = 17,66 for all analyses.

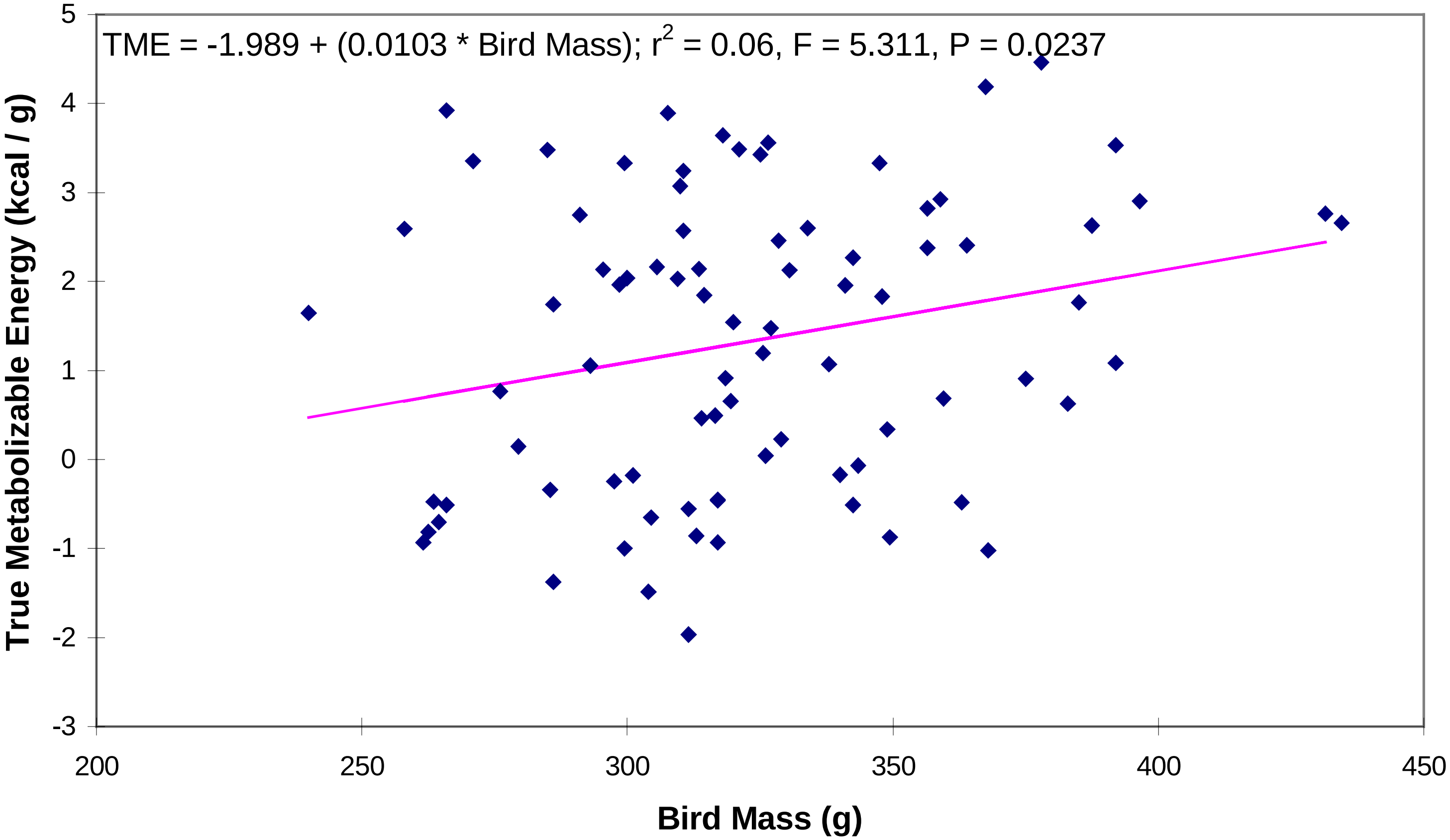

Figure 1.3. Relationship of true metabolizable energy (TME; kcal / g) to Bird Mass (g) for moist-soil seeds and aquatic invertebrates fed to blue-winged teal.

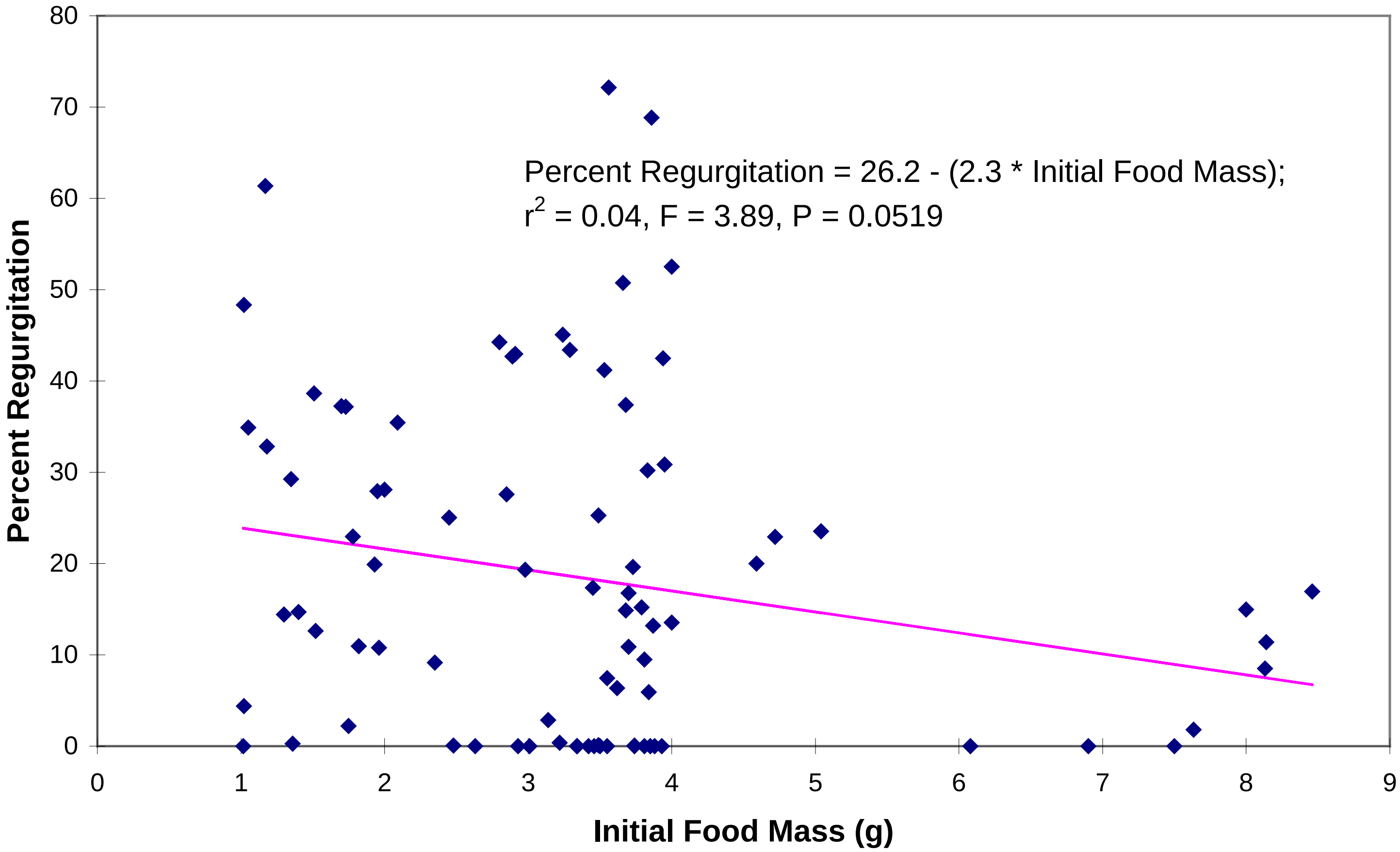

Figure 1.4. Relationship between Percent Regurgitation and Initial Food Mass (g) for moist-soil plant seeds and aquatic invertebrates fed to blue-winged teal.

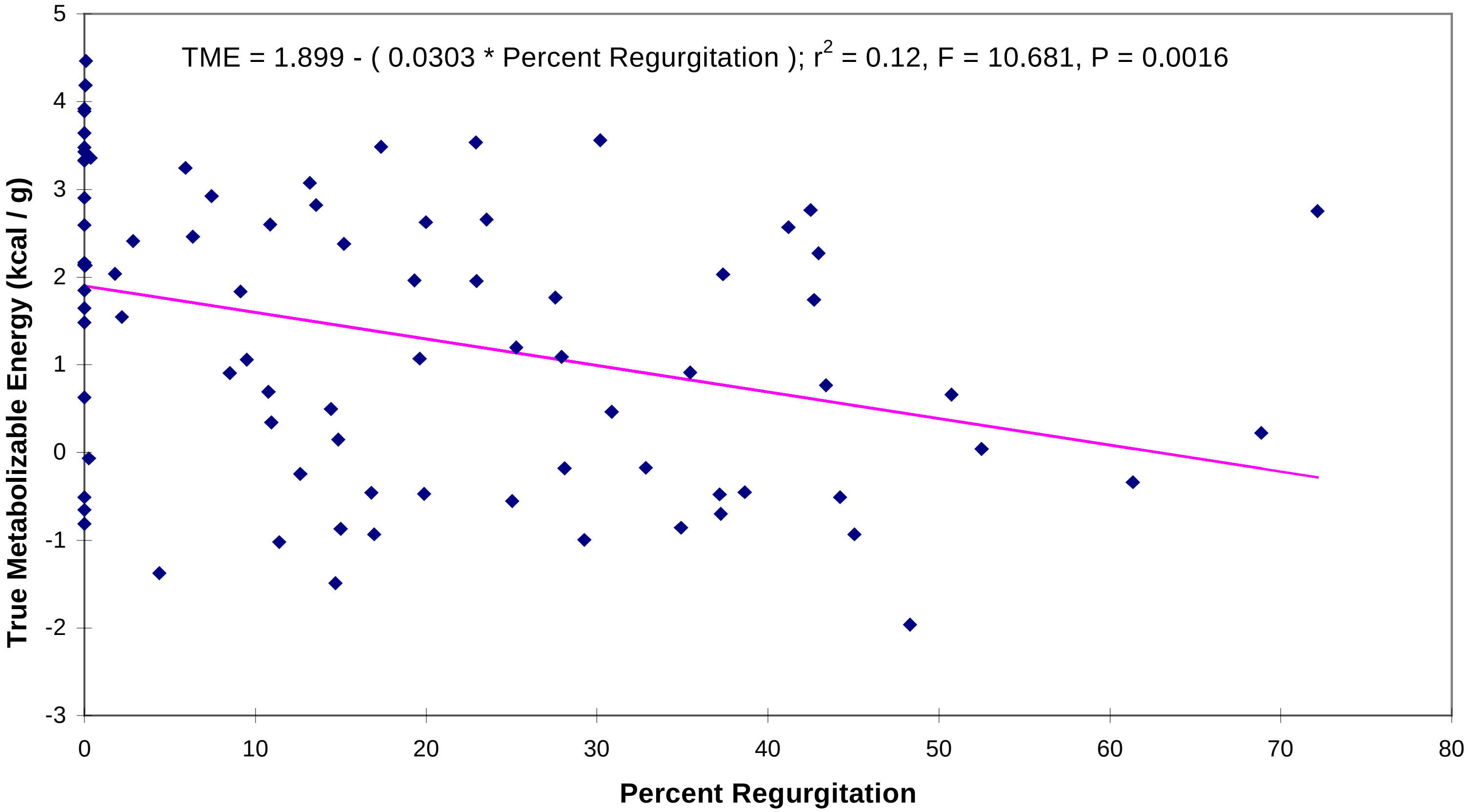

Figure 1.5. Relationship of true metabolizable energy (TME; kcal / g) to Percent Regurgitation ([Regurgitated Feed Mass (g) / Initial Feed Mass (g)] for moist-soil plant seeds and aquatic invertebrates fed to blue-winged teal.

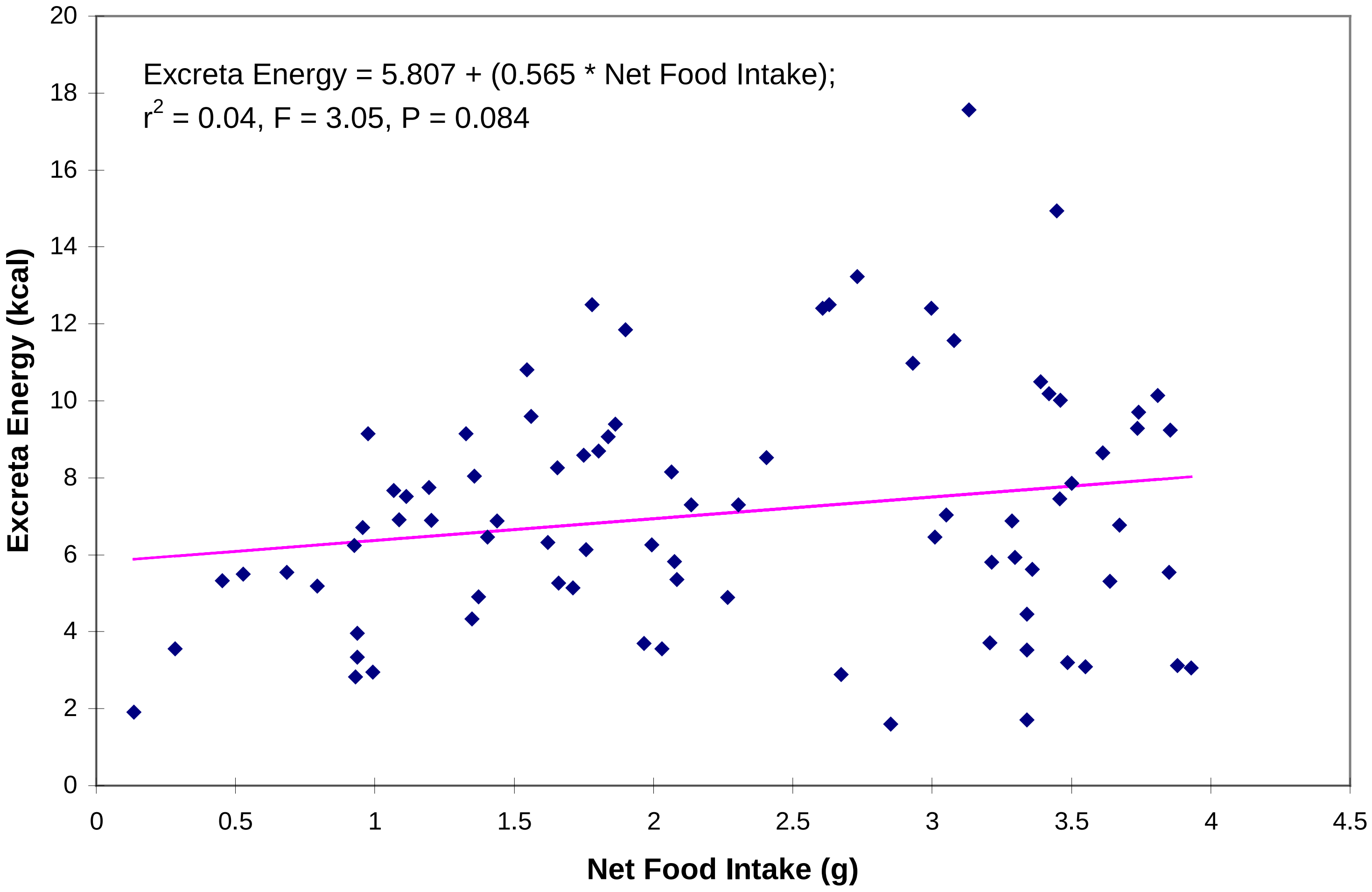

Figure 1.6. Relationship between Excreta Energy (kcal) and Net Food Intake (g) for moist-soil seeds and aquatic invertebrates fed to blue-winged teal.

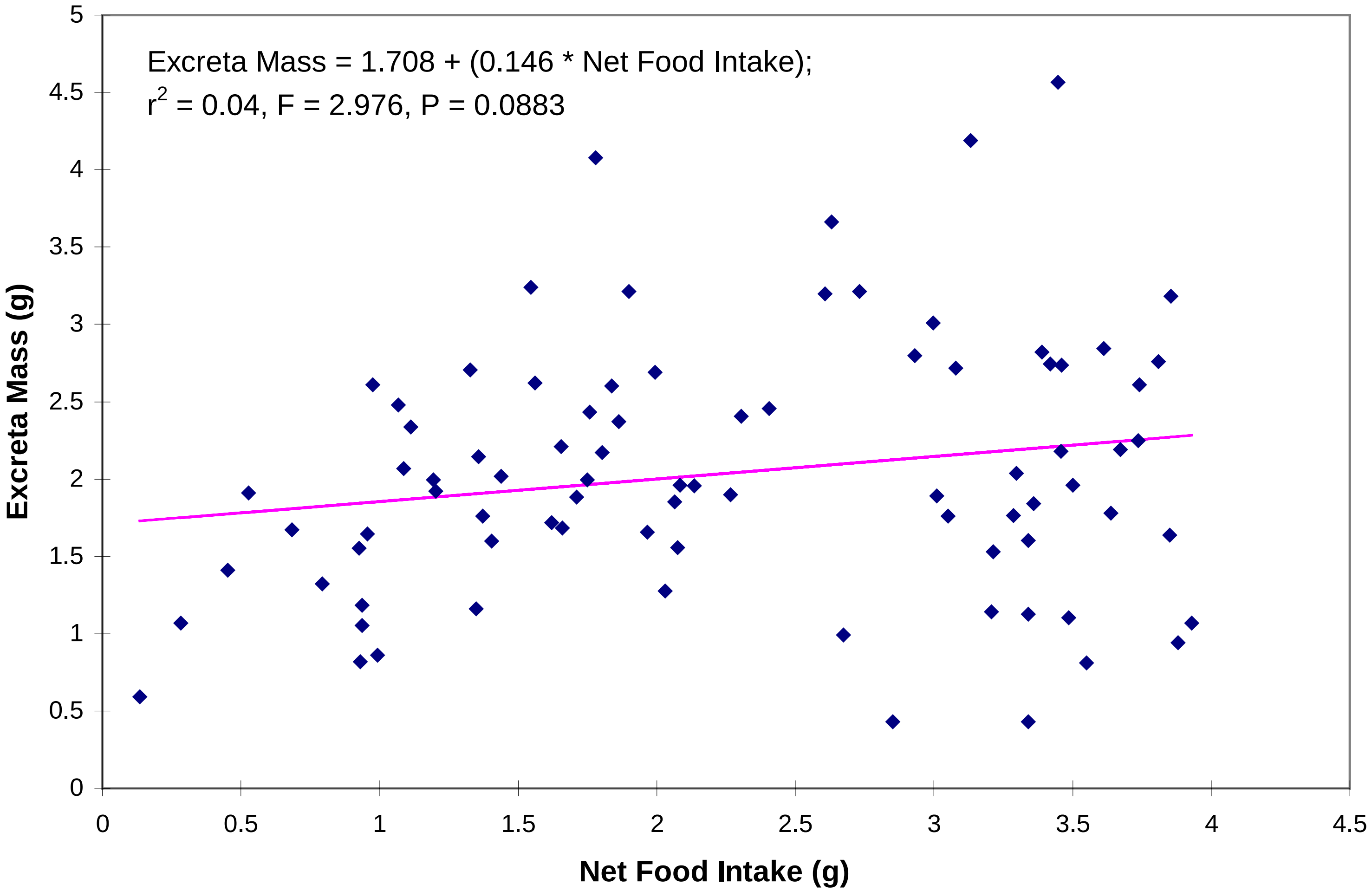

Figure 1.7. Relationship between Excreta Mass (g) and Net Food Intake (g) for moist-soil seeds and aquatic invertebrates fed to blue-winged teal.

Table 1.4. Mean observed values of true metabolizable energy for 13 moist-soil plant seeds, and TME values predicted from 2 regression equations based on acid detergent fiber (ADF) concentration.

		True Metabolizable Energy (kcal / g)		
			Predicted from ADF Regressions	
	ADF (%)	**Mean Observed (All Observations)**	**Full Dataset**[a]	**Reduced Dataset**[b]
Bidens cernua	38.1	0.55	1.20	1.74
Cyperus esculentus	39.0	1.96	1.14	1.69
Echinochloa crusgalli	25.0	2.65	2.08	2.39
Eleocharis obtusa	53.7	-0.18	0.15	0.96
Fimbristylis annua	50.1	0.50	0.40	1.14
Juncus canadensis	50.5	1.21	0.37	1.12
Milo	5.8	3.38	3.37	3.35
Panicum dichotomiflorum	19.7	2.54	2.43	2.65
Panicum virgatum	28.8	2.05	1.83	2.20
Scirpus americanus	31.8	0.64	1.63	2.05
Scirpus pungens	43.3	0.50	0.86	1.48
Spartina patens	51.8	0.05	0.29	1.06
Zizania aquatica	2.8	3.47	3.57	3.49

[a] Generated from means using all observed values.

[b] Generated only from means of species for which CV > 20%.

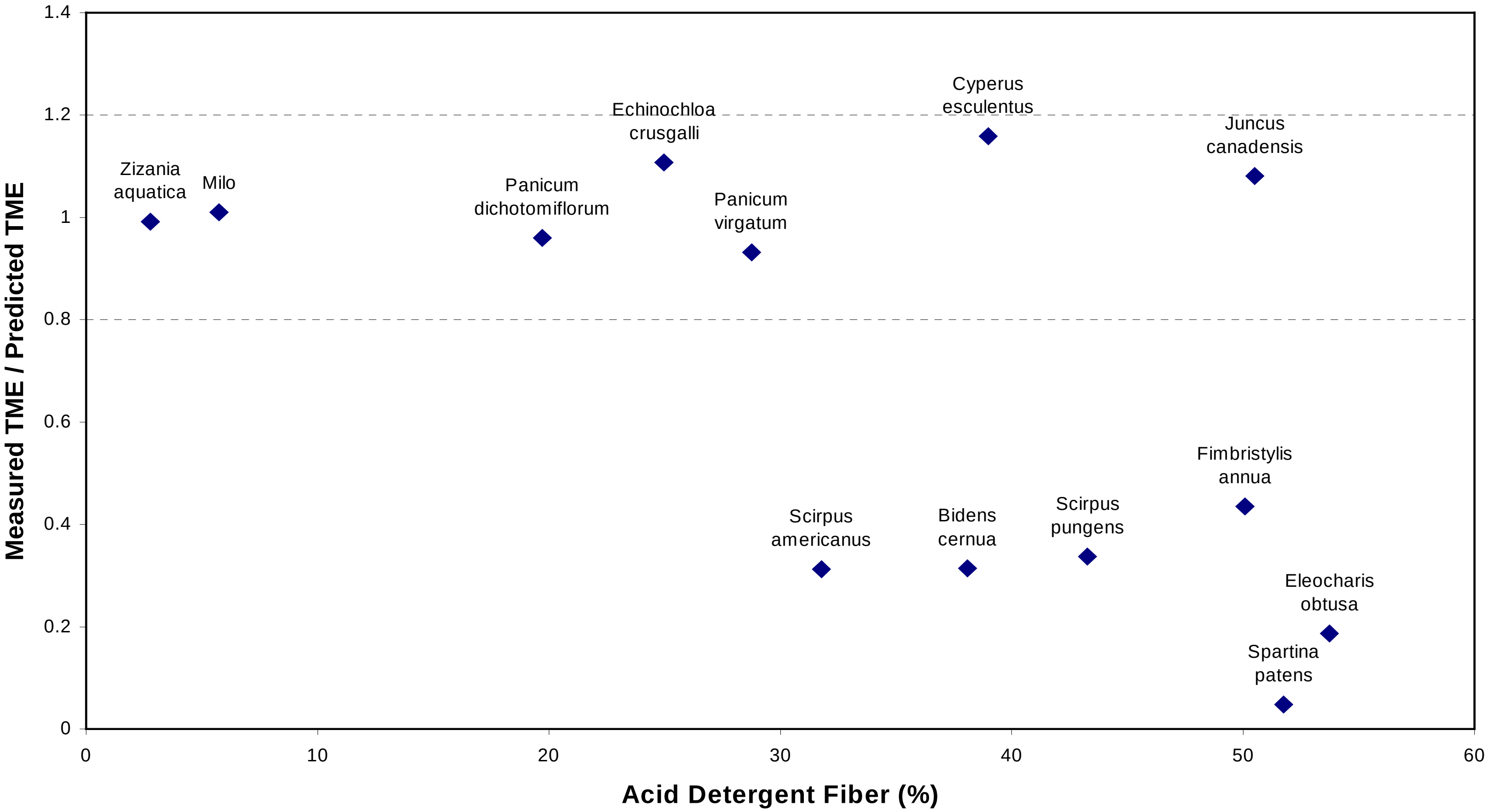

Figure 1.8. Relationship of measured to predicted true metabolizable energy for 13 moist-soil plant seeds of varying fiber content. Horizontal dashed lines indicate the range for which measured TME was within 20% of predicted TME. Predicted TME values were generated from a regression of measured TME on acid detergent fiber concentration for those species with CV of the measured TME mean <20%

Full: $TME = 3.734 - (0.0665 * ADF); r^2 = 0.493, F = 64.16, P < 0.0001$

Reduced: $TME = 3.639 - (0.0513 * ADF); r^2 = 0.724, F = 68.07, P < 0.0001$

Predicted TMEs were > 0.15 kcal / g for the full dataset equation and > 0.96 kcal / g for the reduced dataset equation. For the 2 species with the highest observed TME (Milo and *Zizania aquatica*), both equations produced predicted TMEs within 2% of the observed value. Predicted TMEs were substantially higher than observed TMEs for those species with extremely low observed TMEs (Table 1.4). TME predicted from the reduced dataset equation was higher than that predicted from the full dataset equation for most species (Table 1.4). Measured TME was within 20% of TME predicted from the reduced dataset equation for 7 species; measured TME was 4 - 38 % of predicted TME for the remaining 6 species (Fig. 1.8). The former group had lower mean ADF (24.5 ± 6.5 %) and Percent Regurgitation (14.2 ± 3.0) than did the latter (ADF 44.8 ± 3.5 %; Percent Regurgitation 29.1 ± 3.6).

DISCUSSION

Sources of Variation in TME Estimates

A fundamental assumption of this study was that true metabolizable energy is a quality of the test diet, and not a parameter that varies among bird species. Although no published literature has addressed this assumption for waterfowl, Miller (1984) did not detect differences among 3 species of dabbling ducks in AME of barnyardgrass seeds. Hoffman and Bookhout (1985) presented mean TME data for 4 moist-soil seeds that suggested no differences in metabolizability between mallards and pintails. Similarly, Castro et al. (1989) concluded that assimilation efficiency (i.e., metabolizability) is more strongly determined by food type (e.g., fruits, seeds) than the taxonomic order of the bird. Assuming constancy in analytical methods, the results of this study should therefore be applicable to other *Anas* species.

A regression of Excreta Gross Energy on Net Food Intake should yield a linear relationship in which the intercept equals the excreta energy of an unfed bird (Sibbald and Morse 1982). The equation developed in this study (Fig. 1.6) predicted energy excretion for an unfed bird (5.81 kcal) that was about 2.5x higher than the observed mean for starved birds (2.26 kcal). Several criticisms of the TME approach to evaluating dietary quality have suggested that measurement of endogenous losses in starved birds may not be valid due to the potential for high uric acid excretion in an energy deficient state (du Preez et al. 1981, Farrell et al. 1991). This argument predicts that energy excretion by starved birds would overestimate endogenous losses in an unfed bird, whereas endogenous losses in this study were low relative to predicted values from regression relationships. The slope estimate for the regression of Excreta Gross Energy on Net Food Intake (0.565) was within the range reported for poultry diets by Sibbald (1975) (0.20 - 1.62), but its precision (r^2 = 0.04) was quite low relative to the equations of Sibbald (1975) (r^2 = 0.72 to 0.97). Assuming similar digestive processes among animals, a strong positive relationship between Net Food Intake and energy excretion would be expected. The observed level of variation in energy excretion suggests that substantial among-bird variation in metabolic efficiency occurred.

Precision of TME estimates of nutritional value may be low relative to AME due to among-bird variance in excreta energy of fasted birds (Wolynetz and Sibbald 1984). Shires et al. (1979) and Sibbald (1976) recommend pairing of control and test birds on the basis of weight to reduce this variance. Variance associated with endogenous energy excretion should have been minimized in this study because each bird served as its own control. Variation in mean energy excretion of control birds (mean = 2.24 ± 0.136 kcal, *n* = 22, CV = 28.5%) was lower than variation in mean TME of many experimental foods (Table 1.2). Recalculation of TME using this value as a common estimate of endogenous losses reduced variance for some species, and increased variance for others. Consequently, the observed variation among species in mean TME is not directly attributable to variance among birds in endogenous losses.

Negative AMEs may occur at low intake levels as a consequence of the high relative contribution of endogenous losses to energy excretion, but TME should be similar at low and high intakes (Sibbald 1975). Sugden (1973*b*) found a negative mean AME for 3 foods known to be consumed by wild ducks: aquatic liverwort (*Ricciocarpus natans*), dock (*Rumex maritimus*) and pondweed (*Potamogeton richardsonii*) foliage. Sibbald (1975) recorded a negative AME for wheat in 13 of 48 roosters (27%). No studies of waterfowl foods report negative TME values, but precision of TME estimates is generally much higher than occurred in this study. Distribution of

TME values relative to Net Food Intake (Fig. 1.1, 1.2), Percent Regurgitation (Fig. 1.5) and bird mass (Fig. 1.3) do not show qualitative patterns that suggest a defensible standard for deletion of ‘biologically improbable’ values. Of these relationships, only the regression of TME on Bird Mass became nonsignificant when TMEs <0 were deleted. TMEs near but slightly >0 may be no less biased than negative values, yet have been reported with high precision for waterfowl foods. Jorde and Owen (1988) calculated a TME for periwinkles of 0.30 kcal / g; coefficient of variation for their observations was approximately 5%. The full dataset in this study produced means and variances that are outside the range of expected values. These values are useful in describing the variable physiological responses of captive wild-strain birds to natural diets, yet have little applied value due to their biological improbability.

Kaminski and Essig (1992) detected no differences in TME of commercial mash between wild-strain and game-farm mallards, although variation in TME estimates was slightly higher for game-farm birds. Birds used in this study were of identical origin to the wild-strain birds of Kaminski and Essig (1992), yet within-food variance in this study was substantially higher. However, Kaminski and Essig (1992) fed test birds a pre-ground commercial ration that had also been used as the pretrial maintenance diet. Because digestive tract morphology may change in response to diet composition (Miller 1975, Burton et al. 1979), low variance in TME would be expected for a diet to which test birds had been previously acclimated. Birds in this study were maintained on a diet that contained approximately 33% (v/v) milo for 3 months prior to the start of feeding trials. Percent Regurgitation of milo was among the lowest of all foods (Table 1.3), suggesting that lack of pre-trial exposure to other foods may have contributed to high Percent Regurgitation and variance in TME. Milo is low in fiber (Table 1.2; see also Petrie et al. 1998) and highly digestible (Table 1.2, Petrie et al. 1998), suggesting that changes in digestive morphology associated with pretrial exposure may have been minimal.

Intake Rate and Regurgitation

Theory predicts that AME should vary with intake level, whereas TME should be independent of intake (Sibbald 1975, 1976, 1980, Miller and Reinecke 1984). Jorde and Owen (1988) report nitrogen-corrected TME values for 4 invertebrate taxa that varied inversely with intake level, but did not suggest potential causative factors leading to the observed variation. Studies of domestic poultry also have documented variation in TME with intake level (e.g., Sibbald and Morse 1982, Wolynetz and Sibbald 1984), although the magnitude of variation in these studies was substantially lower than in this study. Among applications of TME methods to wild birds, only Bennett and Hart (1993) have reported data that confirms a lack of relationship between TME and intake. It should be noted that Bennett and Hart (1993) studied TME of fish, a highly digestible, high-protein food, in great blue herons (*Ardea herodias*). This diet composition may more accurately reflect the digestibility and proximate composition of the poultry diets for which TME methods were originally developed. The majority of waterfowl studies have evaluated TME of highly digestible foods such as invertebrates or agricultural seeds. High-fiber moist-soil seeds may have slow passage rates relative to agricultural seeds. Consequently, adjustment of excreta collection times may be necessary for these diets (Sibbald 1979, Parsons 1981).

Sibbald (1976) recommends an intake rate that is approximately equal to 1% of body weight. Initial food masses in this study were intended to approximate this recommendation, but high Percent Regurgitation led to intake rates that were generally <1% (Fig. 1.2). Regurgitation can occur due to high intake, but error in excreta collection is magnified at low intake (Sibbald 1976). Significant positive relationships between intake rate and TME (Figs. 1.1, 1.2) are inconsistent with the predicted relationship (Sibbald 1975, 1976, 1980, Miller and Reinecke 1984).

Correction of food intake for unconsumed food should not bias TME estimates, assuming that 1) collection of regurgitated food is complete and without error, and 2) physiological processes associated with regurgitation do not impact metabolizability. To the contrary, there was a pronounced negative relationship between Percent Regurgitation and TME (Fig. 1.5) that predicted a 33% reduction in TME for the observed mean rate of regurgitation of moist-soil seeds (20.5%). Percent Regurgitation and Net Food Intake are inversely related; as Percent Regurgitation increases, Net Food Intake decreases. Percent Regurgitation did not apparently depend upon Initial Food Mass, yet the relationship between Net Food Intake and TME (Fig. 1.1) suggests that high Percent Regurgitation directly influenced measures of TME. Thus, the assumption that food intake can be corrected for regurgitated food mass without loss of precision or accuracy is probably untenable. Efforts to control regurgitation by manipulating water availability and altering feeding techniques during a preliminary set of feeding trials were unsuccessful. Substantial variation in fiber content between maintenance diets and experimental foods may have contributed to the high Percent Regurgitation observed.

Accuracy of TME Estimates

Because few studies have evaluated TME of natural waterfowl foods, few standards are available for assessing accuracy of this study. Mean TME in this study for milo and barnyardgrass was 11% and 20% lower, respectively, than TME_n measured by Petrie et al. (1998). The estimates of Petrie et al. (1998) were corrected to zero nitrogen balance, whereas limited excreta sample mass in this study precluded this correction. Because nitrogen-corrected TME values are lower than uncorrected estimates (Sibbald and Morse 1982, Wolynetz and Sibbald 1984), departure from estimates of Petrie et al. (1998) can not be attributed to nitrogen correction. Rather, the magnitude of difference in TME estimates between this study and Petrie et al.'s (1998) study would increase if similar expressions of TME were employed. Correction of TME to zero nitrogen balance can improve the precision of estimates (Dale and Fuller 1984, Jorde and Owen 1988, Brugger 1993, M. Petrie, Ducks Unlimited Inc., personal communication), although effects of the correction on accuracy are unknown (Sibbald and Morse 1982). Petrie et al. (1998) did not report intake rates relative to bird mass (i.e., Relative Food Intake), but their mean food and bird mass data correspond to intake rates from 0.1% to 0.5%. These intake rates are at the lower end of the range employed in this study (Fig. 1.2), suggesting that variation in Net Food Intake did not directly cause the observed differences in TME.

Birds in the Petrie et al. (1998) study regurgitated foods with substantially lower frequency than observed in this study and were deleted prior to data analysis. The regression equation relating TME to Percent Regurgitation (Fig. 1.5) suggests that 7% and 12.5% Percent Regurgitation would produce 11% and 20% reduction in mean TME for milo and barnyardgrass, respectively. These predictions are similar in magnitude, and nearly identical for milo, to the observed Percent Regurgitation in this study (Table 1.3). Regurgitation may therefore have contributed substantially to the observed differences in TME between studies. Large birds (e.g., Canada geese) also have higher capacity for fiber digestion than do small birds (e.g., blue-winged teal) due to higher gut residence time (Robbins 1983). The primary evidence for lack of interspecies variation in TME was produced in studies of species that vary relatively little in body size (e.g., mallards and pintails; Hoffman and Bookhout 1985). Conversely, there is an order of magnitude of difference in body size between Canada geese and blue-winged teal. Avian metabolic rate is a power function of body size (Lasiewski and Dawson 1967, Robbins 1983), suggesting that the relationship of other physiological parameters to body size may be similarly nonlinear.

The 2 *Scirpus* genera included in this study both had extremely low TMEs (Table 1.2). Hoffman and Bookhout (1985) report TMEs of 0.85-0.99 for *S. validus* seeds, suggesting that seeds of this genus may be uniformly low in metabolizability. However, coastal marsh management practices are often targeted at providing several *Scirpus* species as duck foods (Hindman and Stotts 1989), including 1 that was included in this study (*S. americanus*). Assuming a daily energy expenditure of 292 kcal / day for an adult mallard (Reinecke et al. 1989), the mean TME for *S. americanus* from this study would produce an estimated maintenance intake requirement of about 456 g / day. This estimate corresponds to about 50% of body mass and is clearly beyond the digestive capacity of mallards, suggesting that the mean TME from this study is not reflective of its true value to waterfowl.

Composition of Foods

Variation in TME was quite low for some foods (e.g., *Echinichloa crusgalli*; CV = 7.5%), but was extremely high for other foods (e.g., *Spartina patens*; CV = 2505.4%). Because experimental foods were interspersed among feeding trials, the observed pattern of variation did not likely result from temporal physiological changes in fed birds or variation in force-feeding techniques. Rather, it is more likely that composition of diets contributed to variability in results. Species that exhibited high variation tended to produce fibrous seeds (e.g., *Juncus canadensis*, *Spartina patens*, *Eleocharis obtusa*) or abundant chaff that was difficult to completely separate from pure seed (e.g., *Bidens cernua*, *Fimbristylis annua*). In contrast, precision was generally high for species that produce relatively large seed kernels that were easily separated from chaff (e.g., *Echinochloa crusgalli*, *Zizania aquatica*, *Panicum dichotomiflorum*, *P. virgatum*). These observations are consistent with the inverse relationship between fiber content and TME of agricultural seeds shown by Petrie et al. (1998).

Stepwise regression models revealed that ADF accounted for most (>92%) of the explained variation in TME. This result is consistent with the analysis by Petrie et al. (1998), who also showed a significant negative relationship between crude fiber content and TME of Canada goose foods. Values of TME predicted by both the full and reduced dataset equations departed substantially from the observed TMEs for some plant species (Table 1.4, Fig. 1.8), suggesting that the TME method does not provide accurate estimates of TME for these foods. In particular, predicted values from the reduced dataset equation (i.e., generated from species with CV < 20%) suggested that the test diets could be assigned to 2 distinct groups. Those species for which Percent Regurgitation and ADF were relatively low had similar observed and predicted TMEs, whereas those species with relatively high Percent Regurgitation and ADF had measured TMEs that were <45% of the predicted value (Fig. 1.8). The high-fiber foods in this study were substantially higher in fiber than species included in other published studies (e.g., Petrie et al. 1998). Thus, the TME method appears to be an unreliable means of assessing dietary quality for high-fiber waterfowl foods. In both this study and that of Petrie et al. (1998), protein and ether extract were nonsignificant predictors of TME, suggesting that these parameters are of little value in describing metabolizable energy. Protein and fat are, however, important dietary constituents that may influence food selection patterns (Alisauskas and Ankney 1992, Jorde et al. 1995, McKnight and Hepp 1998).

Foraging Ecology of Wintering Waterfowl

Evidence from several studies of waterfowl foraging ecology suggests that food abundance may be a more important predictor of use than nutritional value. Euliss and Harris (1987) found that wintering pintails and green-winged teal in southern California generally consume foods in proportion to availability, suggesting that birds may not select for high quality foods. Despite pronounced differences in morphology and foraging strategy, Euliss et al. (1991) showed that ruddy ducks, pintails and shovelers differed in consumption of plant and animal foods, and concluded that the 3 species foraged opportunistically. However, Miller (1987) found that wintering pintails in northern California consumed foods in proportion to their availability in fall when food was abundant, but actively selected several foods, particularly invertebrates, in late winter. Despite substantial variation in proximate composition among foods, the proximate composition of total diets was stable among seasons for ruddy ducks, shovelers and pintails (Euliss et al. 1997). Given that moist-soil plant seeds are generally low in metabolizable energy content relative to agricultural seeds, selection among available moist-soil foods may not be an advantageous foraging strategy for wintering birds. Because nutritionally favorable habitat is not always thermally favorable, birds may forego nutritionally balanced diets during periods of extreme weather in favor of reduced energy expenditure (Jorde et al. 1984).

Petrie et al. (1998) found that crude fiber was the only proximate constituent that significantly predicted true metabolizable energy of 8 Canada goose foods. Jorde and Owen (1988) observed that TME was substantially lower for hard-shelled molluscs (e.g., periwinkles) than for soft-bodied invertebrates (e.g., *Gammarus* spp.; Table 1.5), suggesting that molluscs alone may be insufficient to support wintering black ducks (Albright et al. 1983). Hoffman and Bookhout (1985) found that the dominant food in mallard and pintail crops (rice cutgrass) had the lowest gross energy concentration (4.47 kcal / g) but the highest true metabolizable energy (2.82 - 3.00 kcal / g) of the foods studied. Collectively, the above observations suggest that metabolizable energy may be a more biologically valid measure of dietary quality than proximate composition.

Although agricultural grains are high in metabolizable energy (Petrie et al. 1998), they may lack nutrients essential for egg formation (Krapu 1979) and maintenance of winter body weight (Loesch and Kaminski 1989). Despite their nutritional deficiencies, agricultural habitats provide important sources of abundant high-energy food for wintering birds (Miller 1987, Jorde et al. 1983, Cox and Afton 1997). Because waterfowl maintained on suboptimal diets generally regain weight rapidly when fed nutritionally balanced diets (Loesch and Kaminski 1989, Jorde et al. 1995), agricultural foods may be an important source of food during periods when natural foods are temporarily unavailable. Heitmeyer and Fredrickson (1990) concluded that fatty acid

Table 1.5. Gross energy (kcal / g), true metabolizable energy (TME; kcal / g) and apparent metabolizable energy (AME; kcal / g) of waterfowl foods.

Food	Bird Species	GE	TME	AME	Source
Animal Foods					
Blue mussel	American black duck	0.52	0.01 - 0.04 [a]		Jorde and Owen 1988
Cladocera	Blue-winged teal	2.63		0.850	Sugden 1973*b*
Gammarus	American black duck	3.52	2.12 - 2.32 [a]		Jorde and Owen 1988
Gammarus	Blue-winged teal	3.78		2.320	Sugden 1973*b*
Gammarus	Lesser scaup	3.78		3.050	Sugden 1973*b*
Periwinkle	American black duck	0.27	0.27 - 0.60 [a]		Jorde and Owen 1988
Snails	Blue-winged teal	1.25		0.590	Sugden 1973*b*
Soft-shelled clam	American black duck	0.22	0.26 - 0.93 [a]		Jorde and Owen 1988
Stratiomyidae larvae	Mallard			2.390	Purol 1975
Plant Foods					
Alfalfa	3 species [c]	4.21		1.420	Miller 1984
Barley[b]	Mallard			3.173	Sugden 1971
Barnyardgrass	Canada goose	4.51	3.291 [a]		Petrie et al. 1998
Barnyardgrass	3 species [c]	4.36		2.890	Miller 1984
Barnyardgrass (Coast)	Mallard		2.860		Hoffman and Bookhout 1985
Barnyardgrass (Coast)	Pintail		2.820		Hoffman and Bookhout 1985
Barnyardgrass (Junglerice)	Mallard		2.540		Reinecke et al. 1989
Chufa tubers	Canada goose	5.20	4.030 [a]		Petrie et al. 1998
Corn	Canada goose	4.41	3.901 [a]		Petrie et al. 1998
Milo	Canada goose	4.36	3.781 [a]		Petrie et al. 1998
Rice	Canada goose	4.18	2.811 [a]		Petrie et al. 1998
Rice cutgrass	Mallard	4.47	3.000		Hoffman and Bookhout 1985
Rice cutgrass	Pintail	4.47	2.820		Hoffman and Bookhout 1985
Rye	Mallard			3.336	Sugden 1971
Scirpus paludosus seeds	Blue-winged teal	4.58		0.890	Sugden 1973*b*
Scirpus validus seeds	Blue-winged teal	4.87		0.530	Sugden 1973*b*
Scirpus validus seeds	Mallard	4.91	0.990		Hoffman and Bookhout 1985

Table 1.5. cont'd.

Food	**Bird Species**	**GE**	**TME**	**AME**	**Source**
Scirpus validus seeds	Pintail	4.91	0.850		Hoffman and Bookhout 1985
Smartweed	Canada goose	4.53	1.589 [a]		Petrie et al. 1998
Smartweed (Pennsylvania)	Mallard	4.61	1.080		Hoffman and Bookhout 1985
Smartweed (Pennsylvania)	Pintail	4.61	1.250		Hoffman and Bookhout 1985
Soybean	Canada goose	5.68	3.549 [a]		Petrie et al. 1998
Wheat	Blue-winged teal	4.42		3.070	Sugden 1973*b*
Wheat[b]	Mallard			3.526	Sugden 1971
Winter wheat	Canada goose	4.35	2.400 [a]		Petrie et al. 1998

[a] TME values corrected to zero nitrogen balance (TME_n).

[b] Metabolizable energy calculated as the mean of 3 and 4 varieties for barley and wheat, respectively.

[c] Mean AME for northern pintails, gadwalls and northern shovelers.

composition was an important proximate factor in determining winter diet selection of female mallards. The ability of a winter diet to provide for the specific nutritional needs of waterfowl may subsequently influence survival and reproduction (Alisauskas and Ankney 1992), and may be independent of energy content.

Assessing Waterfowl Diet Quality

True metabolizable energy is recognized as a valid expression of dietary quality that can be measured rapidly and reliably (Miller and Reinecke 1984). True metabolizable energy accounts for the fraction of intake energy metabolized by an animal, yet remains solely a measure of energy content. Specific dietary constituents that positively influence nutritional status (e.g., protein, lipid) or negatively influence metabolizability (e.g., fiber, tannins) may not be directly reflected in TME (but see Petrie et al. 1998). Protein and lipid content of foods are important proximate factors influencing diet selection by waterfowl during clutch formation and pre-migratory fattening (Krapu and Swanson 1975, McKnight and Hepp 1998). Availability of abundant high-energy foods (e.g., agricultural grains) may contribute to survival of wintering waterfowl by mitigating short-term periods of limited access to natural foods, yet these foods may fail to fully provide for seasonal protein and lipid requirements. Thus, TME should not be an exclusive basis for evaluating nutritional value of waterfowl foods. Rather, wetland management practices should consider protein and lipid content of foods, as well as the likelihood that weather or habitat conditions will limit waterfowl access to these foods. Petrie et al. (1998) recommend implementing habitat management practices that provide both agricultural grains and moist-soil plant seeds.

Metabolizable energy generally is measured using seeds collected directly from mature plants. This collection method does not accurately represent food acquisition by waterfowl. Seeds are of greatest significance to waterfowl diets after plants are senescent and seeds have been dropped. Flooding of habitats with high seed production may encourage waterfowl foraging, but extended submergence leads to deterioration of seeds (Nelms and Twedt 1996). Although little research has focused on seed deterioration rates, Fredrickson and Reid (1988) suggest that agricultural seeds deteriorate more rapidly than moist-soil plant seeds. This pattern would be expected, given that many moist-soil plants are adapted for reproduction under seasonally flooded conditions, whereas agricultural grains are not. However, the impact of flood-induced deterioration on nutritional value of seeds is unknown. Short-term flooding may increase nutritional value by softening hard seed coats, whereas nutritional value may be lost under long-term flooding. To the extent that Fredrickson and Reid's (1988) conclusion holds true, differences in TME between agricultural grains and moist-soil seeds observed in captive birds may not accurately reflect differences in value to foraging waterfowl. Investigation of flooding impacts on seed nutritional value would aid in timing of fall floods and would further our understanding of waterfowl nutrition.

Relevance to Shorebird Habitat Management

Availability of invertebrate foods is an important determinant of habitat quality for migrant shorebirds. Due to the narrow window of opportunity for successful breeding in the Arctic, shorebirds must maximize food intake while minimizing stopover time during the northward migration. Abundant invertebrate resources on stopover areas allow migrants to rapidly replenish depleted reserves and enhance the likelihood of optimal timing of arrival on the breeding grounds. Despite the known importance of food to migrant shorebirds, little research has focused on nutritional requirements of shorebirds during spring. Though few studies have addressed direct patterns of selection among invertebrate taxa, selection among habitats may reflect the ability of dominant invertebrate foods to provide for the nutritional needs of shorebirds. Shorebirds generally exploit invertebrate communities that are dominated by one or a few taxa. Higher order selection patterns (i.e., selection among habitats) may therefore be more reflective of shorebird nutritional requirements than selection among available foods within habitats. Davis and Smith (1998) provided evidence that shorebird habitat selection occurs primarily at the landscape scale. Habitat variability evident at this scale may also influence invertebrate distribution, with a subsequent influence on shorebird diet and nutrition.

Investigations of waterfowl foods have shown no differences between bird species in AME (Miller 1984) or TME (Hoffman and Bookhout 1985), suggesting that slight variation within families in gastrointestinal morphology are of little consequence to metabolizability. An adaptation to the generally herbivorous diet in waterfowl is the presence of intestinal ceca; these structures are lacking in shorebirds. Ceca enhance absorption of nitrogen, which may be limited in diets dominated by plant material (Remington 1989, Sedinger 1997). Ceca probably play a minimal role in protein uptake from foods such as invertebrates that are high in protein metabolizability. TME values of invertebrates obtained in waterfowl may therefore not be directly applicable to shorebirds, although these data likely reflect relative value to shorebirds. However, shorebird diets are not strictly limited to animal foods. Seeds and tubers also are consumed by shorebirds (Rundle 1982, Baldassarre and Fischer 1984, Weber and Haig 1997, Davis and Smith 1998), and may be dominant foods for some species (Baker 1977, Alexander et al. 1996). Shorebirds generally favor unvegetated mudflats and use foraging methods that optimize their ability to acquire invertebrate prey, suggesting that consumption of plant matter may be largely incidental to predation on invertebrates. Nonetheless, the potential contribution of plant foods to shorebird energy balance should not be ignored. Given digestive morphology that does not optimize metabolizability of plant foods, TME values for plant foods obtained in waterfowl likely overestimate their value to shorebirds.

CONCLUSIONS

There are marked differences among plant and animal taxa in availability to waterbirds that may be more significant to foraging ecology than TME alone. In temperate zone habitats favored by nonbreeding waterbirds, temporal and spatial distribution are more variable among animal than among plant foods. Plants are largely senescent during the period of residence for wintering waterfowl on the mid-Atlantic coast. Peak biomass of seeds, tubers and vegetative matter roughly corresponds to the arrival of waterfowl on wintering areas. These resources are immobile and are continually depleted throughout the wintering period. In contrast, growth and development of invertebrates may continue through the winter months, providing waterbirds a more renewable source of forage. Moreover, invertebrates exhibit a wide range of habits, including sedentary benthic (e.g., Chironomidae) and highly mobile nektonic (e.g., Corixidae) organisms. Variation in invertebrate size and behavior has been implicated as an important factor in community structure of waterfowl (Nudds and Bowlby 1984, Armstrong and Nudds 1985) and foraging site selection of shorebirds (Hicklin and Smith 1984). The consequences of intra-seasonal variation in availability, combined with seasonal protein and lipid requirements, may render TME a relatively poor predictor of the true value of foods to non-breeding waterbirds.

The TME values observed in this study are likely of limited practical value due to high variation and presence of negative values for some species. Predicted TME values based on ADF concentration, however, are within the range of expected values of TME for waterfowl foods. Given that this study showed similar patterns of TME variation with fiber concentration as did Petrie et al. (1998), predicted values may be more appropriate for use in calculating impoundment carrying capacity based on TME (Reinecke et al. 1989). Such application of these data should, however, be tempered against the uncertain nature of the “true” value of TME for some foods.

Despite the recognition that TME is a desirable means for evaluating dietary quality (Miller and Reinecke 1984), it is clear that caution is warranted in assuming that the technique will produce accurate and precise results for waterfowl foods, particularly those that are high in fiber. The method described by Sibbald (1975) was intended for assessing the value of highly digestible, concentrated diets in domestic animals, and consequently may underestimate the value of high-fiber natural diets to waterfowl. Further, methods commonly employed in TME studies with waterfowl fail to account for flood-induced changes in metabolizability. Future investigators should be aware of the potential for confounding factors in captive wild-strain birds (e.g., regurgitation), and should seek methods that improve accuracy of TME estimates for natural foods (e.g., pre-trial acclimation of test birds to high-fiber diets).

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