Size, Insect Parasitism, and Energetic Value of Acorns Stored by Acorn Woodpeckers
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SIZE, INSECT PARASITISM, AND ENERGETIC VALUE OF ACORNS STORED BY ACORN WOODPECKERS

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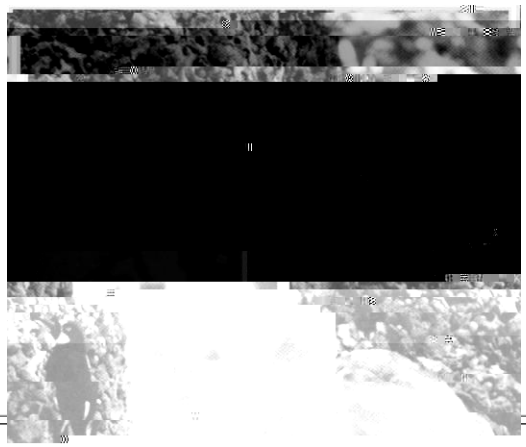
Abstract. We compared species composition, insect parasitism, and mass of acorns stored in 12 granaries with acorns present within the territories of Acorn Woodpeckers (*Melanerpes formicivorus*) at Hastings Reservation in central coastal California. All three species of oaks

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



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

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

existing storage holes in a group's granary (Koenig and Mumme 1987).

If time and energy are relatively unimportant

in which to put those acorns. After all, birds can readily make up an energy deficit by eating more

thus sampling was done relatively late in the season. However, acorns were still abundant in

but building more storage holes requires consid-

tumn.

on separating insect-damaged acorns into those available for storage were of the same species

goal to

of

species

acorns

the cotyledon was destroyed, did not differ sig- assumed that unstored acorns were of the same

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)			
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)			

TABLE 3. Observed vs. hypothetical energetic value of acorns stored by Acorn Woodpeckers occupying 12

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%.

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

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 stood 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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