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Author(s): Walter D. Koenig and Lauryn S. Benedict
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SIZE, INSECT PARASITISM, AND ENERGETIC VALUE OF ACORNS STORED BY ACORN WOODPECKERS

WALTER D. KOENIG[1] AND LAURYN S. BENEDICT
Hastings Reservation and Museum of Vertebrate Zoology, University of California Berkeley,
38601 E. Carmel Valley Road, Carmel Valley, CA 93924

Abstract. We compared species composition, insect parasitism, and mass of acorns stored in 12 granaries with acorns present within the territories of Acorn Woodpeckers (*Melanerpes formicivorus*) at Hastings Reservation in central coastal California. All three species of oaks present in the study area produced excellent crops the year of the study, and thus woodpeckers could readily have filled their granaries with acorns of any one of the species. Nonetheless, species composition of stored acorns was highly variable among territories and at least some acorns of all three species were stored in all granaries. There was no consistent difference in insect parasitism between stored and unstored acorns. Relative to estimated availability, birds preferred to store *Quercus lobata* acorns and avoided *Q. douglasii* acorns, but showed no preference for *Q. agrifolia* acorns even though they are energetically more valuable than the other two species. Stored acorns of two of the three oak species also weighed less, and were thus presumably smaller, than the average unstored acorn. On average, Acorn Woodpeckers did not maximize the energetic value of their stores and could have increased the energy stored in their granaries by 14–108% had they chosen larger acorns or more energetically rich *Q. agrifolia* acorns. Storing may be better understood in a more traditional optimal foraging context in which the costs of harvesting and caching, together with the energetic value of stored acorns, are considered together.

Key words: caching, food storage, granary, insect damage, Melanerpes formicivorus, *oaks.*

Tamaño, Parasitismo por Insectos y Valor Energético de Bellotas Almacenadas por el Carpintero *Melanerpes formicivorus*

Resumen. Comparamos la composición de especies, parasitismo por insectos y masa de bellotas almacenadas en 12 graneros presentes adentro de territorios de *Melanerpes formicivorus*, en la Reserva Hastings en la costa central de California. Las tres especies de roble presentes en el área de estudio produjeron excelentes cosechas durante el año de estudio, por lo que los pájaros carpinteros podrían haber llenado fácilmente sus graneros con bellotas de cualquiera de las especies. A pesar de esto, la composición de especies de las bellotas almacenadas fue altamente variable entre territorios y en todos los graneros fueron almacenadas al menos algunas bellotas de cada una de las tres especies. No hubo una diferencia consistente en el parasitismo por insectos entre bellotas almacenadas y no almacenadas. En relación a la disponibilidad estimada, las aves prefirieron almacenar bellotas de *Quercus lobata* y evitaron las bellotas de *Q. douglasii*, pero no mostraron preferencia por bellotas de *Q. agrifolia*, aunque éstas son energéticamente más valiosas que las bellotas de las otras dos especies. Las bellotas almacenadas de dos de las tres especies de roble fueron menos pesadas, y presumiblemente fueron más pequeñas, que la bellota promedio no almacenada. En promedio, *M. formicivorus* no maximizó el valor energético de sus provisiones, aunque podría haber incrementado la energía almacenada en sus graneros en un 14–108% si hubiera elegido bellotas más grandes y bellotas más energéticas de *Q. agrifolia*. La acción de almacenar puede ser mejor entendida en un contexto de forrajeo óptimo más tradicional, en el que los costos de cosechar y ocultar, junto al valor energético de las bellotas almacenadas, son considerados juntos.

INTRODUCTION

Natural selection is expected to favor behaviors that maximize survival, foraging rate, or some other relevant fitness parameter (Maynard Smith 1978, Stephens and Krebs 1986). Unfortunately, although the goal of greater fitness is unambiguous, the means by which this is best achieved is not. Several possibilities include maximizing efficiency (the ratio of energy obtained to energy expended), maximizing the rate of energy gain, and minimizing errors, each of which yields different predictions in various behavioral contexts (Ydenberg et al. 1994, Waite and Field 2000).

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[1] E-mail: wicker@uclink4.berkeley.edu

Food storage is one such context. Ydenberg et al. (1994) modeled the expected behavior of animals when gathering food for storage given particular time and energy constraints and the necessity of individuals to concurrently feed themselves. They concluded that when energy is limiting, maximizing efficiency ensures the highest total daily amount of food stored, whereas when time is limiting, rate maximization is more likely to predict behavior, particularly as the energy needed for self-maintenance increases. Storing may also be influenced by the fitness consequences of making errors in choosing food items. If the cost is low due to a high rate of energy return, then errors may be common and still entail minimal fitness costs (Waite and Field 2000).

Acorn Woodpeckers (*Melanerpes formicivorus*) provide a unique opportunity to examine behavior in the context of food storage. Acorn Woodpeckers are "larder hoarders" that harvest acorns, and sometimes other nuts, as they mature in the autumn and store them communally in specially modified trees known as granaries (Fig. 1). Although stored acorns provide only a small proportion of the overall energetic needs of groups of Acorn Woodpeckers (Koenig and Mumme 1987, Koenig 1991), they are nonetheless critically important to winter survival and subsequent reproductive success (Koenig and Mumme 1987), a paradox that is consistent with a dynamic model estimating the survival consequences of a relatively small food hoard (Hitchcock and Houston 1994).

The observation that stored acorns provide only a small proportion of the energetic needs of a typical Acorn Woodpecker group during the winter begs the question of what limits acorn storage. Evidence summarized by Koenig and Mumme (1987) demonstrates that only a very small proportion of the available acorns are stored in all but the worst years and thus in general the availability of acorns is unlikely to be limiting. Furthermore, the number of acorns stored by most groups is relatively small, on the order of 300–500 bird^{-1}, or about 1600 group^{-1}. Given that individual birds can readily store upwards of 50 acorns per day, and that acorns are generally available on the trees for 2 to 4 months, this level of storing is unlikely to represent a serious time or energy drain. Instead, the number of acorns stored is, in all but very poor acorn years, limited by the number of preexisting storage holes in a group's granary (Koenig and Mumme 1987).

FIGURE 1. An Acorn Woodpecker on its granary (photo by W. Koenig).

If time and energy are relatively unimportant in limiting acorn storage, then there is little reason to predict that birds should maximize either the efficiency or rate with which they harvest acorns. Instead, birds should be able to spend their time maximizing the energetic content of their stores. This in turn would make it less likely that they would exhaust their stores prior to the following spring's breeding season, when access to stores is important to reproductive success (Koenig and Mumme 1987). Ways to accomplish this include selecting acorns for storage that are large, not parasitized by insects, and of high energy content compared to those available in the habitat. Intuitively, this makes sense: assuming that the acorn crop is at least moderate, neither the amount of energy birds use to find and store an acorn nor the efficiency with which they perform these tasks are likely to be important compared to the limitation imposed by the relatively small number of holes they have in which to put those acorns. After all, birds can readily make up an energy deficit by eating more acorns (limited mainly by their digestion rate), but building more storage holes requires considerable time and energy. Unfortunately, no reliable estimates of the latter are available, but observations suggest that Acorn Woodpeckers can drill at most only a handful of holes a day and that in many cases the production of new holes barely keeps up with those lost when dead limbs fall during winter storms.

Stored acorns do not appear to remain edible for more than a year. Thus, Acorn Woodpeckers are always dependent on the previous autumn's crop. Nonetheless, acorns in general are usually not limiting, to no small extent because Acorn Woodpeckers are restricted to sites containing at least two species of oaks (Koenig and Haydock 1999). Since the acorn crops of different species of oaks are not necessarily synchronous (Koenig, Mumme, et al. 1994, Koenig and Haydock 1999), it follows that in any particular year, birds may have few acorns of one or more species from which to choose. In such years, the lack of available acorns may obscure the preferences of the birds.

Our goal was to investigate the kinds of choices Acorn Woodpeckers make when storing acorns by comparing the mass, frequency of insect damage, and species composition of stored acorns with those available to the birds. By performing the study in a year in which all three species of oaks produced excellent acorn crops, we ensured that acorns of all three species were sufficiently abundant that birds could easily have found enough of any one species to fill their granaries. Thus, although the estimated total productivity of the three species was not identical, choices made by the birds to store acorns of a particular species are more likely to be due to species preferences than differences in availability. Our data allowed us to test for acorn preferences and to contrast the energetic value of observed acorn stores with what the birds could have achieved by being more selective with the acorns they stored.

METHODS

We collected acorns in and around the territories of 12 groups of Acorn Woodpeckers at Hastings Reservation, Monterey Co., California (36°12′N, 121°33′W), from 15–22 November 2000. Acorn storage had begun as early as September, and thus sampling was done relatively late in the season. However, acorns were still abundant in the area due to the excellent acorn crop that autumn.

All 12 territories were contiguous and within an area dominated primarily by three species of oaks: *Quercus lobata* (valley oak), *Q. douglasii* (blue oak), and *Q. agrifolia* (coast live oak). The first two of these species are members of the white oak subgenus (*Quercus*) while the third is a member of the black oak subgenus (*Erythrobalanus*); all mature acorns in a single year. Granaries were sampled by extracting 100 acorns chosen arbitrarily from parts of the tree accessible by ladder. Acorns were separated by species and dried prior to analysis. Available acorns were sampled by arbitrarily choosing productive trees of each of the three species located within 100 m of the granary. From each tree, we sampled 14–29 acorns (mean = 24.3). Acorns were taken at random except that obviously infested or otherwise deformed acorns were avoided. Acorns were taken either from the canopy (n = 50 trees), or directly below the tree on the ground (n = 82 trees). For 10 trees (n = 3, 5, and 2 individual *Q. lobata*, *Q. douglasii*, and *Q. agrifolia*, respectively) we sampled acorns from both the canopy and the ground. In none of these trees was there a significant difference in dry mass (Mann-Whitney U-tests, all $P > 0.2$). There was also no overall difference in the degree of insect damage across all 10 individuals (Wilcoxon signed-ranks test, $z = 0.6$, $P > 0.5$). Consequently, samples taken from the canopy and the ground were combined in subsequent analyses.

Acorns were left at ambient temperature for 2 months, at which point they were shelled and examined for insect damage or obvious malformation. In order to obtain an ecologically meaningful measure of the size of stored and unstored acorns, uninfested acorns taken from granaries, and a sample (usually 10) of similarly undamaged acorns taken from below trees, were dried to constant mass at 50°C. In all, a total of 4443 acorns was examined of which 2342 were dried and weighed.

An index of acorn productivity was obtained from visual surveys of 86 *Q. lobata*, 56 *Q. douglasii*, and 63 *Q. agrifolia* conducted annually since 1980 (Koenig, Mumme, et al. 1994). The survey involves having two observers count as many acorns as they can in different parts of the

TABLE 1. Relative productivity and abundance of three oak species, proportions of their acorns available and stored by Acorn Woodpeckers, and composition and energetic value of their acorns. Composition of acorns from Koenig and Mumme (1987) and Koenig and Faeth (1998). Available energetic value takes into consideration digestive efficiency, which was set at 62.4% (Koenig 1991).

	Quercus lobata	*Quercus douglasii*	*Quercus agrifolia*
Overall mean ± SD acorn productivity index ($n = 21$ years)	20.3 ± 15.9	21.3 ± 21.0	16.8 ± 14.6
Index of acorn productivity in 2000 ($N30_i$)	49.3	48.1	35.5
Percent of oaks in study area (P_i)	15	58	26
Percent of total acorn crop[a]	16	63	21
Percent of stored acorns	45	27	28
Range in percent of stored acorns ($n = 12$ granaries)	7–78	6–72	3–87
Composition of acorns			
% lipid (39.8 kJ g^{-1})	5.6	8.3	24.3
% protein (18.8 kJ g^{-1})	5.5	6.6	7.1
% carbohydrate (16.7 kJ g^{-1})	75.6	71.7	55.1
Total available kJ g^{-1}	9.9	10.3	12.6
Mean mass of stored acorns (g)	1.6	1.4	1.3
Total kJ per stored acorn	14.4	13.3	15.3
Condensed tannins (%)	0.12	0.10	0.64
Hydrolyzable tannins[b]	5.6	31.1	19.0

[a] Estimated as ($N30_i \times P_i / \Sigma(N30_i \times P_i)$. N30 = mean n acorns counted in 30 sec.

[b] Percent dry mass tannic acid equivalents.

tree during a 15-sec period (30 sec total; Koenig, Knops, et al. 1994). Vegetation surveys to estimate tree-species composition in the study area were conducted in 1977–1979 and involved measuring all trees within 0.4-ha circular plots (James and Shugart 1970) at the centers of 61 × 61 m quadrats located throughout the area inhabited by the Acorn Woodpecker groups used in this study. Since regeneration of oaks in this area is minimal (Griffin 1971, 1973), species composition has not changed markedly in the years since the vegetation surveys were conducted. The three species of oaks considered here made up 98% of the oak trees present in the study area. Acorns of the species composing the remaining 2% of trees were not found stored in the granaries and were not considered further. In all, 182 vegetation plots were analyzed.

Statistical analyses were done with nonparametric tests using SPSS (2000). An alpha level of 0.05 (two-tailed) was used to assess significance.

ENERGETIC VALUE OF ACORNS

In most cases, estimates of the composition and energetic value of acorns were taken from Koenig and Mumme (1987) as modified by Koenig (1991). As an estimate of the carbohydrate content of *Q. douglasii*, we assumed that the combined lipid + protein + carbohydrate content of acorns was 86.6% (for *Q. lobata* it was 86.7% while for *Q. agrifolia* it was 86.5%) and estimated the percent carbohydrate as 71.7% (= 86.6% − [%(lipid + protein)] reported for *Q. douglasii* acorns by Koenig and Mumme 1987).

Acorns vary considerably in their composition depending primarily on whether they are in the white oak (*Q. lobata* and *Q. douglasii*) or the black oak (*Q. agrifolia*) subgenus. The former generally have low tannin and lipid content, while the latter have high tannin and lipid content. Among the species considered here, this was true for condensed tannins, which are widely dispersed throughout the plant kingdom, but not hydrolyzable tannins, which appear to be quite high in *Q. douglasii* (Table 1). These differences in tannin content appear to have only a small negative effect on overall digestive efficiency of acorns by Acorn Woodpeckers (Koenig and Heck 1988, Koenig 1991) and do not appear to interact with protein content of acorns during storage in a consistent way likely to affect acorn preferences (Koenig and Faeth 1998).

Based on examination of acorns collected from 300 trees between 1988 and 1995, we estimated that on average, insects consumed or destroyed 54% of the cotyledon of acorns they infested (WDK, unpubl. data). This value, based on separating insect-damaged acorns into those for which less than half and more than half of the cotyledon was destroyed, did not differ significantly among the three oak species after controlling for annual differences. Thus, differences between species in the extent to which insects damage cotyledons is unlikely to influence acorn choice and is not considered further.

COMPARISONS OF STORED VS. UNSTORED ACORNS

Our goal was to test for acorn choice by comparing the species composition, mass, degree of insect parasitism, and energetic value of acorns taken from granaries (stored acorns) to those produced in the environment and that could have been stored (unstored acorns). For species composition, we compared stored acorns with estimates of the proportion of the three species of oaks present in the study area both unweighted and weighted by the mean size of the acorn crop produced by each of the three oak species. For mass and insect parasitism, we compared stored acorns with the means of both unstored acorns of the same species collected from trees within the same territory and to unstored acorns of all trees of the same species sampled across all territories. Since no attempt was made to sample comprehensively within a territory, the latter is probably a better measure of the overall range of acorns available to the birds.

For energetic value of acorns available for storage, a variety of comparisons can be made depending on the assumptions made concerning the size and composition of unstored acorns. Of these comparisons, we performed seven. In the first four, we assumed that groups could have chosen to store only the species of acorn with the highest energetic value per gram (*Q. agrifolia*, see Table 1). Working only with *Q. agrifolia* acorns, we then calculated the resulting energetic value of acorns following four slightly different hypothetical scenarios. These assumed that unstored acorns were of the same mean size as (1) *Q. agrifolia* acorns actually stored, (2) unstored *Q. agrifolia* acorns collected from trees located within the same territory, (3) the complete sample of unstored *Q. agrifolia* acorns collected across all 12 territories, and (4) unstored acorns of the *Q. agrifolia* tree producing the largest acorns sampled within each territory.

The alternative set of three hypothetical scenarios started with the assumption that acorns available for storage were of the same species composition as those actually stored. We then assumed that unstored acorns were of the same mean size as (5) unstored acorns collected from trees of the same species located within the same territory, (6) the complete sample of unstored acorns of each species collected across all 12 territories, and (7) unstored acorns produced by the tree of the same species within each territory with the largest acorns sampled.

Because it combines the same set of trees for all territories, scenario 3 yields a single number for the mean energetic value of unstored acorns. All other scenarios for unstored acorns yield different values for each territory, and thus we present both the mean and the range of calculated estimates. Since the species composition of stored acorns varied among territories, all scenarios yield a mean and range for the estimated percent increase (or decrease) in energy content between hypothetical and actual acorn stores.

RESULTS

SPECIES COMPOSITION

Q. lobata acorns were stored much more frequently, *Q. douglasii* acorns were stored much less frequently, and *Q. agrifolia* acorns were stored in roughly the same frequency as both the estimated relative abundance of the trees and the estimated relative productivity of the species in 2000 (Table 1). Thus, Acorn Woodpeckers stored *Q. lobata* acorns primarily at the expense of *Q. douglasii* acorns. However, variability in the species composition of acorns stored by groups was considerable. For example, while 72% of the acorns stored at group Blomone were *Q. douglasii*, 78% of acorns at Haystack-Blomquist, 0.5 km away, were *Q. lobata*, and 87% of acorns at Knoll, 0.7 km away, were *Q. agrifolia*.

ACORN SIZE AND INSECT PARASITISM

Acorn Woodpeckers stored relatively small *Q. lobata* and *Q. douglasii* acorns, while no significant difference between the mass of stored and unstored *Q. agrifolia* acorns was detected (Table 2). Results were similar regardless of whether stored acorns were compared to trees within the same territory, to all trees sampled, or by comparing the 12 granaries combined to all trees sampled.

In contrast, there were no consistent differences in the degree of insect parasitism rates in stored vs. unstored acorns (Table 2). Stored *Q.*

TABLE 2. Mean ± SD (n) size and rates of insect parasitism of stored and unstored acorns. Mean mass between the two categories were compared with Mann-Whitney U-tests; pairwise comparisons by binomial tests. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

	Quercus lobata	*Quercus douglasii*	*Quercus agrifolia*
Acorn mass (g)			
Stored acorns	1.58 ± 0.50 (12)***	1.41 ± 0.33 (12)***	1.25 ± 0.30 (12)
Unstored acorns	2.50 ± 0.75 (48)	2.01 ± 0.65 (34)	1.38 ± 0.45 (40)
Pairwise comparisons (n = 12 territories)			
Stored acorns smaller than unstored acorns within the territory	12**	12**	7
Stored acorns smaller than all unstored acorns combined	11**	12**	8
Insect parasitism (%)			
Stored acorns	14.7 ± 13.4 (12)	17.0 ± 21.2 (12)	6.0 ± 11.0 (12)
Unstored acorns	12.2 ± 16.1 (48)	5.9 ± 7.7 (34)	5.8 ± 7.1 (40)
Pairwise comparisons (n = 12 territories)			
Stored acorns with less insect damage than unstored acorns within the territory	6	4	10*
Stored acorns with less insect damage than all unstored acorns combined	6	6	8

agrifolia acorns were somewhat less likely (P = 0.04) to be insect damaged than trees within the same territory, but this trend was not significant in either of the other *Q. agrifolia* comparisons. Furthermore, in the nonpairwise comparisons, stored acorns of all three species tended to be more insect infested than unstored acorns (Table 2). Rates of insect parasitism were not significantly different among stored acorn species (Wilcoxon signed-ranks test, both $P > 0.07$), although stored *Q. agrifolia* acorns tended to have lower mean rates of parasitism than the other two species.

ENERGETIC CONSEQUENCES

The higher lipid composition of *Q. agrifolia* acorns made them more energetically valuable per gram than either of the other species (Table 1). This advantage was largely, but not entirely, eliminated by the larger size of stored *Q. lobata* and *Q. douglasii* acorns. The overall estimated energetic value of a stored *Q. agrifolia* acorn was 6% greater than a stored *Q. lobata* acorn and 15% greater than a stored *Q. douglasii* acorn (Table 1).

Given that only 28% of all stored acorns were *Q. agrifolia*, birds did not maximize the energetic value of their stores. This conclusion is enhanced by the considerably smaller mean size of stored vs. unstored *Q. lobata* and *Q. douglasii* acorns (Table 2).

The energetic costs of storing a mix of acorn species of smaller size than those available are summarized by the scenarios in Table 3. The mean observed energetic value of an average stored acorn, taking into account species, size, and probability of insect damage, was 13.9 kJ. The first set of scenarios compared this value with those that would have been theoretically obtained had the birds stored only *Q. agrifolia* acorns. Although estimates varied considerably from territory to territory and among scenarios, 11 of 12 groups (92%) would have benefited by storing only *Q. agrifolia* acorns. On average, groups would have stored 14–59% more energy had they restricted their caching to *Q. agrifolia* acorns, with the relative advantage exceeding 100% on some territories.

The second set of scenarios compared the observed energetic value of stores with what the groups would have obtained had they stored the same mix of species as they did, but chosen the size of the acorns they stored differently. If they had chosen acorns of the same average size as those available either on their territories or overall on the study site, they would have increased the energetic value of their stores by 63–64%, with advantages in some territories well over

TABLE 3. Observed vs. hypothetical energetic value of acorns stored by Acorn Woodpeckers occupying 12 territories at Hastings Reserve, California. Values take into account size and the observed amount of insect damage assuming that infested acorns lose 54% of their cotyledon to insects.

	Mean energetic value in kJ acorn^{-1} (range)	Mean % increase [decrease] over observed (range)
Observed energetic value	13.9 (9.0–20.0)	
If all stored acorns were *Quercus agrifolia* and if they were		
same size as observed acorns stored	15.3 (8.3–21.5)	14 ([19]–103)
same mean size as unstored acorns on the same territory	16.9 (12.7–22.0)	26 ([18]–99)
same mean size as the complete sample of unstored acorns	17.1	30 ([14]–91)
size of the largest *Q. agrifolia* sampled in the territory	21.2 (13.6–28.9)	59 ([16]–160)
If stored acorns were of observed species composition and were		
of mean size for that territory	21.7 (17.1–27.8)	63 (18–138)
of mean size for all sampled trees	21.6 (18.1–23.6)	64 (13–145)
of the size of the largest trees sampled in the territory	27.4 (22.4–33.8)	108 (42–276)

100%. If they had chosen acorns of the same mean size as those of the tree producing the largest acorns of the same species sampled on their territory, they would have stored an average of 108% more energy in their granaries.

DISCUSSION

Acorn Woodpeckers did not discriminate among acorns based on whether or not they were parasitized by insects. However, they preferred to store acorns that were smaller than those available, at least for two of the three oak species. Also, they stored nearly three times more *Q. lobata* acorns and fewer than half as many *Q. douglasii* acorns compared to the overall estimated relative abundance of these species, and failed to prefer *Q. agrifolia* acorns, despite their slightly higher mean energetic value.

The most frequent insect parasites of acorns are beetle larvae of the families Curculionidae and Bostrichidae. Although acorns are clearly stored primarily for the acorn meat rather than the "grubs" that parasitize them (MacRoberts 1974), larvae are readily eaten by Acorn Woodpeckers when they come across them. However, larvae living in stored acorns usually pupate and leave the acorn as it dries, often before they eat the entire contents but before the woodpeckers open the stored acorn. Thus, it would be advantageous for woodpeckers to choose uninfested acorns if they were able to do so. Such acorns are not readily detectable when the larvae are young, at least by humans. Given that many parasitized acorns are stored, it appears likely that the woodpeckers are unable to detect them either.

More problematical is why the birds would choose to store acorns of lower mass than those available in their territories. In general, the size of the storage holes made by Acorn Woodpeckers matches the size of the acorns that are available to them (MacRoberts and MacRoberts 1976). For example, holes in granaries where relatively large *Q. kelloggii* (California black oak) acorns are common are larger than those where smaller *Q. agrifolia* acorns predominate. However, following storage, acorns shrink as they dry and must be moved to smaller holes to avoid falling out or being stolen. Possibly the advantage of having smaller holes available in which to move acorns as they shrink may result in birds making smaller holes than the average acorns available to them, which would then result in smaller acorns being stored even if birds otherwise did not discriminate on size. Alternatively, it is possible that there is an interaction with insect damage such that larger acorns are more likely to be parasitized by insects or incur disproportionately more damage to the cotyledon when infested. Either of these would potentially favor storing acorns smaller than those available.

The reasons for the apparent preference for *Q. lobata* acorns at the expense of *Q. douglasii* acorns are unknown. However, the only major difference in composition between *Q. lobata* and *Q. douglasii* acorns is in their hydrolyzable tannin content (Table 1), suggesting that birds may select acorns in part on the basis of these chemicals, despite having but a relatively small negative effect on digestibility (Koenig 1991).

Birds did not maximize the energetic value of their stores. On average, Acorn Woodpeckers could have increased the energetic value of their stores by 14–30% by restricting storage to lipid-rich *Q. agrifolia* acorns, even without any increased selectivity regarding acorn size. If they had stored the same mix of species as they did, but chosen acorns of the same average size as those present in the study site, they could have increased the energy of their stores by over 60%. Even greater benefits, averaging 108% but as high as 276% in one territory, could have been reaped by storing the same mix of species as they did, but selecting acorns from the trees producing the largest acorns of each species sampled within their territory.

Although these values hold only for the year of the study, prior work examining the species of acorns stored over a period of six years in the same population suggests that birds regularly store a mix of species rather than concentrating on those of high energetic value (Koenig and Mumme 1987). Unfortunately, the extent to which this variability is determined by annual differences in productivity by the species is unknown. However, it is consistent with our results here that birds choose to store a mix of species even when availability is such that they could easily fill their granaries with acorns of the single most energetically valuable species present.

Why do Acorn Woodpeckers prefer to store a mix of acorn species rather than specialize on those with the highest energetic value? Koenig and Heck (1988) found that captive Acorn Woodpeckers were able to subsist for 14 days on a diet of either *Q. lobata* or *Q. agrifolia* acorns. However, the high tannin content of the *Q. agrifolia* acorns apparently affected the ability of the birds to assimilate protein, resulting in the birds losing an average of 0.32 g day^{-1} on the high-tannin *Q. agrifolia* diet, while they gained an average of 0.19 g day^{-1} on the low-tannin *Q. lobata* diet. This suggests that birds may not be able to subsist for long periods of time entirely on *Q. agrifolia* acorns, thus offering an incentive to store other species of acorns. In addition, there is evidence that, at least in some cases, diets consisting of a mix of species may be more beneficial than a diet consisting of only a single item, even though the latter may be more energetically rich (Krebs and Avery 1984).

In support of this latter hypothesis, the range of Acorn Woodpeckers in the western United States is primarily restricted to areas in which there are at least two species of oaks, and population stability increases significantly with increasing oak species diversity (Bock and Bock 1974, Koenig and Haydock 1999). Although the primary explanation for these relationships is the lower probability of an acorn crop failure as oak species diversity increases, it is also possible that the availability of acorns of a mix of species confers nutritional advantages beyond that resulting solely from more consistent acorn availability from year to year.

The primary difficulty with this hypothesis is that, in contrast to species such as Clark's Nutcrackers (*Nucifraga columbiana*) that depend almost exclusively on their stores for relatively long periods of time (Vander Wall and Balda 1977), Acorn Woodpecker caches supply only a relatively small proportion (<20%; Koenig 1991) of their total energetic needs during the winter in our study area. Thus, birds are perforce already acquiring the majority of their nutritional needs from sources other than stored acorns, primarily flying insects and sap. Although this may not eliminate a nutritional advantage to storing a mix of acorn species, it means that the birds are already eating a diversity of foods that would be increased relatively little by the inclusion of additional species of acorns.

In summary, we detected no selectivity with respect to insect damage, selectivity that was largely unrelated to energetic value of the different species, and a preference for smaller acorns of two of the three species involved. These results fail to support the hypothesis that the birds maximize the energetic content of their stores, either by selecting larger acorns, acorns with lower than average insect damage, or high-energy species of acorns. Apparently selection has not facilitated birds storing acorns yielding the most energy possible, despite the limited storage capacity of most territories and the importance of stored acorns to winter survival and subsequent reproduction. Instead, other considerations such as nutritional limitations imposed by the relatively high tannin content of some acorns, constraints resulting from the need to accommodate acorns as they shrink, and advantages of relying on a diversity of species, may play at least as important a role in shaping acorn storage as does energy maximization.

These results also suggest, despite our assumption to the contrary, that storing behavior by Acorn Woodpeckers may be better understood in a more traditional optimal foraging context, such as by maximizing efficiency or maximizing the rate of energy gain (Ydenberg et al. 1994). Both these alternatives assume that the energy needed to harvest and store acorns, rather than just the energetic value of the stores themselves, determines caching behavior. Additional study will be required to test these alternatives.

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