

EFFECTS OF CACHING ON ACORN TANNIN LEVELS AND BLUE JAY DIETARY PERFORMANCE¹

MARK D. DIXON² AND W. CARTER JOHNSON³

Department of Horticulture, Forestry, Landscape and Parks, South Dakota State University,
Brookings, SD 57007

CURTIS S. ADKISSON

Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061

Abstract. Blue Jays (*Cyanocitta cristata*) are important consumers and dispersers of the nuts of oaks and other fagaceous trees in eastern North America. Acorns comprise much of the jay diet, especially during the autumn when jays may spend considerable time harvesting and consuming or caching acorns. However, jays do not appear to possess physiological adaptations for countering the protein-binding properties of secondary compounds (tannins) found in acorns. We tested whether simulated overwinter caching would reduce tannin levels in northern red oak (*Quercus rubra*) and bur oak (*Q. macrocarpa*) acorns, enabling jays to subsist on a cached acorn diet by circumventing the negative effects of high tannin levels in the acorns. After overwinter storage, acorns in simulated caches did not differ significantly in tannin level from uncached acorns, and jays lost weight rapidly on both cached and uncached acorn diets. Thus, simulated caching did not appear to significantly reduce tannin protein-binding activity of acorns, nor enable jays to better subsist on an all-acorn diet.

Key words: *Quercus*, *Cyanocitta cristata*, tannins, oaks, jays, acorns, caching.

INTRODUCTION

The Blue Jay (*Cyanocitta cristata*) may be a keystone species for recruitment of oaks and other nut-bearing trees in eastern North America, functioning both as a seed predator and an important long-distance disperser of nuts (Darley-Hill and Johnson 1981, Johnson and Adkisson 1985, Johnson and Webb 1989). Jays use the temporarily abundant, high-energy food source that acorns provide by storing many for use during winter and spring when other sources of food may be scarce (Bossemma 1979, Vander Wall 1990).

Although the bulk of the fall and early winter jay diet often consists of acorns (Beal 1896, Martin et al. 1951), Johnson et al. (1993) found that Blue Jays were unable to subsist for even a short time on an all-acorn diet in the laboratory. Koenig and Heck (1988) found a similar inability of Western Scrub-Jays (*Aphelocoma californica*) to subsist on an all-acorn diet. In both experiments, the inability of jays to subsist solely

on acorns was attributed to the relatively high concentration of secondary compounds called tannins found in acorns. Tannins bind with dietary proteins and/or digestive enzymes, thereby inhibiting protein digestion (Butler et al. 1986, Robbins et al. 1987), and possibly have direct toxic effects on herbivores (Bernays et al. 1989).

The absence of apparent physiological adaptation to high tannin levels suggests that wild jays must circumvent the effects of tannins behaviorally. Possible foraging strategies include: (1) dietary mixing to dilute or negate the effects of tannins (Bernays et al. 1989), (2) consumption of high-protein foods, such as insects (Semel and Andersen 1988, Bell 1990, Johnson et al. 1993), to overcome protein deficits in the diet (Izhaki and Safriel 1989, 1990, Fleck and Tomback 1996) and perhaps to inhibit protein-binding effectiveness of the tannins (Hagerman and Robbins 1987), (3) manipulation of acorn chemistry via storage (Fleck 1988, Chung-MacCoubrey 1993), and (4) selective consumption of only lower-tannin acorns or lower-tannin portions of acorns (Steele et al. 1993).

Several studies suggest that caching behavior may help animals manage the chemistry and palatability of stored food (Reichman et al. 1986, Roy and Bergeron 1990), and some have speculated that overwinter weathering may cause acorns to undergo changes in tannin levels

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² Current address: Department of Zoology, Birge Hall, University of Wisconsin, Madison, WI 53706, e-mail: mdixon@ravel.zoology.wisc.edu

³ Corresponding author. e-mail: johnsonc@mg.sdstate.edu

(Koenig and Heck 1988, Scarlett and Smith 1991) through leaching or oxidation. Freeze-thaw cycles, snow-melt, fungal attack, and pre- or post-germination chemical changes in the acorn may influence tannin levels.

Studies of the impact of storage on acorn chemistry have had equivocal results (Fleck 1988, Chung-MacCoubrey 1993). The objectives of our study were to determine whether acorns cached in the field undergo changes in tannin levels (as measured by protein-binding activity) during winter storage, and whether such changes enable jays to better subsist on acorns. Specifically, we compared tannin levels between acorns overwintered in the field in simulated "caches" and those stored in a laboratory freezer. Secondly, we compared mass gain/loss of birds fed cached (i.e., weathered) or uncached (frozen) acorns.

METHODS

MATERIALS

Northern red oak (*Quercus rubra*) and bur oak (*Q. macrocarpa*) acorns were used in simulated caches, tannin assays, and dietary trials. Our source of northern red oak acorns was the State Nursery of Iowa in Ames. Bur oak acorns were collected from the ground and from trees at the Northern Plains Biological Field Station and at Oakwood State Park (both in Brookings Co., South Dakota) during September 1992. Flotation tests and visual examination of nuts ensured that most acorns used in simulated caches were sound and not infested by acorn weevil larvae (Coleoptera: Curculionidae). Approximately 90% of the northern red oak and 85% of the bur oak acorns used in caches were uninfested.

ACORN TREATMENTS

We cached acorns in the field to expose them to ambient conditions similar to those that would occur in actual jay caches. In early November 1992, we artificially cached 960 northern red oak and 960 bur oak acorns by placing them under leaf litter and/or by pushing them into the ground. In the field, jays have been observed to cache nuts in either way (Darley-Hill and Johnson 1981). Most caching activity by jays probably occurred somewhat earlier in the fall, in September and October (Johnson et al., unpubl. data), although jays were observed foraging into November on acorns (mostly fallen ones) on the study site.

The artificially cached nuts, in lots of 320 (160 of each species), were covered by screens (one per lot) to prevent predation by small mammals. Seven more exclosures, containing 110 northern red oak acorns each, were put out in late November. All exclosures were placed in old-field/prairie and wooded habitats at the Northern Plains Biological Field Station at Oak Lake.

The first six exclosures were rectangular frames of sheet steel (61 × 61 cm, or 46 × 61 cm), with a wooden sliding top covered with 0.6 cm (¼ inch) hardware cloth. The sheet steel sides were 15 cm high and were buried approximately 10–13 cm into the ground to prevent burrowing. The other seven exclosures were made of 0.6 cm hardware cloth only, folded into a 46 × 46 × 15 cm box with an open bottom. The sides were fastened together at the corners with metal clips.

Seven hundred bur oak and 1,500 northern red oak acorns were kept indoors at low temperatures to serve as a control against potential tannin loss due to weathering of caches in the field. Laboratory-stored acorns were kept at 4°C from November to mid-January in sealed plastic freezer bags. Some acorns (the PRE treatment) were ground and freeze-dried in mid-January, and then stored at -80°C, to serve as a control against possible chemical changes of acorns during further storage in the laboratory. Freeze-drying may be the most effective means to prevent chemical changes in plant material during storage and processing (Martin and Martin 1983, Servello et al. 1987, Hagerman 1988). The rest of the acorns stored in the laboratory (LAB treatment) were left intact (not ground and not freeze-dried) in order to be used for jay dietary trials the next summer. These also were transferred to a freezer and stored at -80°C in mid-January. A summary of the three acorn storage treatments is shown in Table 1.

Because samples were not freeze-dried until mid-January, the tannin levels of laboratory-stored acorns freeze-dried in mid-January (PRE) served as "initial conditions," or the standard against which to compare chemical change due to weathering in the field (CACHE) or due to continued storage in the laboratory (LAB). Differences between the LAB and PRE treatments were expected to be minimal, because both were stored at -80°C. Some changes in tannin level during the initial storage period (at 4°C) were

TABLE 1. Timeline and summary of acorn treatments.

Date	Acorn treatments		
	Pre	Lab	Cache
September 1992	collected, air-dried, stored at 4°C	collected, air-dried, stored at 4°C	collected, air-dried, stored at 4°C
November 1992	kept at 4°C	kept at 4°C	cached in the field
mid-January 1993	freeze-dried, stored at -80°C	stored at -80°C	caches remain in the field
late May 1993	kept at -80°C	kept at -80°C	recovered from field, stored at room temp.
June 1993	tannin assays	tannin assays, dietary trials	tannin assays, dietary trials

possible (Servello et al. 1987), but we believe that these changes were minimal due to the relatively low, constant temperatures. Acorns from all three groups may have changed chemically during ripening (see Fleck and Lane 1990) and air-drying prior to storage in the laboratory or field.

In late May of 1993, acorns previously cached in enclosures were recovered and stored at room temperature. Actual timing and frequency of cache recovery by Blue Jays in the wild is poorly documented, but observations suggest that utilization of cached acorns occurs in the spring (Laskey 1943, Johnson, pers. observ.) and perhaps may coincide with the commencement of nesting (K. G. Smith, pers. comm.). Relatively frequent occurrence of mast during May and June in the diets of birds sampled by Beal (1896) also suggests that some caches are being utilized in middle to late spring. Eurasian Jays (*Garrulus glandarius*) apparently recover caches from winter to early summer, and even provision fledglings partially with stored acorns (Bossemma 1979).

ACORN CHEMISTRY

In June, samples of endosperm from LAB and CACHE acorns were ground in a mortar and pestle over liquid nitrogen and then freeze-dried. Freeze-dried samples were then kept at -80°C prior to extraction and tannin assays.

Endosperm samples were extracted in a 70% acetone solution (70% acetone, 30% water) for 6–10 hr in microcentrifuge tubes, with 200 mg (dry weight) of acorn per 1 ml of solvent. Samples were vortexed for 30 sec at the beginning, midway, and at the end of extraction, and were then spun at high speed in a microcentrifuge for 10 min.

We used the radial diffusion method of Hagerman (1987) to quantify tannin levels. This assay has been widely used because it is relatively simple, fast, and does not require expensive equipment or reagents. Also, as a protein-precipitating technique, it comes closer to measuring the potential biological effects of unknown phenolic compounds than do conventional chemical assays which simply quantify total tannin levels (Mole and Waterman 1987, Wisdom et al. 1987, Hagerman and Butler 1989). In this tannin assay, the relative protein-binding capacity of an extract of plant tissue is correlated with the diameter or area of a ring of precipitated protein formed as the tannin diffuses radially through a protein-laden agarose gel. Tannin levels in different extracts can be compared relative to each other, or to known standards from commercially-available tannin, such as tannic acid (a hydrolyzable tannin) or quebracho (a condensed tannin).

Our methods followed those of Hagerman (1987), except that we used a 5% concentration of bovine serum albumin (BSA, fatty acid-free fraction V; 0.05 g BSA g⁻¹ of gel) in the agarose gel instead of 10%. The lower protein concentration was used in order to generate larger, more easily-measured rings in the gel.

We applied aliquots of the acorn extracts to 4 mm diameter wells in the gel using a 10 µl Hamilton microsyringe. Except for some early tannin assays for red oak in which only 16 µl were applied, we used 24 µl of extract per well (three installments of 8 µl). Wells were produced with a biopsy punch and were placed as far apart as possible, with six per plate. Each plate had three samples of red oak and three of bur oak, with one sample per species of

CACHE, LAB, and PRE acorns. A total of 39 plates was assayed.

After incubating the gels at 30°C for four days, we measured the ring diameters using Videoplan (Zeiss) software with a 4× magnification. We took three measurements of ring diameter per sample by picking points on opposite sides of the ring and digitizing a line between them, with the program automatically measuring the diameter. Measurements were taken to the nearest 0.1 mm. When rings were misshapen (due to proximity to each other or to the edge of the gel) and complete diameters could not be measured, we estimated the ring diameter by measuring the radius on parts of the ring that did not appear misshapen and then multiplying by two.

The protein-precipitating ability of an extract was expressed in tannic acid equivalents (mg tannic acid needed to precipitate as much BSA as 1 mg dry weight of acorn endosperm). We used linear regression to calculate standard curves relating ring size (diameter squared) to different levels of purified tannic acid. To correct for differences among individual batches of gel, we ran tannic acid standards in triplicate and calculated a separate standard curve for each batch. Each batch yielded 9–18 plates of gel. The tannic acid equivalent was calculated for each acorn sample by taking the mean of the three measured diameters, squaring it, and entering it into the standard curve regression equation for that batch.

JAY PERFORMANCE ON ALL-ACORN DIETS

Dietary trials to examine the ability of jays to subsist on cached (CACHE) or uncached (LAB) all-acorn diets were conducted at Virginia Polytechnic Institute and State University because of the availability of aviary and laboratory facilities. Both bur oak and northern red oak occur in Virginia, and we assumed that Virginia jays would respond similarly to acorns from Iowa and South Dakota as to local sources (but see Briggs and Smith 1989). We captured eighteen jays near Blacksburg, Virginia in April 1993 for use in the dietary trials. Jays were housed in an outdoor aviary and kept on a diet of high-protein dog food, sunflower seeds, and acorns previous to trials. In addition to offering acorns as a part of the control diet over a several week period before and between trials, we attempted to acclimate the birds to the all-acorn diets by sub-

jecting them to several short pre-experiment periods of all-acorn diets. This included a 10-day period, just prior to the red oak trials, during which all food except for acorns was removed for 4–8 hr each day.

Dietary trials were conducted as in Johnson et al. (1993), with birds housed in 0.5 m³ wire cages in an indoor experimental room and kept on a 14-hr light:10-hr dark photoperiod. Jays were given an ad libitum diet of CACHE acorns, LAB acorns, or a control diet of lab chow (dog food and sunflower seeds) and acorns. Acorns were halved to ensure that none contained insect larvae. All food was removed just before dark each night and fresh food was offered each morning after the birds were weighed. Trials were ended after three days or sooner if a particular bird lost as much as 20% of its body weight or showed other signs of severe stress.

Diet experiments were conducted separately for the two acorn species, with the northern red oak trial preceding the bur oak trial by three weeks. Birds were kept on control diets between trials until they had regained pre-trial body weight. Five birds were used per treatment in the red oak trial and four in the bur oak trial. In the bur oak trial, one bird from each of the red oak acorn diets, plus two birds that had previously been on a control diet, were assigned to each dietary treatment so that effects of prior exposure to the red oak treatment could be assessed.

STATISTICAL ANALYSES

We compared tannin activity levels (tannic acid equivalents) across acorn species and storage types (CACHE, LAB, PRE) using analysis of variance (ANOVA). The ANOVA model incorporated the effects of acorn species, storage, batch of gel, and individual plate, with acorn species and storage considered fixed effects, and the rest considered random effects. When significant ANOVA results were obtained ($P < 0.05$), multiple comparisons were made using least-squares means (SAS Institute Inc. 1989).

Cumulative weight changes by the third morning (i.e., after two full days on the diet) for birds on different diets also were compared by ANOVA, with least-squares means used for multiple comparisons. Analysis of variance was conducted with the two trials lumped, so that jay performance could be compared across acorn species and diets. The analysis was run as a

TABLE 2. Means (\pm SE) of cumulative jay mass changes (g) after two full days in a dietary trial. For each diet treatment, $n = 4$ for bur oak and $n = 5$ for red oak. Means followed by different letters differ significantly ($P < 0.05$).

Trial	Diet		
	Control	Weathered (Cache)	Unweathered (Lab)
Bur oak	$-0.70 \pm 0.68^* A$	$-13.30 \pm 1.68 B$	$-12.73 \pm 1.41 B$
Red oak	$-0.46 \pm 0.31^* A$	$-12.94 \pm 1.36 B$	$-12.20 \pm 2.74 B$

* Means do not differ significantly from zero.

model I, fixed effects, two-way ANOVA (Zar 1984).

All analyses were run using the General Linear Models (GLM) procedure (SAS Institute Inc. 1989). Multiple comparisons were performed only after significant ANOVA results, but P -values were based on each individual comparison, with no attempt to control for an overall experiment-wise error level. Means \pm SE for acorn tannin levels and bird weight loss are reported below.

RESULTS

Acorns from the two oak species differed significantly in tannin activity ($F_{1,5} = 3,276.6$, $P < 0.001$), with northern red oak acorns approximately three times higher in mean tannin level (mg tannic acid/mg dry weight of acorn endosperm) than bur oak acorns ($\bar{x} = 0.072 \pm 0.001$ and 0.024 ± 0.001 , respectively, $n = 117$ for each). Tannin levels did not differ significantly among storage types ($F_{2,10} = 1.7$, $P = 0.23$; least-squares means across species: CACHE = 0.044 ± 0.002 , LAB = 0.048 ± 0.002 , PRE = 0.050 ± 0.002).

Jay weight loss also did not differ significantly between the diets of CACHE (weathered) and LAB (unweathered) acorns (Table 2). Birds did equally poorly on all of the all-acorn diets, losing an average of 12.2–13.3 g (approximately 14–15% of body weight) by the third morning of the trials (Table 2, Fig. 1). Weight changes of birds on the control diets did not differ significantly from zero, and birds on the all-acorn diets lost significantly more weight than the controls. In the bur oak trial, no significant differences occurred in weight loss among birds that had been on an all-acorn diet in the previous red oak trial and those that had been on a control diet (Fig. 1, $P > 0.50$).

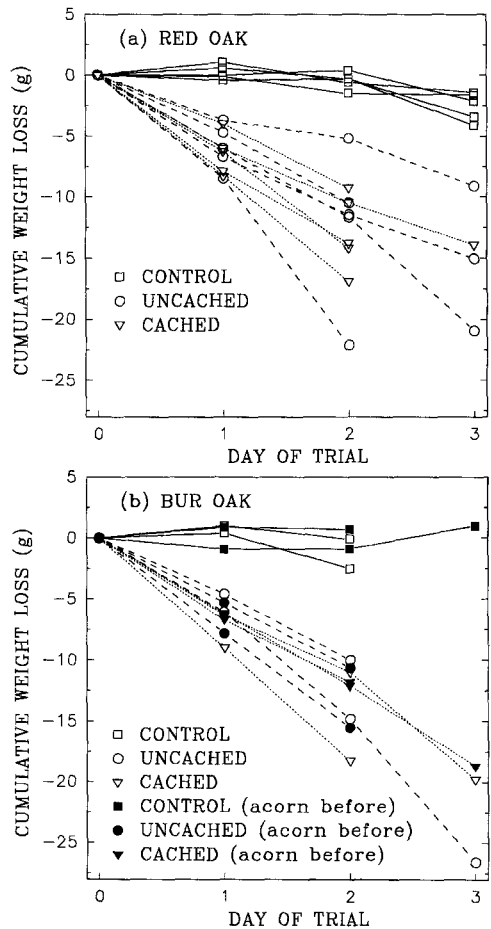


FIGURE 1. Weight change of individual jays in (a) red oak and (b) bur oak trials with control, cached acorn, and uncached acorn diets. Control diets are represented by solid lines, uncached acorn diets by long dashes, and cached acorn diets by short dashes. In (b), "acorn before" denotes birds that had been on all-acorn (cached or uncached) diets in previous (red oak) trials. Trials were discontinued for many birds prior to day three.

DISCUSSION

TANNIN ASSAYS

We found no significant effect of storage on tannin activity levels. Other studies have shown mixed results, with tannin declines in some acorn species, but not in others (Fleck 1988, Chung-MacCoubrey 1993). Our results were similar to those of Chung-MacCoubrey (1993), in that northern red oak showed no significant decline in tannin levels, but differed in that our *Lepidobalanus* species (bur oak) also showed no significant tannin declines. Fleck (1988) found large decreases in tannin level during storage in three of four acorn species examined, including species of both the *Erythrobalanus* and *Lepidobalanus* subgenera.

Our results may differ from Fleck (1988) and Chung-MacCoubrey (1993) because of the use of different species of acorns, differences in how acorns were cached, and large differences in climate and soil conditions between our study site (in South Dakota) and the study sites of Chung-MacCoubrey (in southwestern Virginia) and Fleck (in southern Florida). Additionally, it is possible that tannin changes occurred in our acorns during ripening (Fleck and Layne 1990) or during initial storage prior to freeze-drying (Servello et al. 1987), so that our uncached acorns did not accurately reflect tannin levels in fresh acorns.

DIET TRIALS

Regardless of whether or not acorns declined in tannin level during storage, tannin levels following overwinter storage were apparently still high enough to greatly inhibit performance of the birds on the all-acorn diets. The fact that weight loss of birds did not differ between storage types (CACHE and LAB) was not surprising, because tannin levels between these two groups did not differ significantly. However, no differences in weight loss occurred between groups of birds fed different acorn species, despite a three-fold difference in tannin levels. Johnson et al. (1993) also found similar results across trials with northern red, pin (*Quercus palustris*) and white oak (*Q. alba*), and even with diets supplemented with 1.5 g of weevil larvae (but not with 5.0 g of larvae). Similarly, Koenig and Heck (1988) found that weight loss of Western Scrub-Jays did not differ between diets of high- and low-tannin acorns.

The lack of a correlation of acorn tannin content with magnitude of jay weight loss raises the question whether weight losses are a direct response to tannins, to nutritional deficiencies in the acorns, or to some unknown factor. Acorns are typically rather low in protein and phosphorus, although many acorns species in the *Erythrobalanus* subgenus (including northern red oak and pin oak), are relatively high in lipids (Ofcarcik and Burns 1971, Short 1976, Short and Epps 1976).

The work of Fleck and Tomback (1996) supports the hypothesis that tannins, in concert with inherently low protein levels in acorns, are the cause of weight loss. In their experiments, Western Scrub-Jays were unable to maintain body weight on artificial diets comparable in protein and lipid content to *Lepidobalanus* (*Q. gambelii*) acorns, even at low tannin levels. However, the addition of higher tannin levels doubled the rate of weight loss (from around 2 to 4.5 g day⁻¹), suggesting a significant effect of tannins. No significant weight loss occurred on the high tannin diet when sufficient protein was provided.

Rates of weight loss in our study (around 6 g day⁻¹) and in Johnson et al. (1993) are slightly higher than the range found in the high-tannin, low-protein diets of Fleck and Tomback (1996), and did not differ between the high- and low-tannin groups. However, as Fleck and Tomback point out, the natural mix of tannins in acorns may be more toxic to jays than the commercially available tannic acid used in their artificial diets. Acorns contain both hydrolyzable and condensed tannins (Koenig and Heck 1988), whereas tannic acid is a mix of only hydrolyzable tannins. Koenig (1991) found that both types of tannins adversely affected digestion of acorns by Acorn Woodpeckers, with condensed tannins having the stronger effect. The greater range of tannin types and molecular weights in real acorns (as compared to the artificial diets) may result in more complete binding of dietary protein and deactivation of enzymes, particularly if tannins and proteins interact with the specificity envisioned by Haslam (1988).

Besides the effect of tannins and protein deficiencies, it is possible that the shift from the control diet to the all-acorn diets severely stressed the birds or caused them to drastically reduce food consumption, thus contributing to weight loss. However, birds were subjected to several short intervals of all-acorn diets prior to

experiments and also were offered acorns as a part of their diet both before and between trials, and thus should have been accustomed to handling and eating acorns. Although we were not able to directly measure intake rates, jays on the all-acorn diets were observed vigorously handling and attempting to open and eat whole or half acorns.

CONCLUSIONS

The hypotheses that jays manage the chemical composition of their acorn stores to reduce tannin levels, and that reduced tannin levels enable jays to better subsist on an all- or high-acorn diet were not supported by our experimental findings. Tannin levels were not significantly lower in experimental caches than in acorns kept in cold storage in the laboratory, and birds did equally poorly on diets of cached or uncached acorns, and on both low- and high-tannin species of acorns.

Because our control for tannin change in cached acorns may not have reflected tannin levels at the time jays were caching nuts, and because of the high variability of individual acorn species and ambient conditions to which they might be exposed in jay caches, our conclusions on acorn tannin change during winter storage should be taken with caution. To more rigorously address the question of tannin change in acorns, other work should be done in which acorns at various stages of ripening and at different durations or conditions of storage are compared for tannin content and other chemical constituents. Clearly, however, any tannin changes that might have occurred in this study were still insufficient to enable jays to subsist on an all-acorn diet for even a short time interval.

Although jays performed equally poorly on high- and low-tannin acorn diets in our study, this may not be the case under most natural situations in which jays would rarely have to subsist completely on acorns. At the low protein levels found in all-acorn diets, even relatively low tannin levels may completely bind up dietary protein and digestive enzymes, so that bird performance is little better than that of birds deprived of all food (Johnson et al. 1993). However, the threshold amount or ratio of protein needed to overcome the effects of a diet of low-tannin acorns may be lower than that needed for a diet of high-tannin acorns. This idea could be elucidated with the right set of experiments, sim-

ilar to those of Fleck and Tomback (1996) and Servello and Kirkpatrick (1989), in which diets with different levels of protein and tannin (or acorn content) are presented to the birds.

Our results, and those of Johnson et al. (1993) and Fleck and Tomback (1996), suggest the potential importance of consumption of high-protein foods for jays in conjunction with acorn consumption. Access to some sources of extra protein may be important for jays to benefit from acorn stores even during crucial times when other sources of food are scarce. Without sufficient mixing of high-protein foods with tannin consumption, dietary protein from acorns and perhaps the digestive enzymes in the bird may be effectively bound, resulting in the near negation of nutritional benefit. Consumption of at least a threshold amount of protein may be necessary to overwhelm the effects of tannin and to benefit from the high caloric content found in many acorn species (Ofcarcik and Burns 1971, Short and Epps 1976), make up for deficiencies in protein from both the tannins and the inherently low protein levels in acorns, and prevent damage to the gut wall and absorption of soluble products of tannin hydrolysis into the blood stream (Lindroth and Batzli 1984, Bernays et al. 1989).

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LITERATURE CITED

- BEAL, F. E. L. 1896. The Blue Jay and its food, p. 197-206. *In* Yearbook of the Department of Agriculture. Government Printing Office, Washington, DC.
- BELL, G. P. 1990. Birds and mammals on an insect diet: a primer on diet composition analysis in relation to ecological energetics. *Stud. Avian Biol.* 13:416-422.
- BERNAYS, E. A., G. COOPER-DRIVER, AND M. BILGENER. 1989. Herbivores and plant tannins. *Adv. Ecol. Res.* 19:263-302.
- BOSSEMA, I. 1979. Jays and oaks: an eco-ethological study of a symbiosis. *Behaviour* 70:1-117.

- BRIGGS, J. M., AND K. G. SMITH. 1989. Influence of habitat on acorn selection by *Peromyscus leucopus*. *J. Mammal.* 70:35-43.
- BUTLER, L. G., J. C. ROGLER, H. MEHANSHO, AND D. M. CARLSON. 1986. Dietary effects of tannins, p. 141-157. In J. B. Harborne and E. Middleton [eds.], *Plant flavonoids in medicine: biochemical, pharmacological, and structure-activity relationships*. Alan R. Liss, New York.
- CHUNG-MACCOUBREY, A. L. 1993. Effects of tannins on protein digestibility and detoxification activity in gray squirrels (*Sciurus carolinensis*). M.Sc. thesis, Virginia Polytechnic Inst. and State Univ., Blacksburg, VA.
- DARLEY-HILL, S., AND W. C. JOHNSON. 1981. Acorn dispersal by the Blue Jay (*Cyanocitta cristata* L.). *Oecologia* 50:231-232.
- FLECK, D. C. 1988. Acorn tannin influences on the caching behavior of the Florida Scrub-Jay (*Aphelocoma c. coerulescens*). M.Sc. thesis, Univ. South Florida, Tampa, FL.
- FLECK, D. C., AND J. N. LAYNE. 1990. Variation in tannin activity of acorns of seven species of central Florida oaks. *J. Chem. Ecol.* 16:2925-2934.
- FLECK, D. C., AND D. F. TOMBACK. 1996. Tannin and protein in the diet of a food-hoarding granivore, the Western Scrub-Jay. *Condor* 98:474-482.
- HAGERMAN, A. E. 1987. Radial diffusion method for determining tannin in plant extracts. *J. Chem. Ecol.* 13:437-449.
- HAGERMAN, A. E. 1988. Extraction of tannin from fresh and preserved leaves. *J. Chem. Ecol.* 14:453-461.
- HAGERMAN, A. E., AND L. G. BUTLER. 1989. Choosing appropriate methods and standards for assaying tannin. *J. Chem. Ecol.* 15:1795-1810.
- HAGERMAN, A. E., AND C. T. ROBBINS. 1987. Implications of soluble tannin-protein complexes for tannin analysis and plant defense mechanisms. *J. Chem. Ecol.* 13:1243-1259.
- HASLAM, E. 1988. Plant polyphenols (syn. vegetable tannins) and chemical defense—a reappraisal. *J. Chem. Ecol.* 14:1789-1806.
- IZHAKI, I., AND U. N. SAFRIEL. 1989. Why are there so few exclusively frugivorous birds? Experiments on fruit digestibility. *Oikos* 54:23-32.
- IZHAKI, I., AND U. N. SAFRIEL. 1990. Weight losses due to exclusive fruit diet—interpretation and evolutionary implications: a reply to Mack and Sedinger. *Oikos* 57:140-142.
- JOHNSON, W. C., AND C. S. ADKISSON. 1985. Dispersal of beechnuts by Blue Jays in fragmented landscapes. *Am. Midl. Nat.* 113:319-324.
- JOHNSON, W. C., L. THOMAS, AND C. S. ADKISSON. 1993. Dietary circumvention of acorn tannins by Blue Jays: implications for oak demography. *Oecologia* 94:159-164.
- JOHNSON, W. C., AND T. WEBB III. 1989. The role of Blue Jays (*Cyanocitta cristata* L.) in the postglacial dispersal of fagaceous trees in eastern North America. *J. Biogeog.* 16:561-571.
- KOENIG, W. D. 1991. The effects of tannins and lipids on digestion of acorns by Acorn Woodpeckers. *Auk* 108:79-88.
- KOENIG, W. D., AND M. K. HECK. 1988. Ability of two species of oak woodland birds to subsist on acorns. *Condor* 90:705-708.
- LASKEY, A. R. 1943. The seeds buried by Blue Jays. *Migrant* 14:58.
- LINDROTH, R. L., AND G. O. BATZLI. 1984. Plant phenolics as chemical defenses: effects of natural phenolics on survival and growth of prairie voles (*Microtus ochrogaster*). *J. Chem. Ecol.* 10:229-244.
- MARTIN, A. C., H. S. ZIM, AND A. L. NELSON. 1951. *American wildlife and plants. A guide to wildlife food habits*. Dover, New York.
- MARTIN, J. S., AND M. M. MARTIN. 1983. Tannin assays in ecological studies—precipitation of ribulose-1,5-biphosphate carboxylase/oxygenase by tannic acid, quebracho, and oak foliage extracts. *J. Chem. Ecol.* 9:285-294.
- MOLE, S., AND P. G. WATERMAN. 1987. A critical analysis of techniques for measuring tannins in ecological studies II. Techniques for biochemically defining tannins. *Oecologia* 72:148-156.
- OFCARCIK, R. P., AND E. E. BURNS. 1971. Chemical and physical properties of selected acorns. *J. Food Sci.* 36:576-578.
- REICHMAN, O. J., A. FATTAEY, AND K. FATTAEY. 1986. Management of sterile and mouldy seeds by a desert rodent. *Anim. Behav.* 34:221-225.
- ROBBINS, C. T., T. A. HANLEY, A. E. HAGERMAN, O. HJELJORD, D. L. BAKER, C. C. SCHWARTZ, AND W. W. MAUTZ. 1987. Role of tannins in defending plants against ruminants: reduction in protein availability. *Ecology* 68:98-107.
- ROY, J., AND J. M. BERGERON. 1990. Branch cutting behavior by the vole (*Microtus pennsylvanicus*): a mechanism to decrease toxicity of secondary metabolites in conifers. *J. Chem. Ecol.* 16:735-741.
- SAS INSTITUTE INC. 1989. *SAS/STAT user's guide*. Version 6, 4th ed., Vol. 2. SAS Institute, Inc., Cary, NC.
- SCARLETT, T. L., AND K. G. SMITH. 1991. Acorn preference of urban Blue Jays (*Cyanocitta cristata*) during fall and spring in northwestern Arkansas. *Condor* 93:438-442.
- SEMEL, B., AND D. C. ANDERSEN. 1988. Vulnerability of acorn weevils (Coleoptera: Curculionidae) and attractiveness of weevils and infested *Quercus alba* acorns to *Peromyscus leucopus* and *Blarina brevicauda*. *Am. Midl. Nat.* 119:385-393.
- SERVELLO, F. A., AND R. L. KIRKPATRICK. 1989. Nutritional value of acorns for Ruffed Grouse. *J. Wildl. Manage.* 53:26-29.
- SERVELLO, F. A., R. L. KIRKPATRICK, AND K. E. WEBB. 1987. Predicting metabolizable energy in the diet of Ruffed Grouse. *J. Wildl. Manage.* 51:560-567.
- SHORT, H. L. 1976. Composition and squirrel use of acorns of black and white oak groups. *J. Wildl. Manage.* 40:479-483.
- SHORT, H. L., AND E. A. EPPS, JR. 1976. Nutrient quality and digestibility of seeds and fruits from southern forests. *J. Wildl. Manage.* 40:283-289.
- STEELE, M. A., T. KNOWLES, K. BRIDLE, AND E. L. SIMMS. 1993. Tannins and partial consumption of

- acorns: implications for dispersal of oaks by seed predators. *Am. Midl. Nat.* 130:229–238.
- VANDER WALL, S. B. 1990. Food hoarding in animals. Univ. Chicago Press, Chicago.
- WISDOM, C. S., A. GONZALEZ-COLOMA, AND P. W. RUNDEL. 1987. Ecological tannin assays. Evaluation of proanthocyanidins, protein binding assays and protein precipitating potential. *Oecologia* 72:395–401.
- ZAR, J. H. 1984. *Biostatistical analysis*, 2nd ed. Prentice-Hall, Englewood Cliffs, NJ.