The Condor 98:474–482

TANNIN AND PROTEIN IN THE DIET OF A FOOD-HOARDING GRANIVORE, THE WESTERN SCRUB-JAY[1]

DAVID C. FLECK[2]
Department of EPO Biology, University of Colorado at Boulder, Boulder, CO 80309-0334

DIANA F. TOMBACK
Department of Biology, University of Colorado at Denver, Denver, CO 80217-3364

Abstract. Plant tannins are known to impede vertebrate protein digestion. The severity of their impact on vertebrates, particularly birds, may be a function of the relative presence of lipids and proteins (or individual amino acids) in the diet. We examined the effects on six captive Western Scrub-Jays (*Aphelocoma californica*) of dietary lipids and proteins in artificial diets that varied in tannin activity. Tannin variation in the artificial diets was within the range of concentrations in Gambel oak (*Quercus gambelii*) acorns, an important winter food. Jays lost mass on low-protein diets and lost the most mass on low-protein, high-tannin diets. A significant protein-tannin interaction existed such that tannin effects were eliminated in high-protein diets. No significant changes in weight were associated with any lipid treatments.

Key words: acorns; Aphelocoma; *dietary interactions; oaks; protein;* Quercus; *Scrub-Jay; tannins.*

INTRODUCTION

Tannins are phenolic compounds of variable molecular weight (between 300 and 3000 daltons) that are widespread throughout the plant kingdom and present in high concentrations in certain genera, notably the oaks (*Quercus*). They are regarded as an important component of plant chemical defense (e.g., see Rhoades and Cates 1976, Swain 1977, Fox 1981, Coley et al. 1985, Bernays et al. 1989, Harborne 1991).

In vertebrates, tannins are considered digestibility reducers: that is, they form insoluble precipitates with proteins, including herbivore digestive enzymes and other cellular components (Swain 1979, Hagerman and Klucher 1986), interfering with digestion of plant components (Feeny 1970, Short 1976) and reducing activity of digestive enzymes (Goldstein and Swain 1965, Feeny 1969). In addition, tannins may have direct toxic effects by attacking gut epithelia (Singleton and Kratzer 1973, Bernays 1981) and causing fatal liver necrosis or kidney damage when consumed in high concentrations (Dollahite et al. 1963, Singleton and Kratzer 1973). Tannins' deterrent effects have been noted in many vertebrate species, e.g., reptiles (Swain 1978), ruminants (Cooper-Driver et al. 1977, Cooper and Owen-Smith 1985, Robbins et al. 1987a, Robbins et al. 1987b, Provenza et al. 1990), primates (Wrangham and Waterman 1981, Harborne 1988, Marks et al. 1988), marsupials (McArthur and Sanson 1991), and birds (Tipton et al. 1970, Koenig and Mumme 1987).

Increased interest in the biological importance of tannins has uncovered complications to a previously unambiguous story. It has been argued that tannins' ability to form protein precipitates in vivo probably is minimal and therefore unlikely to be ecologically or physiologically important (Bernays 1981, Martin et al. 1985, Martin et al. 1985, Bernays 1987). In addition, studies have shown that some mammalian species possess the ability to physiologically ameliorate the detrimental effects of tannins (Austin et al. 1989, Mole et al. 1990, Robbins et al. 1991, Hagerman and Robbins 1993).

Among animals that consume large quantities of high-tannin foods, the ability to counteract tannin effects probably is very important (Koenig and Mumme 1987, Robbins et al. 1987a, Robbins et al. 1987b), but there is little evidence of detoxification ability in birds (but see Koenig and Heck 1988). Three papers have specifically addressed the means by which wild birds might

[1] Received 11 January 1996. Accepted 20 May 1996.
[2] Corresponding author. Current address: Division of Natural Sciences, University of Guam, U.O.G. Station, Mangilao, Guam 96923, USA, e-mail: dfleck@uog9.uog.edu

counteract the deleterious effects of acorn tannins. Koenig and Heck (1988) found that acorn woodpeckers (*Melanerpes formicivorus*) could persist indefinitely on low-tannin, low-lipid acorns; Koenig (1991) found that interactions with lipids, as would be found in high-lipid acorns, increased the severity of tannin effects in acorn woodpeckers for unknown reasons. Birds could avoid high-fat, high-tannin species and reduce deleterious tannin effects. Johnson et al. (1993) found that supplementation of an all-acorn diet with acorn weevil larvae (genus *Curculio*) eliminated the adverse affects of acorn tannins on Blue Jays (*Cyanocitta cristata*). They suggested that either the high protein content of the insects, or the insects' own specialized digestive chemistry (adapted for the consumption of acorns), allowed unlimited acorn consumption by the jays.

We performed a series of laboratory feeding trials to address several questions about the importance of variation in food tannins in a granivorous bird, the Western Scrub-Jay (*Aphelocoma californica* Bosc). Western Scrub-Jays in central Colorado store and eat acorns of Gambel's oak, *Quercus gambelii* Nuttall. *Q. gambelii* is a white oak of the subgenus Lepidobalanus, and thus has acorns relatively low in lipids, proteins, and tannins (Ofcarcik and Burns 1976, Fleck 1994). It is the only native oak species in Colorado, and the only oak widely available to Scrub-Jays. We wished to determine whether the range in tannin activity found within an oak species—even a relatively low-tannin species like *Q. gambelii*—was sufficient to influence jay feeding preferences and jay digestive efficiency. Would jays attempt to avoid higher-tannin foods, even when the range in tannin activity was within that found in a single species of oak? Would there be costs for not avoiding high tannin activity? We also wished to determine the effects of increased protein and lipid on jays fed diets varying in tannin activity. If tannins acted by binding protein, greater amounts of dietary protein could reduce tannin effects. If tannin effects were increased by high lipid content, then high lipid content would be associated with increased weight loss.

Our specific hypotheses were:

1. Jays would consume greater amounts of low-tannin food than high-tannin food when presented with both.
2. Jays fed high-tannin diets would lose weight relative to jays fed low-tannin diets.
3. Jays fed high-protein diets would lose less weight than jays fed low-protein diets.
4. Jays fed high-lipid diets would lose more weight than jays fed low-lipid diets.

METHODS

Feeding trials were conducted between 3 March and 12 May 1993, at the Animal Care Facility of the University of Colorado at Denver. Conditions of captivity and experimental protocols were in compliance with guidelines of the University's Institutional Animal Care and Use Committee. We used six Scrub-Jays, caught between 20 and 28 February 1993, at Deadmans Lake (T12S. R67W., Section 9), on the grounds of the United States Air Force Academy, El Paso County, Colorado. The sex and age of the jays were unknown. Jays were housed in separate cages, approximately 0.6 × 0.6 × 1.0 m, in an indoor room with temperature, humidity and light cycle controls. Room air temperature throughout captivity was 25°C, and relative humidity was 45 percent. The light cycle was reset weekly to reflect changes in the natural cycle. Throughout the period of captivity, the jays' water was supplemented with Avitron multivitamin supplement (6 drops/pint). At all times, food and water were available ad libitum. One jay died on 5 May, near the end of the study. Surviving jays were banded and released at the capture site on 15 May 1993.

EXPERIMENTAL DIETS

Real *Q. gambelii* acorns were not used in the experiments because of the high degree of weevil larval damage to acorns collected in the fall of 1992, and the greater difficulty in controlling for tannin activity resulting from weevil presence. Six experimental diets and one tannin-free standard diet were named according to their relative concentrations of lipids, protein, and tannin. For example, lPT designated a low lipid, high protein, high tannin diet, and conversely LPt designated a high lipid, high protein, low tannin diet. Different basic foods were used for each experimental diet pair; LPt and LPT consisted of Eukanuba puppy food, lPt and lPT consisted of Alpo dog treats, and lpt and lpT consisted of whole wheat bread, each with appropriate tannin added (Table 1). The basic foods were chopped

TABLE 1. Diet names are mnemonics based on levels of lipid (L), protein (P), and tannin (T) in each; capital letters represent high levels and lowercase letters represent low levels of a nutrient. % lipid and % protein in base diets obtained from product labels. Tannin activity measured by protein precipitating ability, the ability of an amount of plant tissue to precipitate a given amount of protein.

Diet	Base food	% lipid	% protein	PPA[1]
LP0	A	20	30	0
LPt	A	20	30	0.33
LPT	A	20	30	0.97
lpt	B	7	5	0.30
lpT	B	7	5	0.99
lPt	C	12	30	0.35
lPT	C	12	30	1.10
Gambel oak acorns:	[2]	6.5	10.5	0.70
	[3]	8.2	6.9	—

A: Eukanuba puppy food; B: whole wheat bread; C: Alpo dog treats.
[1] Protein precipitating ability; measured in mm^2 precipitated protein/mg acorn.
[2] Data from Fleck (1994).
[3] Data from Earle and Jones (1962).

or crumbled to the same approximate particle size, about 5mm on a side.

Analyses indicated no consistent pattern of condensed and hydrolyzed tannins either in high-PPA or low-PPA Q. *gambelii* acorns. Because of this inconsistency, tannic acid (Sigma T0125), a readily-available form of hydrolyzed tannin, was used. The experimental diets were made by adding tannic acid to the basic foods so that the diets, when assayed, would precipitate protein to a similar degree as high- and low-tannin activity *Q. gambelii* acorns. *Q. gambelii* acorns range in PPA (protein precipitating activity) from 0.3 mm^2/mg to 1.5 mm^2/mg with a mean value of 0.7 mm^2/mg (Fleck 1994). The low-tannin experimental diets had a PPA of ~ 0.35 mm^2/mg; the high-tannin diets had a PPA of ~ 1.0 mm^2/mg. Tannin activity in experimental diets was determined using Hagerman's (1987) assay (see also Fleck and Layne 1990). Diet lpt most closely mimicked low-tannin *Q. gambelii* acorns, while diet lpT mimicked high-tannin acorns from the studied population.

Diet components were soaked in a solution of 95% ethanol and tannic acid to incorporate tannic acid into the diets. The concentration of tannic acid used and the amount of time soaked depended on the diet (high or low tannin) and how readily the food absorbed the solution. Diets LPT and LPt, and lPT and lPt, were soaked in 40% (weight/volume) and 8% solutions for 90 and 45 min., respectively. Diets lpT and lpt were soaked in 20% and 4% solutions for 45 and 30 min, respectively. The tannin-free standard diet LP0 was soaked in 95% ethanol with no tannic acid for 90 min. After soaking, each diet was air-dried overnight to evaporate ethanol. No adverse effects from soaking food in 95% ethanol are expected; any alteration of water soluble vitamins should be compensated by the supplemental vitamins in water (E. Levy, pers. comm.).

FEEDING TRIALS

Prior to the feeding trials, we fed the jays the tannin-free standard diet LP0, piñon seeds, and sunflower seeds ad libitum. Jays were also fed this diet during recovery from diets which had resulted in significant weight loss. We presented all food to the jays in identical metal trays. Feeding trials were not begun until the jays' weights had stabilized. During each trial period, three birds were fed the low-tannin version of a diet pair while the remaining three birds were fed the high-tannin version. Each bird was provided with measured quantities of diet foods, generally 40 g/day. Birds were kept on a given experimental diet for 14 days, unless a bird showed rapid weight loss (greater than 1 g/day). After jays were taken off of a diet they were allowed to recover, either on diet LP0 if no significant weight loss occurred, or diet LP0 supplemented with seeds (see above) if weight loss was great. Diets were then switched, giving birds previously fed low-tannin diets the high-tannin diet, and vice versa, for 14 days (or until a bird showed rapid weight loss). In this way data were obtained on each bird for each diet.

Over the course of the study, it was not possible to accurately measure the total amounts of food that each bird consumed of each diet. Several jays developed the habit of storing food particles, hiding more than 50 g of food (of all experimental diets combined) this way. The jays were messy eaters and scattered food (of all experimental diets) about their cages and their holding room. On the whole, neither caching nor scattering of food appeared to be affected by nutritional makeup of the food. Although precise assessment of each birds' total consumption on each diet was not possible, food disappeared from food bowls at similar rates; approximately 9–11 g/day, regardless of diet.

Jays were weighed at capture and periodically during captivity. We did not want to stress the jays unnecessarily with frequent weighings, but the potential for rapid weight loss on the high-tannin diets required periodic monitoring of the birds' weight changes. Each bird was weighed every other day, except during the period when diets LPt and LPT were given; then birds were weighed every four days. At weighing, each bird was caught in a hand net, the net twisted shut to immobilize the jay, and the net and jay weighed together with a Pesola 300 g scale.

PREFERENCE TESTS

After the jays had experienced diets lpt and lpT and been allowed recuperation time on the standard diet, all birds were given 30 g each of both lpt and lpT. After 48 hr., all remaining food was weighed. The weight of the remaining food was subtracted from the initial 30 g to determine the total amount of each diet consumed.

STATISTICAL ANALYSES

Weight changes in jays on the different experimental diets lpt, lpT, lPt, and lPT were square-root transformed. Individual variation in weight change and variation due to diet were compared by 2-way ANOVA. Protein, tannin, and interaction effects were compared by 2-way ANOVA using protein and tannin as treatments while controlling for lipid levels. Lipid effects were assessed by 2-way ANOVA comparing lipid and tannin levels on transformed weight changes on diets LPt, LPT, lPt, and lPT. Preference test data (food consumed in 48 hr.) were analyzed by a non-parametric Mann-Whitney U-test. All analyses were conducted using SAS Release 6.09 (SAS Institute 1993).

RESULTS

The experimental diets had marked effects on the jays (Fig. 1, Tables 2–4). No significant variation existed among individual birds in their response to experimental diets (Table 2). Jays on high-lipid, high-protein diets showed no significant weight change, either at no, low, or high levels of tannin in the diet. On average, jays lost weight on all low-lipid diets, and experienced slight weight gains on both high-lipid diets; however, a comparison of high-lipid, high-protein diet weight changes to low-lipid, high-protein weight changes indicated that lipid alone was not associated with significant weight change (Table 3). Weight losses were most severe on the two

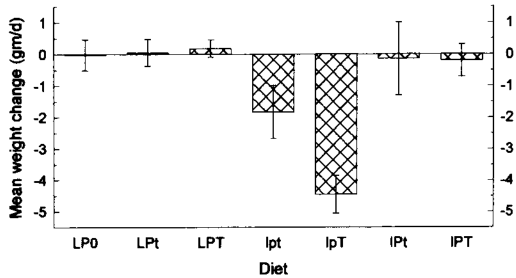

FIGURE 1. Mean weight changes and standard errors for six Western Scrub-Jays on seven experimental diets. Diet names are mnemonics based on levels of lipid (L), protein (P), and tannin (T) in each; capital letters represent high levels and lowercase letters represent low levels of a nutrient.

low-lipid, low-protein diets, which most closely approximated *Q. gambelii* acorns. By far the most severe loss occurred on diet lpT, similar in nutrient content to high-tannin *Q. gambelii* acorns (Fig. 1). An ANOVA using protein and tannin as separate treatments indicated highly significant effects from both protein and tannin diet content, as well as a significant interaction effect (Table 4). High tannin activity in the diet significantly increased weight loss in low-protein diets; the presence of sufficient protein in the diets eliminated weight loss.

The severity of weight losses on diets lpt and lpT meant that none of the jays were able to remain on these diets the full 14 days; jays on diet lpt all had to be returned to a maintenance diet after six days, and jays on diet lpT had to be returned to maintenance diets after four days.

When both foods were available for preference tests, jays consumed significantly more of the low tannin diet (lpt) as compared to the similarly constituted high-tannin diet (lpT) in a 48 hr period (25.56 g of lpt vs. 13.53 g of lpT; Mann-Whitney $U = 34$, $P < 0.01$). These diets were not obviously different in appearance or presentation, apart from diet lpT having a darker brown color—a consequence of higher tannin content.

TABLE 2. ANOVA table of the effects of experimental diets and individual variation on Scrub-Jay weight change.

Source	df	MS	*F*-ratio	*P* value
Bird	5	0.0573	1.04	0.42
Diet	6	1.3631	24.65	<0.01
Error	30	0.0553		

TABLE 3. ANOVA table of the effects of two levels of dietary lipid and dietary tannin on Scrub-Jay weight change. Comparisons of high-protein diets only.

Source	df	MS	*F*-ratio	*P* value
Lipid	1	0.0414	0.59	0.50
Tannin	1	0.0006	0.01	0.95
Interaction	1	0.0195	0.28	0.53
Error	18	0.0702		

DISCUSSION

Previous work (Koenig and Heck 1988, Johnson et al. 1993) found that Western Scrub-Jays and Blue Jays lose weight on acorn-only diets, and that the loss may be more severe on diets composed of the higher-tannin acorns of red oaks (subgenus Erythrobalanus). However, because real acorns were used in these studies, it is not possible to separate out the covarying nutritional effects of these different diets. As Bernays et al. (1989) have indicated, most evidence for tannins as important feeding deterrents is correlative. This is a problem for any attempt to determine the significance of tannins, because many other plant characteristics may covary with tannin activity (Smallwood and Peters 1986, Koenig 1991). Because the base foods in our study were not identical in composition, comparisons among the different diet pairs must be made with care. However, within each diet pair it was possible to assess the effects of tannins alone, because diet pairs (lpt and lpT, lPt and lPT, LPt and LPT) were identical except for the amount of tannin added; changes in weight were correlated to the change in the proportion of tannin in the diet. In addition, because tannins were added to the diets in quantities within the natural range of *Q. gambelii*, the results presumably are relevant to the Western Scrub-Jay-Gambel oak interaction in the wild. It is clear from this study that variation in acorn tannin activity, even the relatively small amount found in natural populations of Gambel oak, is sufficient to cause significant aversion to higher tannin food (all else being equal), and to cause significant differences in rates of weight loss in Scrub-Jays, provided dietary protein is limited.

TABLE 4. ANOVA table of the effects of two levels of dietary protein and dietary tannin on Scrub-Jay weight change. Comparisons of low-lipid diets only.

Source	df	MS	*F*-ratio	*P* value
Protein	1	4.1371	55.92	<0.001
Tannin	1	0.6731	9.10	<0.008
Interaction	1	0.4138	5.59	<0.03
Error	18	0.0740		

In accord with these previous studies, jays on a diet similar to low-tannin acorns (lpt) lost weight, but not as rapidly as jays on a diet similar to higher-tannin acorns (lpT). Because of time and space constraints, we were unable to test the birds on a low-lipid, low-protein, no tannin diet to determine whether the amounts of lipid and protein in these two diets were sufficient to maintain the birds under any circumstances. Regardless, higher tannin concentrations caused the birds to lose weight at nearly double the rate of low tannin concentrations. These data suggest that *Q. gambelii* acorns may not be an adequate food source regardless of tannin, similar to the findings of Koenig and Heck (1988) for other oak species. Colorado Scrub-Jays, like California Scrub-Jays (Koenig and Heck 1988) and Blue Jays (Johnson et al. 1993), probably are not physiologically capable of maintaining themselves on pure acorn diets for more than a few days at a time.

Studies of tannin effects on birds have shown a depression in growth rate, or even weight loss, in experimental domestic animals. Experiments on domestic fowl (*Gallus domesticus*) (Chang and Fuller 1964; Vohra et al. 1966, Yapar and Clandinin 1972, Martin-Tanguy, Guillaume and Kossa 1977, Featherston et al. 1978, Marquardt and Ward 1979, Elkin et al. 1990) and blue tits (*Parus caeruleus*) (Perrins 1976) demonstrate a depression of growth rate in young birds fed tannin-containing foods. Presumably, young birds are unable to assimilate tannin-bound proteins within these foods, although there is evidence that a decrease in consumption of high-tannin foods is at least partly responsible for reduced growth rate (Connor et al. 1969, Marquart and Ward 1979). Tannins also may increase digestion time (Perrins 1976), possibly by deactivating digestive enzymes. Koenig and Heck (1988) showed that adult California Western Scrub-Jays lost 0.30 to 0.39 g body weight per day when fed acorns exclusively. Koenig (1991) found that both condensed and hydrolyzable tannins adversely affected digestion of acorns in acorn woodpeckers

(*Melanerpes formicivorus*); the adverse effects of condensed tannins were greater.

Koenig and Heck (1988) reported that Western Scrub-Jays lost weight at rates of −0.85 to −1.15 g/day after 5 days on diets of low and high tannin acorns, respectively; Johnson et al. (1993) reported that Blue Jays lost weight at much higher rates, −5 to −6 g/day. Johnson et al. suggested that this difference may be an artifact of different experimental conditions; Koenig and Heck's (1988) Scrub-Jays were held in outdoor aviaries and might have had access to insects as supplementary food sources, while Johnson et al.'s Blue Jays were held indoors with no such opportunity. Our results support this idea; our indoor-captive Scrub-Jays, fed only experimental diets, lost weight much more rapidly than those in Koenig and Heck's study, at rates similar to those reported by Johnson et al. (1993).

Elkin et al. (1991) demonstrated that amino acid supplementation of high-tannin diets eliminated adverse tannin effects on weight change in domestic ducks. Similarly, in our study we found that jays fed high-protein diets exhibited no apparent deleterious effects, and no significant weight change on either high- or low-tannin diets.

Assessment of dietary tannin effects from changes in weight admittedly provides limited information. Weight changes signal that individuals are poorly or adequately nourished, but the causes are still obscure. Information on how tannins impact the physiology of digestion would be preferable, but requires well-controlled technical laboratory experiments. We can only guess at the mode of action of tannins from our results.

The presence of a significant protein-tannin interaction such that high levels of dietary protein eliminated the deleterious effects of either high- or low-tannin diets lends support to the hypothesis that in many vertebrates tannins bind to proteins, rendering them unavailable to proteases. The high-protein diets may have provided excess protein to the jays so that all protein-binding components in the diet (i.e., tannins) were bound, and additional protein was available for the jays' nutritional needs.

However, because we could only estimate how much food a jay ate in a day, it is not possible to firmly reject the hypothesis that Scrub-Jays also responded to tannin and protein as feeding cues by reducing consumption rates on some diets and not others, as observed by Connor et al. (1969) and Marquart and Ward (1979). We think this unlikely, because consumption rates for all diets were roughly similar in this study (~ 9.0 to 11.0 g/day).

Ideally, more birds should have been used in this study; conclusions based on six birds must be tentative. But because of the pronounced differences in weight change in response to different diets, and the similar effects on all birds tested (Table 2), we think that the dietary effects are real. In addition, the similar response by different birds to a given diet indicates that the order of presentation was unlikely to influence response; a jay fed a deleterious diet was not likely to fare significantly worse or better on successive diets.

Commercial tannic acid is actually a heterogeneous mixture of low and higher molecular weight hydrolyzable tannins (Hagerman et al. 1992). When commercial tannic acid was added to alfalfa, which was fed in turn to mule deer (*Odocoileus hemionus hemionus*) and Suffolk sheep (*Ovis aries*), Hagerman et al. (1992) observed no inhibition of protein digestion. In contrast, our study showed a distinct effect of tannic acid that could be ameliorated by protein supplementation. This apparent discrepancy may arise because the crude tannin content of their feeds was probably lower than our high-tannin jay diets. Also, as Hagerman et al. (1992) rightly point out, different species are impacted by tannins to a different extent.

Additionally, Hagerman et al (1992) observed greater protein-binding with the higher molecular weight hydrolyzable tannins in the commercial mixture; with higher tannin concentrations in the jay diet, relatively more of these larger compounds are likely to be present. Interestingly, Hagerman et al. (1992) found similar protein-binding abilities in naturally-occurring hydrolyzable and condensed tannins, the former generally of high molecular weight. If anything, their results suggest to us that the tannins in *Quercus gambelii* acorns may be even more deleterious with respect to diet than the tannic acid used in the artificial jay diets.

Western Scrub-Jays may have alternatives to simply avoiding higher tannin acorns altogether. An omnivorous bird such as a Scrub-Jay may consume sufficient animal protein in the form of insects and small vertebrates to offset the detrimental effects of even a high-tannin acorn. Johnson et al. (1993) suggested that Blue Jays are able to offset the tannin effects of *Q. rubra* acorns by the consumption of the larvae of *Curculio* weevils infesting the acorns. However, neither Scrub-Jays in Colorado (D.C. Fleck, unpubl. data) nor Florida (D.C. Fleck and G.E. Woolfenden, unpubl. data) have been observed to consume weevil larvae. Other insects, if caught, were consumed (Woolfenden and Fitzpatrick 1984). Jays probably would not benefit by choosing weevil-infested acorns for storage, as both the weevil and a large proportion of acorn may have disappeared by the time the acorn is recovered.

Koenig (1991) found that an interaction effect existed between dietary lipids and dietary tannins, such that increased lipid concentrations in diets increased the detrimental effects of tannins to acorn woodpeckers. No such effect was seen in our study. Unfortunately, the only comparisons possible with the data from this study were among high-protein diets. The lack of response of birds on these diets may have been the result of the uniformly high protein in these diets. Differences caused by lipid variation may be more apparent in lower-protein diets.

The results from growing numbers of bird studies, both wild and domestic, indicate that for the majority of species tested, dietary tannin can have significant negative effects. In addition, studies that have provided birds with either supplementary amino acids (Elkin et al. 1991) or high-protein foods (Johnson et al. 1993; this study) have demonstrated that these supplements can reduce or eliminate many of these detrimental effects. It seems clear from this evidence that dietary tannin in birds may have protein-inhibiting effects which birds are unable to completely counteract physiologically. The resistance to these effects varies from species to species (Koenig and Heck 1988, Elkin et al. 1991).

ACKNOWLEDGMENTS

Russell DeFusco, Mike Babler, and Greg Speights of the United States Air Force Academy assisted in the location and capture of the Western Scrub-Jays used in this study. Cynthia DeNardo and Constance McDonald helped care for the jays in captivity. David Craig assisted in the release of the jays. Carl Bock and Marc Snyder provided extensive advice on experimental design. Stan Faeth performed condensed and hydrolyzed tannin assays of *Q. gambelii* acorns. Carl Bock, Deane Bowers, and Yan Linhart and anonymous reviewers provided helpful commentary on the manuscript. We thank all these people for their assistance.

LITERATURE CITED

AUSTIN, P. J., L. A. SUCHAR, C. T. ROBBINS, AND A. E. HAGERMAN. 1989. Tannin binding proteins in the saliva of deer. J. Chem. Ecol. 15:1335–1347.

BERNAYS, E. A., G. COOPER-DRIVER, AND M. BILGENER. 1989. Herbivores and plant tannins. Adv. Ecol. Res. 19:263–302.

CHANG, S. I., AND H. L. FULLER. 1964. Effects of tannin content of grain sorghums on their feeding value for growing chicks. Poultry Sci. 43:30–36.

COLEY, P. D. 1986. Costs and benefits of defense by tannins in a Neotropical tree. Oecologia 70:238–241.

COLEY, P. D., J. P. BRYANT, AND F. S. CHAPIN III. 1985. Resource availability and plant antiherbivore defense. Science 230:895–899.

CONNOR, J. K., I. S. HURWOOD, H. W. BURTON, AND D. E. FUELLING. 1969. Some nutritional aspects of feeding sorghum grain of high tannin content to growing chickens. Aust. J. Exp. Agric. Anim. Husb. 9:497–501.

COOPER, S. M., AND N. OWEN-SMITH. 1985. Condensed tannins deter feeding by browsing ruminants in a South African savannah. Oecologia 67: 142–146.

COOPER-DRIVER, G., S. FINCH, T. SWAIN, AND E. A. BERNAYS. 1977. Seasonal variation in secondary plant compounds in relation to the palatability of *Pteridium aquilinum*. Biochem. Syst. Ecol. 5:177–183.

DISTEL, R. A., AND F. D. PROVENZA. 1991. Experience early in life affects voluntary intake of blackbrush by goats. J. Chem. Ecol. 17:431–450.

DOLLAHITE, J. W., G. T. HOUSEHOLDER, AND B. J. CAMP. 1963. Calcium hydroxide, a possible antidote for shin oak (*Quercus havardi*) poisoning in cattle. Southwestern Vet. 16:115–117.

EARLE, F. R., AND Q. JONES. 1962. Analyses of seed samples from 113 plant families. Econ. Bot. 16: 221–250.

ELKIN, R. G., J. C. ROGLER, AND T. W. SULLIVAN. 1990. Comparative effects of dietary tannins in ducks, chicks, and rats. Poultry Sci. 69:1685–1693.

ELKIN, R. G., J. C. ROGLER, AND T. W. SULLIVAN. 1991. Differential Response of ducks and chicks to dietary sorghum tannins. J. Sci. Food Agric. 57: 543–553.

FEATHERSTON, W. R., J. C. ROGLER, AND R. K. GILES. 1978. Studies on the utilization by chicks of sorghum grains with varying tannin contents. Proc. XVI World Poultry Cong. 7:1085–1093.

FEENY, P. P. 1969. Inhibitory effect of oak leaf tannins on the hydrolysis of proteins by trypsin. Phytochemistry 8:2119–2126.

FEENY, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology 51:565–581.

FLECK, D. C. 1994. Chemical mediation of vertebrate-aided seed dispersal. Ph.D. diss., Univ. Colorado, Boulder.

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.

Fox, L. R. 1981. Defense and dynamics in plant-herbivore systems. Amer. Zool. 21:853–864.
Goldstein, J. L., and T. Swain. 1965. The inhibition of enzymes by tannins. Phytochemistry 4:185–192.
Hagerman, A. E. 1987. Radial diffusion method for determining tannin in plant extracts. J. Chem. Ecol. 13:437–449.
Hagerman, A. E., and K. M. Klucher. 1986. Tannin-protein interactions, p. 67–76. *In* J. B. Harborne and E. Middleton [eds.], Plant flavonoids in medicine: biochemical, pharmacological, and structure-activity relationships. Alan R. Liss, New York.
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.
Hagerman, A. E., and C. T. Robbins. 1993. Specificity of tannin-binding salivary proteins relative to diet selection by mammals. Can. J. Zool. 71: 628–633.
Hagerman, A. E., C. T. Robbins, Y. Weerasuriya, T. C. Wilson, and C. McArthur. 1992. Tannin chemistry in relation to digestion. J. Range Manage. 45:57–62.
Hanley, T. A., C. T. Robbins, A. E. Hagerman, and C. McArthur. 1992. Predicting digestible protein and digestible dry matter in tannin-containing forages consumed by ruminants. Ecology 72:537–541.
Happe, P. J., K. J. Jenkins, E. E. Starkey, and S. H. Sharrow. 1990. Nutritional quality and tannin astringency of browse in clear-cuts and old-growth forests. J. Wildl. Manage. 54:557–566.
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.
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.
Koenig, W. D., and R. L. Mumme. 1987. Population ecology of the cooperatively breeding Acorn Woodpecker. Princeton Univ. Press, Princeton, NJ.
Marks, D. L., T. Swain, S. Goldstein, A. Richard, and M. Leighton. 1988. Chemical correlates of rhesus monkey food choice: the influence of hydrolyzable tannins. J. Chem. Ecol. 14:213–235.
Marquart, R. R., and A. T. Ward. 1979. Chick performance as affected by autoclave treatment of tannin-containing and tannin-free cultivars of fababeans. Can. J. Anim. Sci. 59:781–789.
Martin, J. S., M. M. Martin, and E. A. Bernays. 1987. Failure of tannic acid to inhibit digestion or reduce digestibility of plant protein in gut fluids of insect herbivores: implications for theories of plant defense. J. Chem. Ecol. 13:605–621.
Martin, M. M., D. C. Rockholm, and J. S. Martin. 1985. Effects of surfactants, pH, and certain cations on precipitation of proteins by tannins. J. Chem. Ecol. 11:485–494.
Martin-Tanguy, J., J. Guillaume, and A. Kossa. 1977. Condensed tannins in horse bean seeds: chemical structure and apparent effects on poultry. J. Sci. Food Agric. 28:757–765.
McArthur, C., and G. D. Sanson. 1991. Effects of tannins on digestion in the common ringtail possum (*Pseudocheirus peregrinus*), a specialized marsupial folivore. J. Zool. Lond. 225:233–251.
Mole, S., L. G. Butler, and G. Iason. 1990. Defense against dietary tannin in herbivores: a survey for proline rich salivary proteins in mammals. Biochem. Syst. Ecol. 18:287–293.
Ofcarcik, R. P., and E. E. Burns. 1971. Chemical and physical properties of selected acorns. J. Food Sci. 36:576–578.
Perrins, C. M. 1976. Possible effects of qualitative changes in the insect diet of avian predators. Ibis 118:580–584.
Provenza F. D., E. A. Burritt, T. P. Clalusen, J. P. Bryant, P. B. Reichardt, and R. A. Distel. 1990. Conditioned flavor aversion: a mechanism for goats to avoid condensed tannins in blackbrush. Am. Nat. 136:810–828.
Rhoades, D. F. 1979. Evolution of plant chemical defense against herbivores., p. 4–55. *In* G. A. Rosenthal and D. H. Janzen [eds.], Herbivores: their interaction with secondary plant metabolites. Academic Press, New York.
Rhoades, D. F., and R. G. Cates. 1976. Toward a general theory of plant antiherbivore chemistry. Rec. Adv. Phytochem. 10:168–213.
Robbins, C. T., T. A. Hanley, A. E. Hagerman, O. Hjeljord, D. L. Baker, C. C. Schwartz, and W. W. Mautz. 1987a. Role of tannins in defending plants against ruminants: reduction in protein availability. Ecology 68:98–107.
Robbins, C. T., S. Mole, A. E. Hagerman, and T. A. Hanley. 1987b. Role of tannins in defending plants against ruminants: reduction in dry matter digestion? Ecology 68:1606–1615.
Robbins, C. T., A. E. Hagerman, P. J. Austin, C. McArthur, and T. A. Hanley. 1991. Variation in mammalian physiological responses to a condensed tannin and its ecological implications. J. Mamm. 72:480–486.
SAS Institute, Inc. 1993. Release 6.09. Cary, NC.
Short, H. L. 1976. Composition and squirrel use of black and white oak groups. J. Wildl. Manage. 40: 283–289.
Singleton, V. L., and F. H. Kratzer. 1973. Plant phenolics, p. 309–345. *In* Committee on Food Protection [ed.], Toxicants occurring naturally in foods. National Acad. Sciences, Washington, DC.
Smallwood, P. D., and W. D. Peters. 1986. Gray squirrel food preferences: the effects of tannin and fat concentration. Ecology 67:168–174.
Swain, T. 1977. Secondary compounds as protective agents. Ann. Rev. Plant Physiol. 28:479–501.
Swain, T. 1979. Tannins and lignins, p. 657–682. *In* G. A. Rosenthal and D. H. Janzen [eds.], Herbivores: their interaction with secondary plant metabolites. Academic Press, New York.
Tipton, K. W., E. H. Floyd, J. C. Marshall, and J. B. McDevitt. 1970. Resistance of certain grain

sorghum hybrids to bird damage in Louisiana. Agron. J. 62:211–213.

VOHRA, P., F. H. KRATZER, AND M. A. JOSLYN. 1966. The growth depressing and toxic effects of tannins to chicks. Poultry Sci. 45:135–142.

WRANGHAM, R. W., AND P. G. WATERMAN. 1981. Feeding behaviour of vervet monkeys on *Acacia tortilis* and *Acacia xanthophloea*: with special reference to reproductive strategies and tannin production. J. Anim. Ecol. 50:715–731.

YAPAR, Z., AND D. R. CLANDININ. 1972. Effects of tannins in rapeseed meal on its nutritional value for chicks. Poultry Sci. 51:222–228.