

TRUE METABOLIZABLE ENERGY FOR WOOD DUCKS FROM ACORNS COMPARED TO OTHER WATERFOWL FOODS

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Abstract: Acorns of bottomland red oaks (*Quercus* spp.) are an important food of North American wood ducks (*Aix sponsa*). Barras et al. (1996) demonstrated that female wood ducks selected willow oak (*Q. phellos*) acorns over other species. We measured true metabolizable energy (TME) derived by captive, wild-strain, adult female wood ducks from acorns of willow oak, water oak (*Q. nigra*), cherrybark oak (*Q. pagoda*), and pin oak (*Q. palustris*) to determine whether female wood ducks' preference for willow oak acorns was related to TME. Estimates of TME within acorn species were relatively precise, yet we did not detect variation in TME among acorn species ($P = 0.31$); hence, we estimated TME across species (2.76 ± 0.033 [SE] kcal/g dry mass; $n = 34$). We concluded that TME apparently did not explain female wood ducks' preference for willow oak acorns and hypothesized that morphological characteristics of willow oak acorns may be proximate cues related to selection by wood ducks. We also summarized known TME estimates for acorns fed to wood ducks and mallards (*Anas platyrhynchos*), and natural and agricultural foods fed to mallards, northern pintails (*A. acuta*), blue-winged teal (*A. discors*), and Canada geese (*Branta canadensis*). We found that acorns and moist-soil plant seeds and tubers provided, on average, about 76% of the TME in agricultural seeds. Thus, bottomland-hardwood and moist-soil habitats have potential to provide significant amounts of dietary energy, as well as greater diversity of foods and nutrients than croplands. Researchers should continue to determine TME of common foods (plant and animal) of waterfowl, and use TME in estimating waterfowl habitat carrying capacity (e.g., Reinecke et al. 1989). Additionally, large-scale, reliable estimates of plant and animal food availability in bottomland-hardwood and moist-soil habitats are needed to evaluate carrying capacity of landscapes important to waterfowl, such as the Mississippi Alluvial Valley (MAV).

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Barras (1993:34–37) reviewed literature on use of acorns by wood ducks, mallards, and several species of birds and mammals. He quoted Bellrose (1976:194), who stated, "Acorns are the favored foods of more wood ducks in more places than any other plant food from New Hampshire to South Carolina to Mississippi to Wisconsin." Acorns have been reported to account for as much as 74% (of total dry mass) of the esophageal contents of wintering wood ducks (Delnicki and Reinecke 1986). Wood ducks consume acorns from a variety of bottomland red oaks (Bellrose and Holm 1994), including cherrybark oak (Hall 1962), Nuttall oak (*Q. nuttallii*; Delnicki and Reinecke 1986), pin oak (McGilvrey 1966, Drobney and Fredrickson 1979), water oak

(Hall 1962, McGilvrey 1966, Allen 1980, Delnicki and Reinecke 1986), and willow oak (Hall 1962, Drobney and Fredrickson 1979, Allen 1980, Delnicki and Reinecke 1986). Acorns are important sources of energy for migrating, wintering, and prebreeding wood ducks, because these nuts contain relatively high levels of fatty acids (Heitmeyer and Fredrickson 1990) and nitrogen-free extract (Ofcarcik and Burns 1971, Short 1976, Landers et al. 1977).

Barras et al. (1996) fed acorns of several red oak species to captive, wild-strain, adult female wood ducks and reported that the ducks selected willow oak acorns over equally available water oak, cherrybark oak, and Nuttall oak acorns, whether the nuts were presented in mixed- or single-species aggregations. Barras et al. (1996) speculated that small size and a high mass ratio of meat to shell for willow oak acorns facilitated ingestion and energy assimilation by wood ducks compared to larger acorn species. They recom-

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mended that future research determine TME of red oak acorns commonly consumed by wood ducks to learn whether species-specific TME values of acorns were related to differential use by wood ducks. Therefore, we conducted a controlled experiment, also using captive, wild-strain, adult female wood ducks, to estimate and compare mean TME acquired by wood ducks that consumed willow, water, cherrybark, and pin oak acorns. True metabolizable energy provides a more accurate estimate of metabolized energy than apparent metabolizable energy (AME), because TME accounts for endogenous losses of energy from nondietary sources (Miller and Reinecke 1984, Karasov 1990). We were unaware of any TME data for red oak acorns ingested by wood ducks. Moreover, differences in acorn size, shape, and nutrient and tannin contents may influence TME acquired by wood ducks and birds that forage on acorns (Koenig 1991, Barras et al. 1996). We also desired estimates of TME acquired by wood ducks from these acorns to complement similar estimates from mallards (K. J. Reinecke, U.S. Geological Survey, unpublished data) for use in assessing winter carrying capacity of bottomland-hardwood forests for waterfowl in the MAV and elsewhere in the southeastern United States (e.g., Reinecke et al. 1989, Loesch et al. 1994).

METHODS

Study Area

We conducted acorn feeding trials indoors at the College of Veterinary Medicine, Mississippi State University (MSU). We confined wood ducks in a manufactured metal brooder unit (12 compartments) housed inside a thermally controlled room (approx 20 °C) with 1 window and a ceiling light (Kaminski and Essig 1992). We exposed the birds to a natural photoperiod, except during feeding trials and daily husbandry (approx 1–2 hr), when we artificially illuminated the room. We conducted nutritional assays of acorns and analyzed excreta from wood ducks in the Department of Animal and Dairy Sciences laboratories at MSU.

Acorn Collection and Preservation

We collected fresh cherrybark, water, willow, and pin oak acorns on the MSU campus and in Starkville, Mississippi, during autumn 1994. Because Barras et al. (1996) included Nuttall oak acorns in their experiment, we also attempted to collect this species. However, we could not collect any Nuttall acorns because of widespread mast

failure by this species in 1994. Instead, we collected pin oak acorns, which were intermediate-to-large sized acorns (Olson 1974), similar in size to Nuttall oak acorns, and commonly consumed by wood ducks (Bellrose and Holm 1994). After collection, we placed cupless acorns in a bucket containing water, discarded those that floated (i.e., cracked or insect-damaged acorns; Allen 1989), and froze intact acorns until we fed them to wood ducks (Barras et al. 1996). We used only intact acorns in an effort to control nutrient variation among acorns of a species. Cracked acorns may have been in various stages of decomposition when collected, and those acorns harboring weevil larvae (e.g., *Curculio* spp.) may have had different nutrient quality (e.g., enhanced protein) than intact acorns (Johnson et al. 1993).

Experimental Birds and Husbandry

We used wild-strain, female wood ducks (3 yr-of-age) hatched from artificially incubated eggs collected from nest boxes at Noxubee and Yazoo National Wildlife Refuges in east-central and west-central Mississippi (Demarest et al. 1997, Vrtiska 1995). We used adult females to be consistent with Barras et al. (1996), whose research motivated our study. Additionally, we found no evidence that TME varied by sex in captive domestic fowl (Sibbald 1976b). When the birds used in our study were ducklings, we reared them 4–6 weeks in an indoor brooder unit, then placed them in an outdoor aviary about 2 km from the MSU campus (Loesch and Kaminski 1989). While our study birds were in the aviary, we provided them with fresh water daily in livestock troughs and a commercial ration (Purina®) ad libitum ($\geq 30\%$ crude protein, $\geq 2.5\%$ crude fat, $\leq 6\%$ crude fiber; Demarest et al. 1997). We assumed that birds had ad libitum access to grit from the graveled floor in the aviary. We maintained birds in the aviary until we selected them for acorn feeding trials; we then moved the birds to the brooder unit in the College of Veterinary Medicine. We followed standard rearing procedures for waterfowl (Ward and Batt 1973, Hofman 1985) and a protocol approved by the MSU Institutional Animal Care and Use Committee (Study 91–065).

Acorn Feeding Trials

We replicated acorn feeding trials 3 times on separate groups of wood ducks: 21 January, 17 February, and 18 March 1995. For each of the 3 feeding trials, we randomly selected 12 different wood ducks ($n = 36$ ducks) from the outdoor

aviary and randomly assigned each bird to 1 of 12 compartments in the brooder unit. We maintained ducks in the brooder unit for approximately 2 weeks before we initiated acorn feeding trials to acclimate the ducks to indoor captivity. During this period, we provided ducks with the same commercial ration fed outdoors and fresh water ad libitum. We placed commercial grit in each bird's water trough daily but did not measure amount of grit consumed by individual ducks.

Within each feeding trial, we randomly assigned each of the 12 ducks to 1 of 4 test species of acorns, resulting in 3 replicate ducks per acorn species and feeding trial ($n = 9$ ducks per acorn species). We force-fed each duck its randomly designated acorn species 3 times over a period of about 3 weeks within each of the 3 primary feeding trials. Our feeding schedule within each week was as follows: day 1, withheld food from ducks; day 2, collected excreta after food deprivation (approx 42 hr in total) and fed about 15 g (wet mass) of intact acorns to birds in both morning and afternoon (total = 30 g) to minimize regurgitation; days 3–4, collected excreta; days 5–6, fed commercial ration ad libitum; and day 7, removed commercial ration about midday.

After food was withheld and immediately before acorn feeding, we weighed each wood duck using a hand-held spring scale (± 10 g). During each acorn feeding trial, we inserted individual nuts by hand into each duck's buccal cavity and then gently massaged each nut downward into the esophagus. Petrie et al. (1997) investigated TME of foods fed to Canada geese and recommended feeding intact foods and providing test birds with grit to derive accurate TME values; although Sherfy et al. (2001) did not detect an effect of grit on TME of foods fed to blue-winged teal.

We fed different numbers of acorns to each treatment group of wood ducks because of species-specific variation in size and mass of acorns (Barras et al. 1996; R. M. Kaminski, Mississippi State University, unpublished data). For example, 30 g of cherrybark acorns would approximate 20–24 nuts compared to 23–31 willow oak acorns. Sometimes ducks regurgitated all or part of their acorn gavage during a feeding trial or the subsequent 24 hr. We omitted 2 birds from our analysis that regurgitated all acorns (e.g., Petrie et al. 1997). For wood ducks that regurgitated part of an acorn gavage, we recovered disgorged acorns and subtracted their mass from the initial force-fed mass (Sherfy et al. 2001). We deemed this approach justified,

because TME is theoretically independent of food-intake level (Sibbald 1975, Miller and Reinecke 1984, cf. Sherfy 1999:19, Sherfy et al. 2001).

We used net intake of acorn dry mass in calculations of TME. We estimated proportional dry mass of acorns from a representative sample (100 g, wet mass) of each acorn species fed to the wood ducks and multiplied each proportion times the wet mass of fed and retained acorns to determine net intake. We dried acorns to a constant mass in a forced-draft oven at 105 °C.

We lined fecal catchment trays under each duck's holding compartment with clean aluminum foil to collect excreta during periods of food deprivation and after acorn feeding. We collected excreta from unfed ducks to determine endogenous energy loss (i.e., fecal and urinary energy of nondietary origin; Miller and Reinecke 1984) for use in calculating TME of ingested acorns. Using this approach, we let each bird serve as its own control (Sibbald 1986, Kaminski and Essig 1992). We collected excreta for 48 hr after acorn feeding to ensure complete collection of feces for determination of TME (Parsons et al. 1982, Dale and Fuller 1986, Sibbald 1986, Petrie et al. 1997, Checkett et al. 2002). We removed feathers from excreta and examined excreta for presence of grit (Petrie et al. 1998). We dried excreta to a constant mass as described above and ground samples of excreta and acorns with a mortar and pestle before analysis for energy content. We determined gross energy of excreta and of each test acorn species with a Parr adiabatic oxygen bomb calorimeter.

We calculated TME (kcal/g) as (Sibbald 1976a):

$$\text{TME} = ([\text{GEF} * X] - [\text{YEF} - \text{YEC}]) / X,$$

where GEF was the gross energy (kcal/g, dry mass) of the samples of each acorn species fed to wood ducks; X was the dry mass (g) of acorns retained by each duck (i.e., net intake); YEF was the energy (kcal) voided as excreta 48 hr after each duck was fed acorns; and YEC was the energy (kcal) voided by the same duck after being deprived of food.

Statistical Analyses

We analyzed TME data using a mixed model analysis of variance (ANOVA; PROC MIXED; Littell et al. 1996) employing $\alpha = 0.05$. We discovered that initial body mass of wood ducks assigned to the 4 treatment groups of acorns differed ($F_{3,6} = 5.55$, $P = 0.036$). However, this dif-

ference was due to random assignment of heavier birds to 1 acorn test group (i.e., mean masses of wood ducks assigned to the acorn groups were willow oak, 510.3 g; cherrybark oak, 481.8 g; pin oak, 460.7 g; and water oak, 453.4 g). Because body mass of ducks may influence TME (e.g., Sherfy 1999:19), we used mean mass of individual wood ducks ($n = 3$ measurements per duck) as a covariate in ANOVA of TME data.

We averaged the 3 TME estimates from each wood duck to provide an independent and representative value for each bird. We treated acorn species as fixed and feeding trial as random effects. Using the Shapiro–Wilk test (SAS Institute 1988), we found that average TME values did not depart from normality for cherrybark oak, pin oak, and willow oak acorns ($0.199 \leq P \leq 0.543$), but we rejected normality for average TMEs of water oak acorns ($P = 0.006$). Nevertheless, we did not view lack of normality as a problem because (1) TME data for 3 of 4 acorn species were adequately modeled by a normal distribution, (2) averages tend toward normality due to the central-limit theorem, and (3) ANOVA is robust to departures from normality (Miller 1986:80). We assumed equal variances of TME data among acorn species, because Akaike’s Information Criterion (Anderson et al. 2000), reported in the ANOVA output, favored a model with equal rather than unequal variances.

We also expressed TME values of each acorn species as a percentage of their gross energy (GE) to estimate metabolizability (Petrie et al. 1998). We performed simple correlation analysis (Zar 1999) between TME and GE and computed mean percent metabolizability across acorn species. We multiplied mean TME estimates for acorn species by the proportional dry mass of the species to express TME on the basis of wet mass. We thereby gained an improved understanding of energy potentially available to wood ducks from acorns in natural environments.

RESULTS

We did not detect a relationship between acorn TMEs and mean mass of wood ducks ($F_{1, 23} = 0.11, P = 0.74$), suggesting that TME was not a function of body mass in our experiment. Hence, we deleted body mass as a covariate in the subsequent ANOVA. Mean values of TME did not differ among acorn species ($F_{3, 6} = 1.51, P = 0.31$); the maximal difference between mean TMEs was 7% (Table 1). The overall estimate of TME across acorn species was 2.76 ± 0.033 ($\bar{x} \pm SE; n = 34$)

kcal/g. Mean TME correlated positively with GE among acorn species ($r = 0.98, P < 0.02, n = 4$), and metabolizability across species was 50.3 \pm 0.004% ($\bar{x} \pm SE; n = 4$).

Percent dry matter was similar among species of acorns fed to wood ducks (willow oak: 71.5%, water oak: 70.5%, pin oak: 70.1%, cherrybark oak: 69.7%; $\bar{x} = 70.5\%$, $SE = 0.39\%$, $n = 4$). Estimates of TME adjusted to reflect the effect of water content on energy availability were 1.99 kcal/g (wet) for cherrybark, 1.98 for willow, 1.95 for water, and 1.86 pin oak acorns ($\bar{x} = 1.95$ kcal/g). Thus, wood ducks in our experiment metabolized about 2 kcal for each gram of fresh, whole acorn ingested.

DISCUSSION

Estimates of TME (dry and wet bases) were similar among willow, water, cherrybark, and pin oak acorns fed to female wood ducks during our study. Hence, we concluded that wood ducks in our study metabolized similar amounts of energy from the red oak acorns tested, and TME did not explain the strong preference by female wood ducks for willow oak acorns observed in free-choice trials by Barras et al. (1996). Wood ducks in the Barras et al. (1996) study were confined outdoors during winter in cages similar in size to those used in our study. We have no reason to believe, however, that indoor or outdoor confinement would cause a difference in energy metabolized from acorns by wood ducks. Willow oak acorns were smallest among the red oak acorns used in both studies. Thus, we concur with the hypothesis of Barras et al. (1996) that the small size, thin shell, and high meat-to-shell ratio of willow oak acorns may reduce handling time

Table 1. Gross energy (GE; kcal/g dry mass) and least-squares predicted means and standard errors (SE) of true metabolizable energy (TME; Kcal/g dry mass) of red oak acorns fed to adult female wood ducks (n) in captivity indoors at Mississippi State University, Mississippi, USA, Jan–Apr 1995.

Acorn species	GE	TME		
		\bar{x} ^a	SE ^b	n
Pin oak	5.19	2.65	0.067	7 ^c
Water oak	5.45	2.77	0.067	9
Willow oak	5.54	2.77	0.067	9
Cherrybark oak	5.78	2.85	0.067	9
Mean	5.49 (0.122)	2.76	0.033	34

^a Means adjusted for unequal samples sizes among acorn species.

^b Estimates of SE computed from model based on pooled estimates of variability.

^c Sample size reduced because of 2 missing values due to regurgitation of all fed acorns.

(Stephens and Krebs 1986:14) of these acorns and, therefore, enhance net energy assimilation. Additionally, efficient consumption of willow oak acorns may decrease time required by wood ducks to fill their esophagi. These time savings could accrue energetic and survival values to free-ranging wood ducks by decreasing time spent foraging and the associated vulnerability to predation. Our study was not designed to test these hypotheses, but they represent interesting questions for further experiments that examine trade-offs between energy acquisition and risk of mortality during foraging (Schoener 1971, Pyke 1984, Stephens and Krebs 1986).

Wood ducks in our study metabolized the greatest TME on average from cherrybark oak acorns and not willow oak acorns, which were selected by wood ducks in the Barras et al. (1996) study. Barras et al. (1996) reported results of proximate nutrient analysis of red oak acorns collected from many of the same trees and locations used in our study and showed that cherrybark oak acorns had greater levels of crude fat and lower levels of tannic acid than willow, water, and Nuttall oak acorns. In our study, slightly greater TME from cherrybark oak acorns may be related to these or other nutrient characteristics. Heitmeyer and Fredrickson (1990) reported that cherrybark oak acorns were relatively high in unsaturated fatty acids (e.g., linolenic acid [18:2]) and thus were important sources of energy for mallards and wood ducks. Moreover, tannin levels have been shown to lower TME of acorns in other birds (Koenig 1991). Willow and water oak acorns had intermediate TME values and levels of crude fat (Barras et al. 1996), and pin oak acorns had the lowest mean TME. Pin oak acorns contained lower GE and crude fat and had greater fiber content than willow and water oak acorns (Fredrickson and Reid 1988, Bellrose and Holm 1994:398), possibly explaining the low TME value for pin oak acorns fed to wood ducks in our study.

Availability of TME estimates for natural and agricultural foods of waterfowl has increased in recent years but remains limited (Checkett et al. 2002). We assembled 42 TME estimates for plant foods fed to several species of waterfowl (Tables 1, 2). Average TME for red oak acorns fed to wood ducks or mallards (2.67 kcal/g) was slightly greater (7%) than average TME for moist-soil plant seeds and tubers fed to mallards, northern pintails, blue-winged teal, or Canada geese (2.49 kcal/g). Our mean TME for red oak acorns fed to wood ducks (2.76 kcal/g) was equal or similar

(1–3%) to (1) average TME derived by mallards from a nutritionally complete, commercial ration (2.76 kcal/g); (2) the TME derived by Canada geese from pin oak acorns (2.72 kcal/g); and (3) average TME for seeds of moist-soil grasses, pigweed (*Amaranthus* spp.), and curly dock (*Rumex crispus*) fed to mallards, northern pintails, blue-winged teal, or Canada geese (2.83 kcal/g). Thus, for the purpose of generalization, red oak acorns and seeds of the latter moist-soil plants were intermediate in TME between agricultural seeds (3.38 kcal/g) and seeds of smartweeds (*Polygonum* spp.), horned beakrush (*Rhynchospora corniculata*), and paspalum grass (*Paspalum leave*) (1.45 kcal/g).

MANAGEMENT IMPLICATIONS

Our mean TME for red oak acorns fed to wood ducks and mallards resulted in a precise estimate (i.e., 2.67 kcal/g, CV = 8.3%, $n = 7$). Thus, managers and researchers may use 2.67 kcal/g as a reasonable estimate of TME for red oak acorns (dry-matter basis) for wood ducks and mallards, or 2 kcal/g if TME calculations were performed on a wet-mass basis. We suggest these estimates for updating calculations of carrying capacity of bottomland-hardwood forests for waterfowl wintering in the MAV and elsewhere in the southeastern United States where lowland red oaks exist (Reinecke et al. 1989, Loesch et al. 1994), provided estimates of acorn availability are in consistent units (i.e., wet or dry mass). Additionally, we recommend that researchers and managers use TME estimates instead of estimates of AME, because AME always underestimates TME ($\geq 3\%$), and AME varies with energy intake (Miller and Reinecke 1984). The net effect is that population and habitat requirements are overestimated by using AME.

Managers also need reliable estimates of acorn availability in bottomland-hardwood forests to estimate foraging carrying capacity of these habitats for waterfowl. Studies of acorn availability in bottomland-hardwood forests are limited in spatial and temporal scales (e.g., McQuilkin and Musbach 1977, Young 1990); hence, long-term studies should be initiated to provide reliable estimates at landscape scales. These data are necessary for evaluating habitat conservation strategies of the Lower Mississippi Valley Joint Venture of the North American Waterfowl Management Plan (Loesch et al. 1994).

Our summary of TME data from natural and agricultural plant foods of waterfowl indicated

Table 2. True metabolizable energy (TME; kcal/g dry mass) estimates for foods fed to waterfowl and respective references.

Food type/name	Species				Reference
	Mallard	Northern pintail	Blue-winged teal	Canada goose	
Acorn					
Pin oak	a			2.72	Petrie (1994:23)
Willow oak	2.91				K. J. Reinecke (unpublished data)
Water oak	2.38				K. J. Reinecke (unpublished data)
Nuttall oak	2.35				K. J. Reinecke (unpublished data)
Mean ^b	2.67				
Moist-soil plant parts					
Chufa tuber (<i>Cyperus esculentus</i>)				4.03	Petrie et al. 1998
Seeds					
Wild rice (<i>Zizania aquatica</i>)			3.47		Sherfy (1999:18) ^c
Hairy crabgrass (<i>Digitaria sanguinalis</i>)	3.09				Checkett et al. (2002)
Smooth crabgrass (<i>D. ischaemum</i>)	3.10				Checkett et al. (2002)
Rice cutgrass (<i>Leersia oryzoides</i>)	3.00	2.82			Hoffman and Bookhout (1985)
Pigweed (<i>Amaranthus</i> spp.)	2.97				Checkett et al. (2002)
Yellow bristlegrass (<i>Setaria lutescens</i>)	2.88				Checkett et al. (2002)
Coast barnyardgrass (<i>Echinochloa walteri</i>)	2.86	2.82			Hoffman and Bookhout (1985)
Fall panicum (<i>Panicum dichotomiflorum</i>)	2.75				Checkett et al. (2002)
Switchgrass panicum (<i>P. virgatum</i>)			2.54		Sherfy (1999:18) ^c
Curly dock (<i>Rumex crispus</i>)	2.68		2.05		Sherfy (1999:18) ^c
Barnyard grass (<i>E. crusgalli</i>)	2.61				Checkett et al. (2002)
			2.67		Sherfy et al. (2001)
				3.29	Petrie et al. (1998)
Junglerice (<i>E. colonum</i>)	2.54				Reinecke et al. (1989)
Horned beakrush (<i>Rhynchospora corniculata</i>)	1.86				Checkett et al. (2002)
Paspalum (<i>Paspalum laeve</i>)	1.57				Checkett et al. (2002)
Curltop ladsythumb (<i>Polygonum lapathifolium</i>)	1.52				Checkett et al. (2002)
Pennsylvania smartweed (<i>P. pennsylvanicum</i>)	1.08	1.25			Hoffman and Bookhout (1985)
			1.30		Sherfy et al. (2001)
Mean	2.47	2.30	2.41	1.59	Petrie et al. (1998)
Agricultural seeds/forage				2.44	
Corn	3.67				Reinecke et al. (1989)
				3.90	Petrie et al. (1998)
Milo			3.49		Sherfy et al. (2001)
				3.76	Petrie et al. (1998)
Cultivated rice	3.34				Reinecke et al. (1989)
				2.81	Petrie et al. (1998)
Soybean	2.65				Reinecke et al. (1989)
Wheat					
Grain	3.38				Reinecke et al. (1989)
Forage				2.40	Petrie et al. (1998)
Mean	3.26			3.49 ^d	
Commercial ration	2.76				Kaminski and Essig (1992)

^a Blanks denote unavailable data.

^b Mean TME under mallard includes species-specific acorn TMEs for wood ducks from Table 1.

^c TME estimates with CV ≤ 15%.

^d Average includes TME values for grain only, not green forage.

that acorns and moist-soil plant parts together provided, on average, about 74–78% of the metabolizable energy of agricultural seeds (also see Checkett et al. 2002). Thus, bottomland-hardwood and moist-soil habitats provide significant amounts of dietary energy and greater diversity of natural foods and nutrients than croplands, as well as seeds that resist decomposition (Gray et

al. 1999, Manley 1999, Checkett et al. 2002). Moreover, a growing amount of evidence suggests the decreasing availability of waste grain (e.g., rice) for migrating and wintering waterfowl as a result of changing agricultural practices and germination, decomposition, and granivory of waste grains by birds and mammals during fall (e.g., Miller and Wylie 1996; Manley 1999:114; J. D.

Stafford, Mississippi State University, unpublished data). Therefore, natural wetlands may play an increasingly important role as foraging habitats for migrating and wintering waterfowl. Thus, managers should restore and manage these habitats on public and private lands to increase waterfowl food production (e.g., Gray et al. 1999, Batema et al. 2003) and integrate agricultural and natural wetlands to produce foods of diverse energy and nutrient content (Petrie et al. 1998). Additionally, researchers should determine TME of aquatic invertebrates commonly used by waterfowl (e.g., Jorde and Owen 1988, Sherfy 1999), because invertebrates also provide metabolizable energy and meet important seasonal needs for protein (e.g., Krapu and Reinecke 1992, Heitmeyer 1988, Heitmeyer and Fredrickson 1990, Barras et al. 2001).

We found no difference in TME among oak species, but acorn production can vary among years (e.g., 7–405 kg/ha; McQuilkin and Musbach 1977) and likely geographically due to species- and environmental-specific differences. Gross energy could be assayed for samples of acorns from different sites and years to determine if reasons existed to test annual or spatial variation in TME of acorns. If GE did not vary, then TME likely would not vary and research could focus on interactions between acorn consumers (e.g., ducks) and acorn availability. Although challenging, future studies might assess use, spatial distribution, proximity, and richness of foraging patches (e.g., Lovvorn and Gillingham 1996, Nolet et al. 2001), or extent of patch depletion and time of patch abandonment (e.g., Tome 1989).

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