

THE EFFECTS OF TANNINS AND LIPIDS ON DIGESTION OF ACORNS BY ACORN WOODPECKERS

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ABSTRACT.—The effects of tannins and lipids on the metabolizable energy coefficient (MEC; i.e. energy ingested minus energy excreted, divided by energy ingested) of Acorn Woodpeckers (*Melanerpes formicivorus*) fed acorn meal of known composition was determined by feeding trials on captive birds. Adding tannins decreased MEC, while adding acorn lipid increased it. Quebracho (a condensed tannin) had a stronger detrimental effect on MEC than did tannic acid (a hydrolyzable tannin). There was a significant interaction (associative digestion) between tannic acid and lipid, such that the detrimental effects of tannic acid were enhanced in the presence of increased lipid. Despite the detrimental effects of added tannin, MEC of acorns, which are naturally high in tannins, was similar to the MEC of crickets, which are low in tannins. The amount of energy Acorn Woodpeckers derived from acorns (net energy value) averaged 69.0% of their maximum estimated energetic content based on composition and 60.5% of their total gross energy based on bomb calorimetry. The study indicates that stored acorns are more important to Acorn Woodpeckers than previously estimated. On average, however, acorns supply only a small proportion of the energetic needs of this species during the winter in central coastal California. Received 16 January 1990, accepted 17 July 1990.

TANNINS are water-soluble phenolic compounds that precipitate proteins (Ribéreau-Gayon 1972; Swain 1979a, b; Martin and Martin 1982). Consequently, they often have the deleterious effect of reducing protein availability (Rhoades and Cates 1976, Zucker 1983, Freeland et al. 1985, Robbins et al. 1987a). This allelo-chemic effect has been noted in a variety of animals including insects (Feeny 1968, 1970), chickens (Chang and Fuller 1964, Ford and Hewitt 1979, Chami et al. 1980), and mammals (Pigeon et al. 1962, Almond et al. 1979, Griffiths and Mosely 1980, Robbins et al. 1987a) and may have important effects on food preferences of herbivores (Freeland and Janzen 1974, Rosenthal and Janzen 1979, Tempel 1981, Smallwood and Peters 1986, Servello and Kirkpatrick 1989).

There is less support for the hypothesis that tannins have detrimental effects on digestibility of material other than protein. Most of the extensive work in this area involves *in vitro* fermentations (Waterman et al. 1980, Kumar and Singh 1984, Palo 1985, Palo et al. 1985, Risenhoover et al. 1985), although there are some *in vivo* studies of ungulates (Barry and Manley 1984, Barry et al. 1986, Robbins et al. 1987b). Generally there is reduced protein digestibility as a correlate of tannin content. However, Robbins et al. (1987b) found no effect of tannins on

cell wall digestion in deer. These authors present evidence that deer can effectively neutralize tannins by producing salivary proteins that bind tannins in a highly specific manner. Similar means of reducing or neutralizing the detrimental effects of tannins might be expected in other species highly dependent on tannin-containing plant tissues.

One such species is the Acorn Woodpecker (*Melanerpes formicivorus*), a common resident of montane regions of California south to Colombia. Based on monthly stomach content samples, Beal (1911) found an average of 53% acorns by weight in the diet of Acorn Woodpeckers, with a high of 94% acorns found in November. Although these values overestimate the importance of acorns relative to more rapidly digested food items, acorns are clearly a major dietary item for this species. Use of acorns, which are only seasonally available throughout most of their range, is facilitated by the unique habit of storing large numbers of acorns in specialized storage trees, or granaries. The birds are highly dependent on these caches and eat them during periods of food shortage throughout the subsequent winter and spring (MacRoberts and MacRoberts 1976, Koenig and Mumme 1987). Granaries, and the stored acorns, are a focus of activity for Acorn Woodpecker behavior

TABLE 1. Composition of foods (% dry mass) used in feeding trials. Composition of *Q. agrifolia*, dog chow, crickets, and the *Q. lobata* standard was assayed directly; that of *Q. lobata* tissue with added lipid or tannin was estimated from the known standard. ADR = acid detergent residue (primarily cellulose and lignin). Rows do not sum to 100% because nonstructural and ADR are subsets of "total" carbohydrates. For details of proximate analyses, see text.

Diet	Ash	Lipid	Protein	Carbohydrate			Tannin	
				Total	Non-structural	ADR	Condensed	Hydrolyzable
<i>Q. lobata</i>	1.9	9.7	2.0 (5.5 ^a)	75.6	13.6	3.0	0.89	9.96
+10% lipid (L)	1.7	18.7	1.8	68.0	12.2	2.7	0.80	8.96
+20% lipid (L)	1.5	27.8	1.6	60.5	10.9	2.4	0.71	7.97
+3% quebracho (QT)	1.8	9.4	2.0	72.7	13.2	2.9	3.86	9.66
+8% quebracho (QT)	1.7	8.9	1.9	67.8	12.5	2.8	8.82	9.16
+3% tannic acid (T)	1.8	9.4	2.0	72.7	13.2	2.9	0.86	12.66
+8% tannic acid (T)	1.7	8.9	1.9	67.8	12.5	2.8	0.82	17.16
+10L3T	1.6	18.4	1.8	65.1	11.8	2.6	0.77	11.67
+10L8T	1.5	18.0	1.7	60.2	11.2	2.5	0.73	16.17
+20L3T	1.4	27.5	1.6	57.5	10.5	2.3	0.69	15.67
+20L8T	1.3	27.0	1.5	52.7	9.8	2.2	0.64	15.17
<i>Q. agrifolia</i>	0.7	16.8	7.1 ^a	55.1	13.2	3.0 ^b	1.27	19.00
Dog chow	0.7	10.1	27.0 ^c	—	56.3	—	—	—
Crickets	12.2	16.4	63.8 ^d	—	7.6	—	—	—

^a Crude protein value as assayed by micro-Kjeldahl method, not BioRad method.

^b Not measured; estimate is the value for *Q. lobata*.

^c From composition listed on package.

^d Levey and Karasov (1989).

(Mumme and de Queiroz 1985) and are critical to virtually all aspects of their biology including survival, reproductive success, and social behavior (Hannon et al. 1987, Koenig and Mumme 1987, Stacey and Ligon 1987). Because all species of acorns thus far analyzed contain significant amounts of tannins (e.g. Ofcarcik and Burns 1971, Pratini 1989), Acorn Woodpeckers are excellent candidates to have evolved physiological means of reducing the detrimental effects of tannins on digestibility.

Prior work has shown that Acorn Woodpeckers can survive in captivity, apparently indefinitely, when fed *ad libitum* exclusively on low tannin, low lipid *Quercus lobata* acorns, but that they gradually lose weight when fed only high tannin, high lipid *Q. agrifolia* acorns (Koenig and Heck 1988). Acorns of both these species are low in protein (Table 1), and these results suggest that tannins may have adverse effects on long-term protein assimilation. I performed a series of feeding trials designed to determine the effects of tannins and lipids on the metabolizable energy coefficient (Robbins 1983) attained in Acorn Woodpeckers. I also calculated the net energetic value of the two acorn species to Acorn Woodpeckers. These estimates allow a reevaluation of Koenig and Mumme's (1987)

calculations that estimated the importance of stored acorns to the energetic needs of Acorn Woodpeckers.

METHODS

Subjects.—I conducted feeding trials between 26 October and 18 December, 1987, at Arizona State University in Tempe. I used 5 (2 males and 3 females) Acorn Woodpeckers, born in the wild at Hastings Reservation, Monterey County, California. All but one, a first-year bird, were 3 yr old or older, and all were acclimated to captivity. While in captivity, birds were fed high-protein dog chow supplemented irregularly with acorns. Birds were housed separately in small (approx. 0.5 × 0.8 × 0.8 m) cages lined with aluminum foil. Cages were placed outside, sheltered from sun and weather. Mean air temperature during the trials ranged from 25.3 to 34.0°C.

Feeding trials.—In each trial I provided birds with a known quantity of food and water *ad libitum*. Food used in the trials included dog chow, crickets, and acorn meal. Acorn meal was derived from either *Q. lobata* or *Q. agrifolia* acorns collected 17–18 October 1987 at Hastings Reservation. Acorns were shelled, and those not damaged by insects were ground in a meat grinder and dried at 65°C.

I performed two sets of trials using the ground meal from each of the two species of acorns, chosen because they represent the major subgenera of oaks: *Quercus* ("white" oaks [*Q. lobata*]) and *Erythrobalanus* ("red" or

"black" oaks [*Q. agrifolia*]). Additional trials were performed with *Q. lobata* acorn meal to which a known quantity of lipids, tannins, or both had been added. The mixtures were thoroughly mixed before use. I chose *Q. lobata* as a standard because, as a member of the white oak subgenus, it is relatively low in tannins and lipids (Ofcarcik and Burns 1971, Short and Epps 1976). Lipids were extracted by petroleum ether from *Q. agrifolia* acorns.

In the absence of any detailed analysis of the precise tannins present in acorns, I chose commercially available representatives of the two major types: (1) tannic acid, a hydrolyzable tannin (Mallinckrodt), and (2) quebracho, a condensed tannin (Los Angeles Chemical Corp.). Hydrolyzable tannins contain a carbohydrate core (usually glucose) bound by an ester linkage with gallic, m-digallic, or hexahydroxyphenic acid, and are found only in dicotyledonous plants. Condensed tannins, or proanthocyanidins, are formed by the condensation of flavan-3-ols and flavan-3, 4-diols, lack the carbohydrate core, and are widely dispersed throughout the plant kingdom. More complete discussion of tannin chemistry can be found in Ribéreau-Gayon (1972), Swain (1979b), and Pratini (1989). Tannins were added in biologically realistic quantities (Table 1).

Before each trial, birds fasted for 3 hours. Although passage time for different foods is not known for Acorn Woodpeckers, all birds were fed dog chow between trials, and thus no systematic bias should have resulted from any residual food in their digestive tracts. At the end of the fast period, I cleaned the cage, weighed the bird, and added the food. There was no precollection period. Additional food was added as necessary. Limited time and availability of acorn meal restricted trials to 3 (sometimes 4) days. At the end of a trial, birds again fasted for 3 h, were weighed, and were removed from the cages. Excreta was separated carefully from any remaining food. I dried the remaining food to constant weight and subtracted its weight from the amount of food used during the trial, while excreta was dried at 65°C and a sample kept for bomb calorimetry. Because excreta was left in the cages during trials, microbial action may have altered the chemical and energetic composition of feces. However, I noted no evidence of such microbial action in either feces or the food used in trials, and because all trials were treated similarly, this factor is unlikely to have systematically influenced the results.

Three trials with three different individuals were performed using each food type (only one trial was performed with dog chow). In all, I performed 40 trials (8 on each bird) that involved 14 different diets (listed in Tables 1 and 2). Birds used for particular trials were chosen randomly from the five available for simultaneous testing. Trials were performed at weekly intervals. As noted above, birds were fed dog chow between trials.

Proximate analyses.—Analyses of gross energy content, lipid, protein, carbohydrate, and ash were performed on the *Q. lobata* standard. Tannins were measured in both acorn species. Otherwise, for *Q. agrifolia*, dog chow, and crickets, I measured only gross energy content, lipid, and ash. All food was dried before analysis.

I determined lipid content by extraction of a 1–3 g sample for 3 h with petroleum ether, ash by incineration of a 0.5–3.5 g sample at 550°C in a muffle furnace, and total energetic value with a Phillipson microbomb calorimeter. I made 2–3 replicate analyses of lipid content and total energetic value of the *Q. lobata* standard and of the *Q. agrifolia* used in trials. Other analyses of lipid, ash, and total energetic content were performed once.

Condensed tannins were determined by a modified acidified vanillin method (Broadhurst and Jones 1978) and hydrolyzable tannins by a modified iodate technique (Bate-Smith 1977). Protein content of the *Q. lobata* standard was quantified by the BioRad method, which is the most reliable method known when large amounts of phenolics are present (Robinson 1979). Tannin and BioRad assays were run in triplicate (for additional information on these methods, see Faeth 1986). Unfortunately, I did not perform the BioRad analysis on the *Q. agrifolia* sample, and protein content for this sample was estimated by the micro-Kjeldahl technique.

Direct determination of nonstructural carbohydrates (performed on a different sample of *Q. lobata* than that used in the trials) was measured by digestion in 0.2 M NH_4SO_4 (Smith et al. 1964). Structural carbohydrates of the *Q. lobata* standard were determined by the methods of Van Soest (1982). A summary of the composition of the items used in the feeding trials along with their energetic values is presented in Table 1.

The total gross energy (TGE) value of ingredients fed during the trials was determined by bomb calorimetry, and the metabolizable energy (CME) estimates are based on the proximate analyses of composition. The "minimum" CME estimate assumes that, of the total carbohydrates present in the sample, only those assayed as nonstructural are digestible, and the "maximum" CME estimate assumes that only ash, the acid detergent residue (primarily lignin and cellulose, see Van Soest 1982), and tannins are *not* digestible. Standard energetic values ($39.6 \text{ kJ}\cdot\text{g}^{-1}$ for lipids, $23.7 \text{ kJ}\cdot\text{g}^{-1}$ for protein, and $17.2 \text{ kJ}\cdot\text{g}^{-1}$ for carbohydrates) were used for CME calculations (Brody 1945).

Analysis of the metabolizable energy coefficient.—For each treatment, I determined the energy value of a sample of the acorn meal fed during the trial by bomb calorimetry. For each trial, a sample of the excreta (feces plus uric acid) produced was analyzed by bomb calorimetry. Gross energy value of food ingested and waste produced was the energy value per gram times the dry weight of food ingested and excreta produced,

TABLE 2. Metabolizable energy coefficients, intake rates, and percent body mass change for feeding trials. All values are $\bar{x} \pm \text{SD}$; range is in parentheses; $n = 3$ for all trials except dog chow ($n = 1$). Initial body mass of birds was 77.2 ± 4.9 g (range 69.8–87.4 g).

Diet	MEC (%)	Intake rate (kJ·day ⁻¹)	Body mass change (%)
<i>Q. lobata</i>	60.3 ± 3.2 (56.6–62.3)	160.0 ± 38.2	-1.5 ± 3.2
+10% lipid (L)	71.6 ± 5.4 (65.3–74.9)	193.4 ± 9.6	-1.0 ± 5.7
+20% lipid (L)	74.1 ± 0.9 (73.4–75.1)	191.9 ± 47.3	-2.4 ± 1.7
+3% quebracho (QT)	50.2 ± 4.6 (47.0–55.5)	187.9 ± 14.7	-1.7 ± 2.8
+8% quebracho (QT)	46.4 ± 5.5 (41.1–52.1)	214.4 ± 33.8	-5.6 ± 1.2
+3% tannic acid (T)	60.6 ± 4.3 (56.4–65.0)	155.6 ± 31.0	-3.6 ± 0.6
+8% tannic acid (T)	54.1 ± 1.6 (52.4–55.4)	171.0 ± 55.5	-1.1 ± 5.7
+10L3T	64.5 ± 2.5 (62.9–67.4)	196.1 ± 4.3	-2.3 ± 3.1
+10L8T	55.1 ± 2.8 (53.1–58.3)	225.6 ± 32.2	-5.1 ± 2.1
+20L3T	63.2 ± 2.7 (60.9–66.1)	188.8 ± 21.7	-1.4 ± 1.6
+20L8T	61.1 ± 4.4 (56.6–64.7)	223.3 ± 9.0	-0.8 ± 1.0
<i>Q. agrifolia</i>	64.5 ± 5.6 (59.0–70.2)	179.1 ± 21.5	-2.2 ± 3.9
Dog chow	79.8	122.5	-3.7
Crickets	64.4 ± 1.4 (62.8–65.4)	193.4 ± 8.5	-0.1 ± 2.4

respectively. Net energy intake was the energy value of food ingested minus that of waste produced. The metabolizable energy coefficient (MEC) was then calculated as the net energy intake divided by the total energy value of food ingested multiplied by 100 (Robbins 1983). As in other studies of avian digestion, excreta could not be separated into feces and urine; therefore estimates of digestive efficiency can be expected to be low by 2–5% (Drodz 1967). However, mass loss during trials was usually small (<5%; Table 2), which indicates that birds were usually in protein balance. Under such conditions, the error caused by mixing of urinary and digestive wastes is likely to be minimal (Levey and Karasov 1989).

Metabolizable energy coefficient values were arcsine transformed and compared by ANOVA. Given the small number of replicates, this procedure provides more power than nonparametric procedures, although comparable nonparametric tests generally yielded similar results. Value presented are $\bar{x} \pm \text{SD}$ (range).

RESULTS

Mean values of metabolizable energy coefficients for the diets ranged from 46.4% for the *Q. lobata* standard acorn mash + 8% quebracho to 79.8% for the single trial with dog chow (Table 2).

Effect of tannins on metabolizable energy coefficients.—The mean and range of MEC varied according to the amount and kind of tannin added to the *Q. lobata* standard (Fig. 1a). Overall, there was no significant effect of added tannic acid on MEC (ANOVA, $F_{2,6} = 3.8$, $P = 0.09$). In contrast, added quebracho significantly decreased MEC ($F_{2,6} = 7.5$, $P = 0.02$). There was no overlap

between the ranges in MEC of added tannic acid and quebracho at either the +3% or +8% levels, which supports the conclusion that quebracho has a greater adverse effect than the addition of a comparable amount of tannic acid.

The effects of added tannic acid (T), not significant in the above trials, was pronounced in the trials in which acorn lipid (L) was also added (Fig. 1b). ANOVAs of MEC comparing the trials with 10% added lipid (+10L, +10L3T, and +10L8T) and those comparing the trials with 20% added lipid (+20L, +20L3T, and +20L8T) were both highly significant ($F_{2,6} = 13.5$ and 17.1, respectively; both $P < 0.01$). Tannic acid has adverse effects on MEC when combined with additional acorn lipid.

Effect of lipids on MEC.—I divided trials into three categories based on the amount of tannic acid added, and then I graphed the results according to the percent added lipid (Fig. 2). With no tannic acid added, there were significant differences among these three categories by ANOVA ($F_{2,6} = 11.8$, $P < 0.01$). There were no significant differences in MEC with increased lipid among the three categories with 3% added tannic acid (+3T, +10L3T, +20L3T) or among those with 8% added tannic acid (+8T, +10L8T, +20L8T) (for 3% added tannic acid: $F_{2,6} = 1.1$, NS; for 8% added tannic acid: $F_{2,6} = 5.0$, $P = 0.052$).

Interaction of added tannic acid and lipid.—The analyses described above revealed the possibility of an interaction (associative digestion) between added tannic acid and lipids. Additional lipid appeared to magnify the effects of tannic

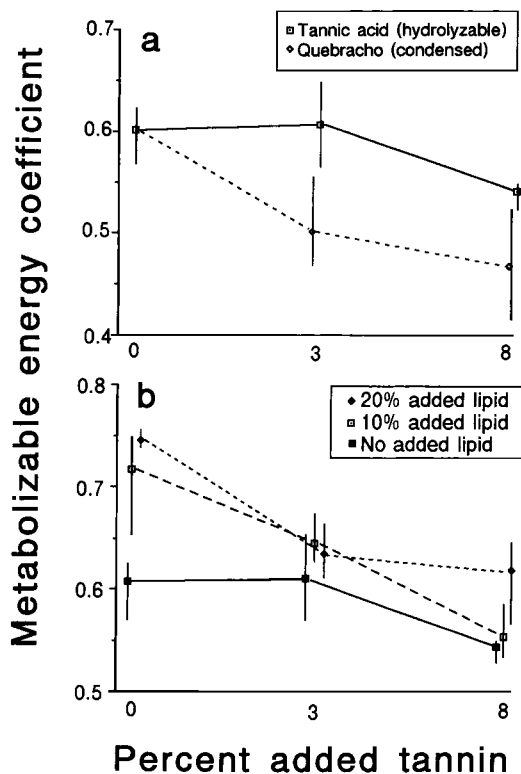


Fig. 1. The relationship between the metabolizable energy coefficient and added tannins (a) according to type of tannin added (tannic acid or quebracho), and (b) according to the amount of lipid added, excluding trials with added quebracho. Means are plotted; vertical lines represent ranges, $n = 3$ trials for each category.

acid. Alternatively, added tannic acid tended to inhibit the otherwise beneficial effect of additional lipids. To test the statistical validity of this interaction, I performed a two-way ANOVA on the 27 trials involving the *Q. lobata* standard alone and in combination with added lipid or added tannic acid, which were analyzed as main factors.

The results confirm that lipids and tannic acid have highly significant effects on MEC (Table 3). Based on the mean squares and F -values, I also suggest that the adverse effects of increased tannic acid are more potent than the positive effects of increased lipids. There is also a significant ($P < 0.05$) interaction between these factors, which confirms associative digestion between them.

Comparative metabolizable energy coefficients of acorns.—Despite their considerable difference in lipid and tannin composition, there were no

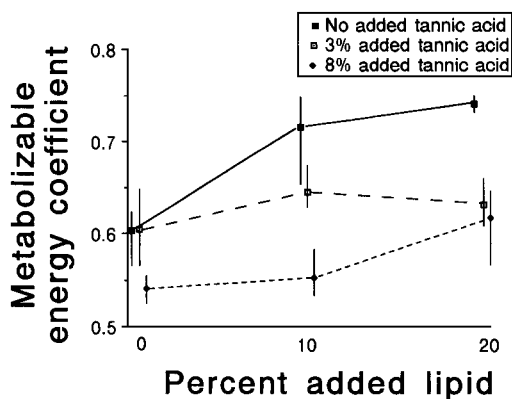


Fig. 2. The relationship between the metabolizable energy coefficient and the percent lipid added, excluding trials with added quebracho. Values plotted as in Fig. 1.

significant differences in MEC between the two acorn species (*Q. agrifolia* and the unadulterated *Q. lobata*) or among the trials using *Q. lobata*, *Q. agrifolia*, and crickets (ANOVA; $F_{2,6} = 1.2$, NS) (Table 2).

Energy value of acorns to Acorn Woodpeckers.—I did not perform any direct metabolic measurements during the course of this study. Still, the metabolizable energy (ME) of food used in trials was readily calculated by subtracting the energetic value of excreta from the gross energetic value of food eaten (Robbins 1983). Metabolizable energy estimates for the four trials that involved dog chow or crickets averaged $64.7 \pm 9.5\%$ of the estimated energy requirements of free-living birds (TDEE) that do not forage in flight. Estimates were based on body

TABLE 3. Analysis of variance of the effects of added tannic acid and acorn lipid (analyzed as main factors) to the metabolizable energy coefficient of *Q. lobata* acorn meal. A total of 27 trials (3 replicates for each of the 9 categories (0, +3%, +8% tannic acid, and 0, +10%, +20% lipid in all permutations) were performed. Metabolizable energy coefficient was arcsine transformed before analysis. Overall $R^2 = 0.75$; * = $P < 0.05$; *** = $P < 0.001$.

	df	Mean square	F-value	Direction of relationship
Lipid	2	0.016	13.2***	+
Tannic acid	2	0.034	27.7***	-
Lipid \times tannic acid	4	0.004	3.5*	
Explained	8	0.015	12.0***	
Total	26	0.005	—	

TABLE 4. Estimated energy present and net energy value ($\text{kJ}\cdot\text{g}^{-1}$) of foods used in feeding trials. Total gross energy (TGE) based on bomb calorimetry; CME = metabolizable energy based on chemical composition. Total gross energy and CME measure the amount of energy present in the acorns; net value is an estimate of the amount of energy obtained from the acorns by birds ($n = 3$) during trials. For details of calculations, see text.

Diet ^a	TGE	CME		Net value ($\bar{x} \pm \text{SD}$)	Net value divided by		
		Min	Max		TGE	CME Min	CME Max
<i>Q. lobata</i>	18.81	6.66	17.32	11.34 \pm 0.61	0.603	1.703	0.655
+10L	20.64	9.95	19.55	14.78 \pm 1.12	0.716	1.485	0.756
+20L	23.31	13.25	21.77	17.27 \pm 0.21	0.741	1.303	0.793
+3QT	18.38	6.46	16.69	9.23 \pm 0.85	0.502	1.429	0.553
+8QT	20.25	6.13	15.63	9.39 \pm 1.11	0.464	1.532	0.601
+3T	18.14	6.46	16.69	10.99 \pm 0.79	0.606	1.701	0.658
+8T	18.48	6.13	15.63	10.00 \pm 0.29	0.541	1.631	0.640
+10L3T	20.52	9.75	18.92	13.23 \pm 0.51	0.645	1.357	0.699
+10L8T	21.91	9.42	17.86	12.06 \pm 0.62	0.550	1.280	0.675
+20L3T	21.60	13.05	21.14	13.65 \pm 0.58	0.632	1.046	0.646
+20L8T	22.79	12.72	20.09	14.03 \pm 0.99	0.616	1.103	0.698
<i>Q. agrifolia</i>	25.16	10.62	17.82	16.22 \pm 1.41	0.645	1.527	0.910
Dog chow	20.22	—	20.08	—	—	—	—
Crickets	23.35	—	22.92	—	—	—	—
Mean	—	—	—	—	0.605	1.425	0.690
SD	—	—	—	—	± 0.081	$+0.215$	± 0.094

^a L = % lipid; T = % tannic acid; QT = quebracho tannin.

mass averaged at the start and end of each trial and calculated from Walsberg's (1983) formula. This value is virtually identical to the ratio of ME to TDEE ($\bar{x} = 63.8 \pm 13.4\%$) obtained from the 36 trials in which acorns were used. Thus, ME values did not differ in birds that ate dog chow or crickets compared with acorns. The ME values ($\times 0.64$) were apparently good estimates of the usable energy Acorn Woodpeckers derived from acorns during the trials.

Dividing metabolizable energy by the mass of acorns consumed yields the energetic value ($\text{kJ}\cdot\text{g}^{-1}$) of acorns (here called "net value"). I compared net values with three estimates of the available energy contained in the acorns. These were (1) total gross energy, (2) minimum metabolizable energy derived from composition, and (3) maximum metabolizable energy derived from composition. Total gross energy was based on bomb calorimetry of each trial food and provides a maximum estimate of the energy present. Both the minimum and the maximum metabolizable energy values were based on the composition of acorns, as discussed earlier.

On average, Acorn Woodpeckers obtained 69.0% of maximum metabolizable energy derived from composition and 60.5% of the total gross energy present in acorns (Table 4). These values compare favorably with the observed metabolizable energy coefficient for unadulter-

ated acorns of between 60.3 and 64.5% (Table 2).

DISCUSSION

Metabolizable energy coefficients.—Digestion of acorns by Acorn Woodpeckers is adversely affected by tannins (Fig. 1). Quebracho (a condensed tannin) has a stronger negative effect on metabolic energy coefficient (MEC) than tannic acid (a hydrolyzable tannin) at comparable concentrations. Condensed tannins were present in concentrations lower in acorns than in hydrolyzable tannins (Table 1). This suggests that Acorn Woodpeckers are better able to deal with the tannin types found naturally in higher concentrations in acorns. The strong detrimental effect of quebracho on MEC does not support the hypothesis (e.g. Zucker 1983) that condensed tannins function primarily to deter microbial decomposition rather than to defend against herbivory, although the first function may also be important. Additional study is necessary to determine the precise mechanisms by which tannins decrease MEC. They may either bind with proteins present in the gut and decrease overall apparent MEC, or directly inhibit assimilation by accelerating gastrointestinal transit time.

Addition of acorn lipid significantly in-

creased digestive efficiency, at least in the absence of additional tannic acid (Fig. 2). However, there was significant associative digestion between added tannic acid and lipid such that tannic acid tended to counteract the beneficial effects of lipids more than expected based on their separate influences on MEC (Fig. 2). Because these two components generally covary in acorns (cf. *Q. lobata* and *Q. agrifolia* in Table 1), this interaction enhances the antipredatory effects of tannins in those acorns which, because of their high lipid content, would otherwise be most desirable to seed predators. Additional work will be necessary to determine the mechanism by which acorn lipid influences MEC.

Because of the opposite effects of added lipids and tannins, MEC was no greater when birds were fed low-tannin, low-lipid *Q. lobata* acorns than when they were fed high-tannin, high-lipid *Q. agrifolia* acorns. Overall, the mean MEC of birds fed unadulterated acorns (*Q. lobata* and *Q. agrifolia* trials combined) was 62.4%, very close to the 64.5% "estimated true dry matter digestibility" for 11 species of acorns calculated by Short and Epps (1976) using the methods of Goering and Van Soest (1970).

Mean MEC of Acorn Woodpeckers fed crickets was 64.4%, comparable to the 71–73% values reported by Levey and Karasov (1989) for American Robins (*Turdus migratorius*) and European Starlings (*Sturnus vulgaris*). The slightly lower values I found are probably in part an artifact of my protocol, which did not include a pre-collection period. Levey and Karasov (1989) found MEC values significantly increased following acclimation. Indeed, MEC for robins fed crickets was 58% during the first 3 days of their trials, slightly lower than the values found here. Metabolizable energy coefficient values lower than the 70–80% values normally cited for insectivorous species are probably typical for birds fed insects with heavy exoskeletons (Krebs and Avery 1984).

The lack of any difference between MEC in Acorn Woodpeckers fed crickets compared with those fed acorns suggests that, although sensitive to added tannic acid and quebracho, Acorn Woodpeckers can cope reasonably well with the naturally occurring tannins present in *Q. lobata* and *Q. agrifolia* acorns. This conclusion holds especially for *Q. lobata*, as birds fed this species not only had good MEC but also appeared able to maintain themselves indefinitely (Koenig and

Heck 1988). This ability is especially impressive given the low protein content (2.0% in the sample used here) of *Q. lobata* acorns. This value is considerably less than the 4% dietary protein needed for maintenance by Tree Sparrows (*Spizella arborea*; Martin 1968) or the 7% needed by adult chickens (*Gallus gallus*; Fisher 1972). Overall MEC was also high for Acorn Woodpeckers fed *Q. agrifolia* acorns, but feeding trials indicated that birds could not maintain their body mass when fed exclusively on acorns of this species (Koenig and Heck 1988). I suggest that protein assimilation is adversely affected by the high tannin levels of this oak species. Additional work to examine the protein balance of Acorn Woodpeckers fed acorns is clearly desirable.

The detrimental effects of tannins on the growth and digestive physiology of chickens is well documented. Chami et al. (1980) found reduced digestion in chickens fed soybean or corn meal with as little as 1% added tannic acid. However, I am aware of only one prior study that looked at the effects of tannins in wild birds. Perrins (1976) examined the influence of eating tannin-contaminated caterpillars on growth of Blue Tit (*Parus caeruleus*) nestlings and found some evidence of a detrimental effect, but he did not examine MEC.

Net energetic value of acorns.—Stored acorns are critically important to Acorn Woodpeckers (e.g. Koenig and Mumme 1987, Stacey and Ligon 1987), yet no prior attempt has been reported that measures directly the energy value to this species. Based on their finding that the proportion of nonstructural carbohydrates in acorns was very small, Koenig and Mumme (1987) used low energetic estimates, comparable to the minimum values calculated here for ME derived from composition, in their analysis of acorn storage at Hastings Reservation. For example, they found only 13.6% nonstructural carbohydrates in *Q. lobata* acorns and thus estimated the energetic value of this species to be only 5.53 kJ·g⁻¹. However, direct analysis of the *Q. lobata* standard I used yielded only 3.0% structural carbohydrates (the acid detergent residue). Based on the above results, Acorn Woodpeckers are apparently able to digest much of the large carbohydrate fraction (approx. 59% for *Q. lobata*) not accounted for by either analysis. I do not know the reason for the considerable discrepancy in carbohydrate composition yielded by the two different analyses.

The net energetic value of *Q. lobata* acorns was $11.34 \pm 0.61 \text{ kJ} \cdot \text{g}^{-1}$, 2.05 times the estimated energetic content listed by Koenig and Mumme (1987). Net energetic value of *Q. agrifolia* acorns, in which carbohydrates contribute a smaller proportion of the total gross energy value, was $16.22 \pm 1.41 \text{ kJ} \cdot \text{g}^{-1}$, 1.23 times that listed by Koenig and Mumme (1987). Koenig and Mumme (1987) further assumed 70% MEC of these already low energetic values. From the net values I obtained, *Q. lobata* acorns provide approx. 2.93 times the energetic values used by Koenig and Mumme (1987), and *Q. agrifolia* acorns provide 1.75 times the values.

The effect of this error on subsequent calculations depends on the proportion of each species of acorn used and is beyond the scope of this paper. However, based on the values presented above, the estimates of Koenig and Mumme (1987) for the energetic value of stored acorns are probably off by a factor of between 2 and 2.5. They estimated that when granaries in the Hastings Reservation population were full, they held an average of only 6.5% of the total energetic needs of the population between 1 December, when acorn storage is usually complete, and 1 June, by which time most young have fledged. Assuming that the net energetic value of acorns is 2.5 times greater, this proportion would be increased to 16.3%. This is still a relatively small value and does not qualitatively change the conclusions of Koenig and Mumme (1987), contrary to the doubts of Brown (1987). Given the importance of stored acorns to overwinter survival and reproductive success, stored acorns still apparently supply a surprisingly small fraction of the total energetic needs of Acorn Woodpeckers.

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