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ABILITY OF TWO SPECIES OF OAK WOODLAND BIRDS TO SUBSIST ON ACORNS[1]

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Acorns are an extremely important food resource for bird populations in temperate North America (Martin et al. 1951). However, relatively little is known about the ability of animals to digest and maintain themselves on acorns. Nowhere is this ignorance more blatant than in California, where 15 species of oaks (*Quercus* spp.) dominate millions of hectares of land area (Griffin and Critchfield 1972, Griffin 1977), and serve (via their fruit) as a primary food resource for at least 16 species of birds (Martin et al. 1951).

Of the birds dependent on acorns in foothill woodland regions of California, two of the most characteristic are the Acorn Woodpecker (*Melanerpes formicivorus*) and Scrub Jay (*Aphelocoma coerulescens*). The former is well known for its habit of caching large numbers of acorns in specially modified storage trees or granaries (MacRoberts and MacRoberts 1976). Acorns comprise over 50% of this woodpecker's total diet (Beal 1911), and are critical to overwinter survival and subsequent spring breeding (Koenig and Mumme 1987). Acorns also comprise over 50% of the fall and winter diet of Scrub Jays (Beal 1910; W. J. Carmen, unpubl. data).

Despite the dependence of these species on acorns, it is unknown to what extent, if any, they are able to circumvent the effects of tannins, a key secondary metabolite present in acorns. Tannins bind with proteins (Martin and Martin 1982) and are generally accepted as defense compounds against herbivory (Bate-Smith 1973, Tempel 1981). This study was conducted in order to obtain preliminary data on the ability of Acorn Woodpeckers and Scrub Jays to overcome tannins and to maintain their body mass exclusively on acorns.

METHODS

Three Acorn Woodpeckers and three Scrub Jays were captured at Hastings Reservation, Monterey County, California, during autumn 1985 and maintained in outdoor flight aviaries (2 m × 4 m × 3 m) containing several dead tree limbs (and a roost box for the woodpeckers) for the duration of the study, which took place December 1985 to March 1986. The woodpeckers consisted of a first-year male and two adult females; the jays included three first-year birds of unknown sex. (First-year Scrub Jays at Hastings Reservation spend as high a proportion of their time foraging for and handling acorns as do adults [W. J. Carmen, unpubl. data], and thus the lack of any adults in this sample is unlikely to have been misleading.) No attempt was made to control the diet of birds prior to the study; all birds were fed a mixture of high-protein dog food and acorns for several weeks before trials started.

Prior to each trial, cages were cleaned and all traces of edible items removed. Birds were weighed daily and given water and acorns ad libitum during trials. Because of acorn storage by experimental birds in locations which resulted in loss of acorns from the cages, it was not possible to measure the mass of acorns eaten during trials. Individual trials were of variable length, but generally lasted 13 to 15 days or until a bird lost approximately 10% of its body mass. Four trials were terminated prematurely because of mass loss by the subject, while an additional four were stopped after 4 to 8 days for unrelated reasons. A total of 25 trials (12 for Acorn Woodpeckers; 13 for Scrub Jays) were performed. In order to avoid pseudoreplication (Hurlbert 1984), trials on the same individual for the same acorn species were averaged prior to analysis.

Three species of acorns were used in trials: coast live oak (*Quercus agrifolia*; five trials for Acorn Woodpeckers and seven for Scrub Jays), valley oak (*Q. lobata*; five trials for Acorn Woodpeckers and six for Scrub Jays), and canyon live oak (*Q. chrysolepis*; two trials for Acorn Woodpeckers only). These acorn species were chosen for their abundance at Hastings Reservation and because each is a member of a different subgenus (*Erythrobalanus* ["red" or "black" oaks, hereafter designated as BO], *Quercus* ["white" oaks, hereafter WO], and *Protobalanus* ["intermediate" oaks], respectively; Tucker 1980). Acorns were collected in autumn 1985 and frozen until used. Composition of the species used here, determined from analysis of acorns collected at Hastings Reservation, are presented in Table 1.

Except for total available carbohydrates, which were virtually identical in the three species, acorns differed

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TABLE 1. Composition of acorns collected at Hastings Reservation.[a]

Species	Subgenus	Tannins: Condensed	Tannins: Hydrolyzable	Percent lipids	Percent protein	Percent available carbohydrates	Energy content (kJ/g)
Coast live oak (*Quercus agrifolia*)	*Erythrobalanus*	1.27	19.00	24.3	7.1	13.2	13.23
Canyon live oak (*Q. chrysolepis*)	*Protobalanus*	0.84	8.29	16.7	3.9	12.6	11.39
Valley oak (*Q. lobata*)	*Quercus*	0.89	9.96	5.6	5.5	13.6	5.53

[a] Crude protein was measured by the micro-Kjeldahl method, nonstructural carbohydrates by digestion in 0.2 M NH_2SO_4 (Smith et al. 1964), and lipids by extraction in SkellySolve F. 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). For additional details on tannin assays, see Faeth (1986).

considerably in composition (Ofcarcik and Burns 1971). Protein content was relatively low in all three species, but was highest in *Q. agrifolia.* Lipid content varied the most, being over four times higher in *Q. agrifolia* than in *Q. lobata,* with *Q. chrysolepis* intermediate. Both condensed and hydrolyzable tannins were also highest in *Q. agrifolia,* and were approximately equivalent in *Q. lobata* and *Q. chrysolepis.* Largely because of higher lipid content, the estimated energetic value of *Q. agrifolia* acorns (per gram) is over twice that of *Q. lobata* acorns. However, this difference comes at the cost of 43% more condensed and 91% more hydrolyzable tannins (Table 1).

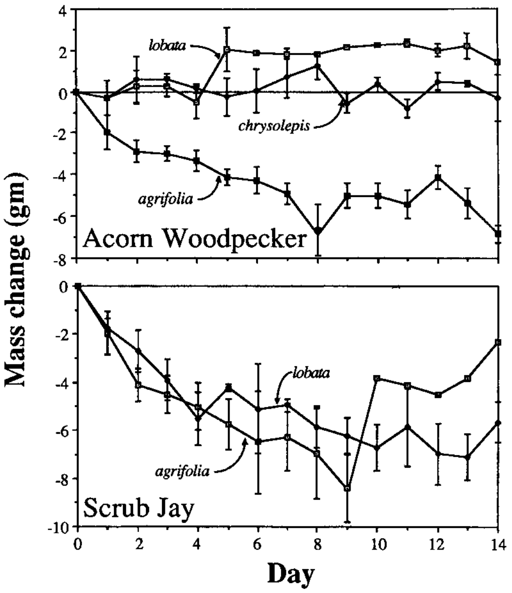

FIGURE 1. Mean (±SE) mass change of Acorn Woodpeckers (top), and Scrub Jays (bottom) fed exclusively on acorns of the *Quercus* species indicated for the number of days given on the x-axis. Each day is considered separately for each trial, but multiple trials in the same category using the same individual bird are averaged. Premature termination of some trials results in reduced sample sizes after day 4.

RESULTS

The mean change in body mass experienced by the subjects during the trials are presented in Table 2; mean values for each day are plotted in Figure 1. Acorn Woodpeckers (Table 2 and Fig. 1) maintained their body mass for the duration of the trials when fed either *Q. lobata* or *Q. chrysolepis* acorns; woodpeckers even gained mass on the former. In contrast, woodpeckers lost an average of 0.32 g day^{-1} when fed *Q. agrifolia* acorns. However, none of the five trials in which *Q. agrifolia* acorns were fed to Acorn Woodpeckers had to be terminated prior to the 14-day maximum duration of our trials.

We tested for differences in treatments by an analysis of covariance (ANCOVA) in which the species of acorn was treated as a factor and day of the trial as a covariate. Results of this analysis indicate that the ability of Acorn Woodpeckers to maintain their body mass varied significantly with acorn species ($F_{2,109} = 148.3, P < 0.001$).

In contrast with these results, Scrub Jays lost significant body mass when fed either *Q. lobata* or *Q. agrifolia* acorns (Table 2, Fig. 1). The ANCOVA analysis showed no significant difference in their ability to maintain body mass on these two acorn species ($F_{1,79} = 0.8, P > 0.25$). (The apparent rise in body mass among Scrub Jays fed *Q. agrifolia* acorns between days 9 and 10 occurs because several trials were terminated at day 9, leaving a reduced sample on subsequent days.) Similar ANCOVAs comparing the two species of birds (again controlling for the day of the trial) suggest that Acorn Woodpeckers were better able than Scrub Jays to subsist on both *Q. agrifolia* ($F_{1,79} = 4.7, P < 0.05$) and especially *Q. lobata* ($F_{1,79} = 177.0, P < 0.001$) acorns.

DISCUSSION

Different species of acorns vary significantly in composition (Ofcarcik and Burns 1971, Short and Epps 1976). Differences in lipid and tannin content, particularly evident between the WO and BO subgenera, may be dominant factors influencing preference and digestibility of acorns (but see Briggs and Smith, in press). However, there is currently no consensus as to whether animals usually prefer WO acorns, with their relatively low tannins and lipids, or BO acorns, with their high lipids and tannins.

The majority of work in this area has been done on squirrels. Short (1976), for example, found that fox

TABLE 2. Average mass change per day (in grams) for two oak woodland species fed exclusively acorns.[a]

	Coast live oak (*Quercus agrifolia*)	Canyon live oak (*Q. chrysolepis*)	Valley oak (*Q. lobata*)
Acorn Woodpecker	−0.32 ± 0.46***	−0.01 ± 0.03	+0.19 ± 0.38***
Scrub Jay	−0.30 ± 0.12*	—	−0.39 ± 0.06***

[a] Data are the slopes (±SE) and significance of the regressions of change in body mass from start of trial on day of trial. Each day is considered separately for each trial, but multiple trials in the same category using the same individual bird are averaged.
* = $P < 0.05$; *** = $P < 0.001$; other $P > 0.05$.

squirrels (*Sciurus niger*) preferred acorns from the relatively low-tannin, low-lipid WO species. In contrast, Smith and Follmer (1972) found that digestive efficiency and preference was greater for Shumard oak (*Q. shumardii*) acorns, a BO species, than for white oak (*Q. alba*) acorns for both fox and grey (*Sciurus carolinensis*) squirrels. More recently, Smallwood and Peters (1986) demonstrated that adding tannins to processed acorn meal decreased, and adding lipids increased, acceptability of experimental food balls to grey squirrels.

There are as yet no comparable studies using birds. However, several studies, including Perrins (1976) on Blue Tits (*Parus caeruleus*), Marquardt and Ward (1979) on domestic chickens (*Gallus domesticus*), and Koenig (unpubl.) on Acorn Woodpeckers, indicate that tannins adversely affect growth rate or digestibility of acorns by birds. This negative influence is presumably a consequence of the ability of tannins to bind with proteins, thereby making the protein unavailable to seed predators (Bate-Smith 1973, Tempel 1981, Martin and Martin 1982).

In the trials performed here, both Acorn Woodpeckers and Scrub Jays lost body mass when fed exclusively high-tannin, high-lipid *Q. agrifolia* acorns, while Acorn Woodpeckers, but not Scrub Jays, were able to maintain body mass for 2 weeks on low-tannin, low-lipid *Q. lobata* acorns (Table 2, Fig. 1). Acorn Woodpeckers were also able to subsist on *Q. chrysolepis* acorns, which have levels of tannins comparable to *Q. lobata*, lipids intermediate to the other two acorn species, and the lowest protein concentration of the three species (Table 1). Thus, tannins are most likely to have been responsible for the significant difference in the ability of Acorn Woodpeckers to maintain their body mass on these species of acorns.

Increased lipids did not appear to increase the ability of either species to subsist on acorns. Scrub Jays showed no significant difference in their ability to maintain themselves on either *Q. lobata* or *Q. agrifolia* acorns despite their four-fold difference in lipid content, while Acorn Woodpecker performance was inversely correlated with lipid content of the acorns used in the trials. More precise conclusions of the independent consequences of lipid and tannin content on the ability of the species to maintain body mass would have to be made using experimental food items such as those created by Smallwood and Peters (1986).

One prediction from these results is that Acorn Woodpeckers should choose acorns with relatively low tannin content. Surprisingly, there is some evidence that this is not the case, and that Acorn Woodpeckers prefer *Q. agrifolia* acorns over alternative, low-tannin species at Hastings Reservation and elsewhere in California (N. Pratini, unpubl. data). The resolution of this paradox may lie at least in part in differences between natural conditions and those offered by our feeding trials. In our experiments, food was unlimited, and birds were therefore probably able to compensate for the decreased energetic value of *Q. lobata* acorns by simply eating more. However, in the wild, reproductive success of Acorn Woodpeckers is often limited by the size of the storage facilities in which they can cache acorns (Koenig and Mumme 1987). Under these conditions, greater energetic content might be of much greater importance to the birds than lower tannin levels, especially if birds need only rarely depend exclusively on acorns for sustenance during the winter. In addition, the antibacterial properties of tannins (Grant and McMurtry 1978) may make tannin-rich acorns such as *Q. agrifolia* particularly well-suited to the long-term storage needs of Acorn Woodpeckers.

In contrast with the Acorn Woodpeckers, Scrub Jays were apparently not able to sustain themselves indefinitely on either species of acorn, a result probably, although not conclusively, attributable to a lower tolerance for tannins. Scrub Jays also store acorns extensively (Grinnell 1936), but do so in the ground where storage space is not limited. These two differences suggest that Scrub Jays should prefer low-tannin acorns more than do Acorn Woodpeckers, and that Scrub Jays should be more dependent on alternative, low-tannin food resources than are Acorn Woodpeckers.

However, at least three considerations argue for caution before drawing conclusions about the ecological influence of tannins on Scrub Jays in the wild. First, although storage space for Scrub Jays may not be limited, the bonus of the higher energetic content of a recovered BO acorn may still be more important than the lower tannin levels of a WO acorn. Second, tannins may leach out of acorns into the soil following storage, thus reducing the initial difference in tannin concentrations found between acorn species. Third, the tendency of WO acorns to sprout soon after falling to the ground, whereas BO acorns tend to remain dormant for much of the fall and winter (USDA 1974), may also make BO species, such as *Q. agrifolia*, more attractive to ground-caching species such as Scrub Jays (Smallwood and Peters 1986).

Thus, the ecological significance of our results, in terms of acorn preference and use by either Acorn Woodpeckers or Scrub Jays, is unclear. Additional studies, both in the field on acorn use and in the laboratory on acorn preference and digestibility, will be necessary in order to understand the coadaptations of these birds to the oaks and acorns on which they depend.

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