

Acorns and Acorn Woodpeckers: Ups and Downs in a Long-Term Relationship¹

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Abstract

Acorn woodpeckers are one of the most conspicuous and abundant birds in California oak forests due to their unique dependence on acorns, a food resource eaten directly and stored in specialized structures on their territories for later use when acorns are no longer present on trees. Parallel long-term studies of the demography and behavior of this species and of patterns of acorn production by oaks at Hastings Reservation in central coastal California have revealed many ways that acorn crops influence the ecology and behavior of acorn woodpeckers. We present results focusing on the large-scale effects of oaks on the geographical ecology of acorn woodpeckers and how the acorn crop influences woodpecker demography, including the probability that young remain as helpers and the corresponding fitness consequences of this decision.

Key words: acorns, acorn woodpeckers, masting, *Melanerpes formicivorus*, oaks

Introduction

One need not study acorn woodpeckers (*Melanerpes formicivorus*), a common avian resident and by far the most common woodpecker in California, for very long before it becomes apparent that their dependence on acorns, as suggested by their common name, is far more appropriate than their proclivity to eat ants, as suggested by their scientific name. Indeed, except perhaps for a brief period during late summer, it is difficult to not be struck by the degree to which the lives of acorn woodpeckers revolve around oak trees and their acorns, as much of their time involves harvesting acorns, storing them in unique structures known as ‘storage trees’, or ‘granaries’, located on their territories, defending granaries from both conspecifics and other species, and eating acorns when conditions are unsuitable for flycatching or obtaining otherwise more nutritious food.

Early in our long-term study of the social behavior of acorn woodpeckers, which we began in 1974 by continuing a study initiated in 1968 by Michael and Barbara MacRoberts (1976), it became obvious that many aspects of acorn woodpecker population ecology were dependent on what was clearly a highly variable acorn crop. This was not surprising; not only had Carl and Jane Bock demonstrated that the geographical ecology of acorn woodpeckers was dependent on oak species richness (Bock and Bock 1974), but numerous studies dating back at least 30 years had reported data suggesting that oaks frequently produced highly variable acorn crops (Burns and others 1954, Downs and McQuilkin 1944, Tryon and Carvell 1962).

¹ An abbreviated version of this paper was presented at the Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World, November 3-6, 2014, Visalia, California.

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Despite these prior studies, including ongoing work examining oak regeneration at our study site by Jim Griffin that involved work quantifying acorn fall under a number of valley oaks (*Quercus lobata*, Griffin 1971), we soon decided that more detailed investigation of the acorn crop and its effects on the acorn woodpecker population were warranted.

Here we briefly summarize some of those effects, extracted from what has become parallel long-term studies of the social behavior and population ecology of acorn woodpeckers and variable seed production in California oaks (Koenig and Mumme 1987, Koenig and others 1994b, Koenig and others 2011, Koenig and others 2015). We present results illustrating the effects of the acorn crop on the demography of the acorn woodpecker population, summarize some of the large-scale biogeographical effects of oaks on acorn woodpeckers, and briefly discuss effects the acorn crop has on their social behavior.

Methods

Our study site is Hastings Natural History Reservation in central coastal California, a field station run by the Museum of Vertebrate Zoology, University of California Berkeley. Acorn woodpeckers are cooperative breeders, living in family groups of 2 to 16 individuals generally consisting of both multiple breeders of both sexes and offspring that remain in their natal group as nonbreeding helpers, often for many years (Koenig and others 1984). Acorn woodpeckers at Hastings have been individually color-banded and monitored continuously since 1971; studies quantifying the acorn crop were initiated in October 1980 (Koenig and others 1994a). Thus, most of our analyses include bird data from 1981 (the first year for which we had acorn data from the prior fall) through 2012 or 2013. Weather data are from Hastings Reservation headquarters (36° 23' N, 121°, 33' W).

Our measure of the acorn crop is based on a modified version of the visual survey technique introduced by Graves (1980). Each autumn two observers counted as many acorns in 15 seconds as they could on each tree using binoculars; counts were then combined (N30) and ln-transformed ($\ln[N30+1] = LN30$) for subsequent analysis. Surveys were performed on an initial sample of 250 marked trees (several of which have since died) spread throughout the field site and divided among the five tree oak species present in at least part of the study site (currently 86 *Q. lobata*, 56 *Q. douglasii*, 63 *Q. agrifolia*, 21 *Q. chrysolepis*, and 20 *Q. kelloggii*). Trees were located near established acorn woodpecker territories, and although unequally divided among the species, provide a reasonably unbiased sample of the importance of not only the acorn crop for the different species but the relative importance of the species to the acorn woodpecker population. Thus, we took the mean of LN30 values in year x for all individuals of the same species for an estimate of that species' acorn crop, and the mean of LN30 values for all 250 individuals in year x for an estimate of the overall size of the acorn crop in a given year. For a few analyses, we divided trees based on where they were located within the study site; we were particularly interested in differences in areas where only three of the oak species were generally present (*Q. lobata*, *Q. douglasii*, and *Q. agrifolia*; all "1-year" species that mature acorns in a single year) compared to sites where four species were present (the prior three plus *Q. chrysolepis*, a "2-year" species that matures acorns in 2 years) and those where all five were common (the prior four plus *Q. kelloggii*, also a 2-year species).

In order to keep track of timing, we refer to the calendar year of an event as taking place in 'year x ', where x ranges from -1 to +1. The primary effects of the acorn crop in the fall of one year (typically 'year -1') are manifested on the woodpecker

population the following spring (typically ‘year 0’). Lagged effects are referenced similarly.

Statistical analyses, described in the text, were conducted in R 3.0.3 (R Core Team 2014).

Results

Variability in the acorn crop

As expected, the acorn crop varied considerably from year to year; the mean acorn crop for *Q. lobata* as estimated by our annual survey is graphed in fig. 1a. Variability as measured by the coefficient of variation (CV = standard deviation x 100 / mean) for the five species individually at Hastings between 1980 and 2013 ranged from 55.3 percent for *Q. douglasii* to 74.5 percent for *Q. kelloggii*. Acorn production is typically asynchronous among species, however, particularly among those that require different number of years to mature crops (Koenig and Haydock 1999, Koenig and others 1994b). Consequently, the overall variability in the number of available acorns from any of the five species in the oak community (‘community variability’), although still variable from year to year (fig. 1b), was considerably less so than that of any one of the species by itself. The mean CV for the five individual species at Hastings was 62.7 percent, nearly 50 percent greater than the community variability as estimated by considering all five species together (fig. 1b).

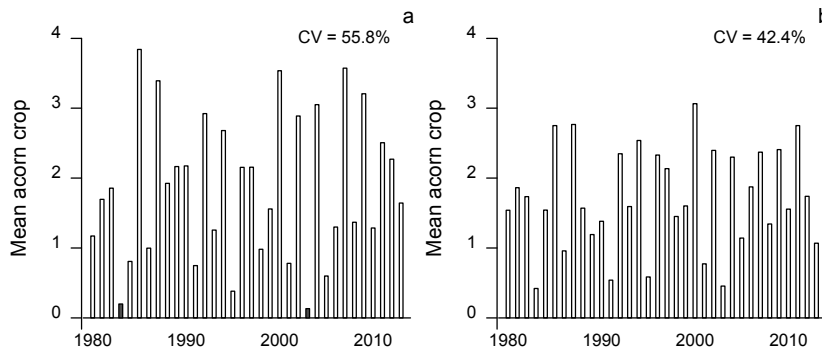


Figure 1—The mean number of acorns counted in 30-sec per tree (\ln transformed) for (a) *Quercus lobata* and (b) all species combined, Hastings Reservation, 1980 to 2013 ($N = 34$ years.) Variability, measured by the coefficient of variation (CV), is listed.

Acorn woodpeckers exhibit little to no preference for different species of acorns (Koenig and Benedict 2002, Koenig and others 2008a) and territories in our study have access to between three and five species of oaks. As a result, years when few acorns of any species are available to groups are rare. Three to four such years are evident from fig. 1b; when sufficiently bad, poor years resulted in the disintegration of many groups, with the proportion of birds of different classes disappearing being inversely related to their status in the dominance hierarchy (Hannon and others 1987). Conversely, when the overall acorn crop was very good, some groups were able to produce a fall nest. Such nests, which start in August or September and fledge young as late as early November, occurred in about one-third of years and contributed only 4.3 percent of the population’s total productivity overall. In 1984,

however, following the bad acorn crop of 1983 and a poor 1984 spring acorn woodpecker breeding season, 50 percent of the calendar-year's productivity of fledglings was attributed to fall nests (Koenig and Stahl 2007).

Long-term effects of the acorn crop

Good acorn crops were not only accompanied by occasional fall nests but were followed by early and highly productive breeding seasons the following spring, including significantly larger clutch sizes ($r = 0.37$, $P < 0.05$), significantly more groups having successful second nests ($r = 0.64$, $P < 0.001$), and significantly more young fledged per group ($r = 0.76$, $P < 0.001$; fig. 2b).

When high productivity in year 0 followed a good acorn crop in year -1, groups had more helpers the following spring in year +1 ($r = 0.59$, $P < 0.001$) and larger mean group size ($r = 0.61$, $P < 0.001$; fig. 2c). Thus, the effects of a good acorn crop were detectable in the population over 2 years later. It is likely that such effects might be felt even longer, but the negative lag-1 correlation between annual acorn crops (the correlation between the overall mean acorn crop in year 0 and year +1 = -0.49 , $P = 0.005$) resulted in a significant inverse correlation between the acorn crop in year -1 and fledging success 2 years later (fig. 2d). Going backwards in time, however, the overall mean acorn crop, which was strongly weighted in our sample by the productivity of *Q. lobata*, a 1-year species, was significantly correlated with mean maximum temperature the prior April (fig. 2a), apparently due to a complex relationship linking mean temperature to phenological synchrony, pollen availability, and fertilization success (Koenig and others 2015). Thus, based on mean maximum temperature during a particular April, it was possible to predict the overall acorn crop that fall (fig. 2a), fledging success of the acorn woodpecker population the following year ($r = 0.42$, $P = 0.01$), and mean group size 2 years later ($r = 0.35$, $P = 0.05$).

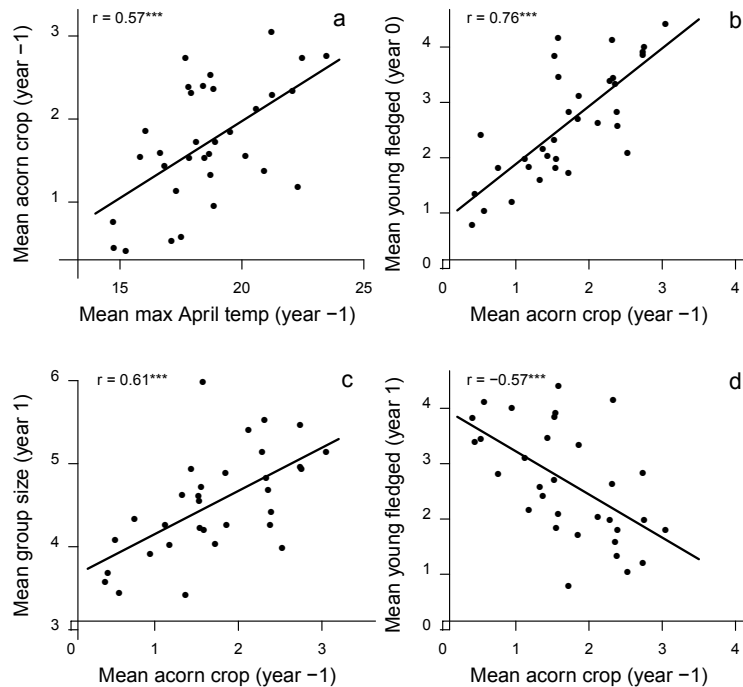


Figure 2—Scattergrams of (a) the mean acorn crop in year -1 vs. maximum April temperature in year -1; (b) the mean number of young fledged per group in year 0 vs. the mean acorn crop in year -1; (c) mean group size in year 1 vs. the mean acorn crop in year -1 and; (d) the mean number of young fledged per group in year 1 vs. the mean acorn crop in year -1. Pearson correlations (all $P < 0.001$) listed.

Role of oak richness

A reanalysis and updating of Bock and Bock's (1974) study of the relationship between acorn woodpeckers reported on the Audubon Christmas Bird Counts confirmed that the distributional limit of the species along the Pacific Coast is set not by the limit of oaks, but by sites where oak richness drops to a single species (Koenig and Haydock 1999). Moreover, results supported the intuitively pleasing conclusion that mean woodpecker population size is determined by the extent of oak woodland in an area (resource abundance), while annual variability in population size is inversely correlated with oak species richness (resource variability). The rationale for this finding is that annual variability in the overall acorn crop decreases as the number of oak species increases due to asynchrony in acorn production, as illustrated in fig. 1. No such relationship was detected by either study among sites in the southwestern United States. Although the reasons for this difference are unclear, it is possibly related to the relatively rare co-occurrence of 1-year and 2-year species of oaks in the Southwest. With a high proportion of sites containing only species of oaks that mature acorns in the same number of years, there is quite possibly greater synchrony of acorn production, and thus higher overall acorn variability, in the Southwest compared to the Pacific Coast (Koenig and Haydock 1999).

There is similar evidence that variability associated with oak species richness may be detectable even within a limited geographic scale such as our Hastings study site. By dividing the study area into regions within which different numbers of oak species (three, four, or five) were common, we tested their effects on woodpecker productivity. Among the three categories of oak richness, mean woodpecker group

size increased with increasing oak richness (Kruskal-Wallis test, $\chi^2 = 8.8$, $df = 2$, $P = 0.01$) whereas annual variability in group size decreased significantly (Kruskal-Wallis test, $\chi^2 = 12.3$, $df = 2$, $P = 0.002$) with oak richness (fig. 3). The latter result was due to a sharp decrease in CV among sites with access to four or more oak species, the areas that included both 1-year and 2-year species of oaks.

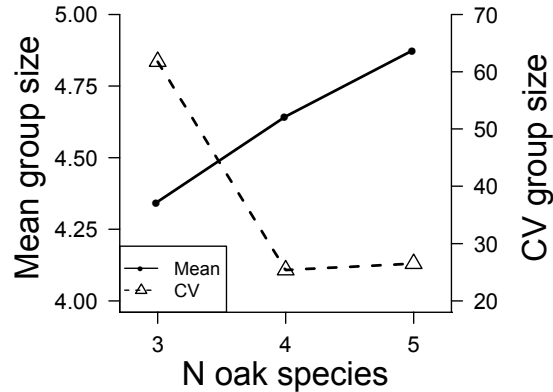


Figure 3—Mean and coefficient of variation in the size of acorn woodpecker groups at Hastings Reservation, 1975 to 2013, depending on the number of oak species to which they had ready access. The three oak species in the first category are all ‘1-year’ species that mature acorns in a single year; additional species are ‘2-year’ species requiring 2 years to mature acorns.

Crop size and helping behavior

Young acorn woodpeckers typically delay dispersal as a ‘best of a bad job’ strategy when they are unable to fill a reproductive vacancy in the population (Koenig and Mumme 1987). The availability of such vacancies, and thus the proportion of helpers able to become breeders in any one year, was influenced by the acorn crop. Specifically, when the acorn crop was good (year -1), a higher proportion of helpers survived the subsequent winter to become helpers the next spring (fig. 4a). This was presumably because the high reproductive success in spring of year 0 resulted in more offspring being produced, and with a limited number of territories, a higher proportion of birds were forced to remain as helpers in year +1. This relationship remained significant even after controlling for the acorn crop in year 0. In contrast, the proportion of helpers that remained as helpers into the next breeding season decreased with larger acorn crops in the same year (year 0) (fig. 4b). This relationship may once again be a side-effect of the lag-1 correlation in the acorn crop, since it was not significant in an analysis that included both the acorn crop in year -1 and in year 0, but to the extent it is real it was possibly the result of favorable food conditions resulting in an increased number of vacancies in otherwise poor-quality territories that were then colonized by older helpers. In any case, the acorn crop clearly had important effects on the probability of helpers obtaining reproductive vacancies and, conversely, continuing to help in their natal group.

The acorn crop also influenced the degree to which helpers influenced the reproductive success of groups. Prior work in other cooperative breeding species has suggested that in many cases, helpers are most important when conditions are poor, allowing pairs to breed successfully when they otherwise would be unable to acquire sufficient resources for themselves and their offspring (Covas and others 2008, Magrath 2001). In contrast, in acorn woodpeckers, evidence indicates that helpers

significantly increase survivorship and reproductive success of breeders when conditions are good—that is, following large acorn crops—rather than when conditions are poor (Koenig and others 2011). Perplexingly, this effect was only observed for helper males (fig. 5a); the statistical effect of a helper female on reproductive success was nonsignificantly positive and independent of the acorn crop.

This result becomes even more difficult to explain when looked at in greater detail. First, assuming that the different effects of helpers are due to differences in their provisioning behavior, we would expect to see feeding rates that parallel the above patterns. In contrast, there was no relationship between provisioning rates of helpers and environmental conditions—that is, the prior fall’s acorn crop—for either male (fig. 5b) or female helpers. How, then, did helper males benefit their group? If we restrict the analysis to first spring nests only, the strong positive relationship between the effect size of a helper male and the acorn crop disappears (fig. 5c). The probability of having two successful nests in a season, however, increased significantly among breeding pairs when they had helper males (fig. 5d).

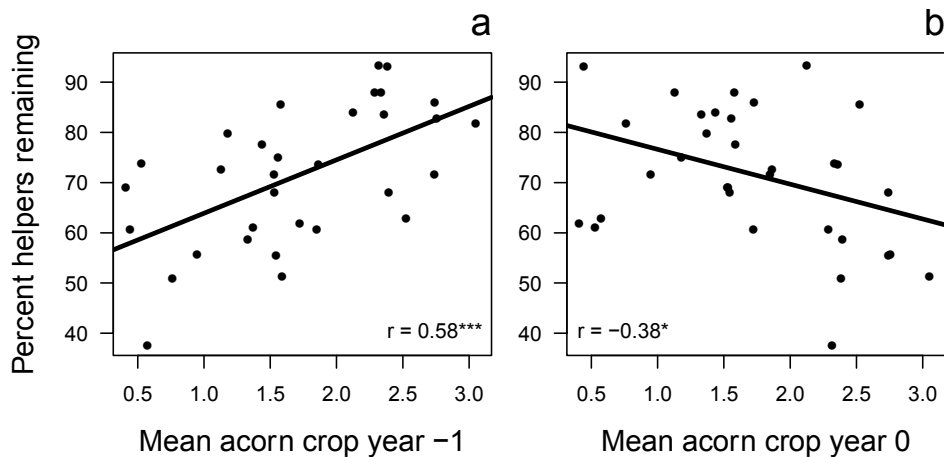


Figure 4—Scattergrams of (a) the percent of helpers that remained as helpers from year 0 to year +1 versus the mean acorn crop in year -1, and (b) the percent of helpers that remained as helpers from year 0 to year +1 versus the mean acorn crop in the fall of year 0; Pearson correlations and significance (* $P < 0.05$; *** $P < 0.001$) listed.

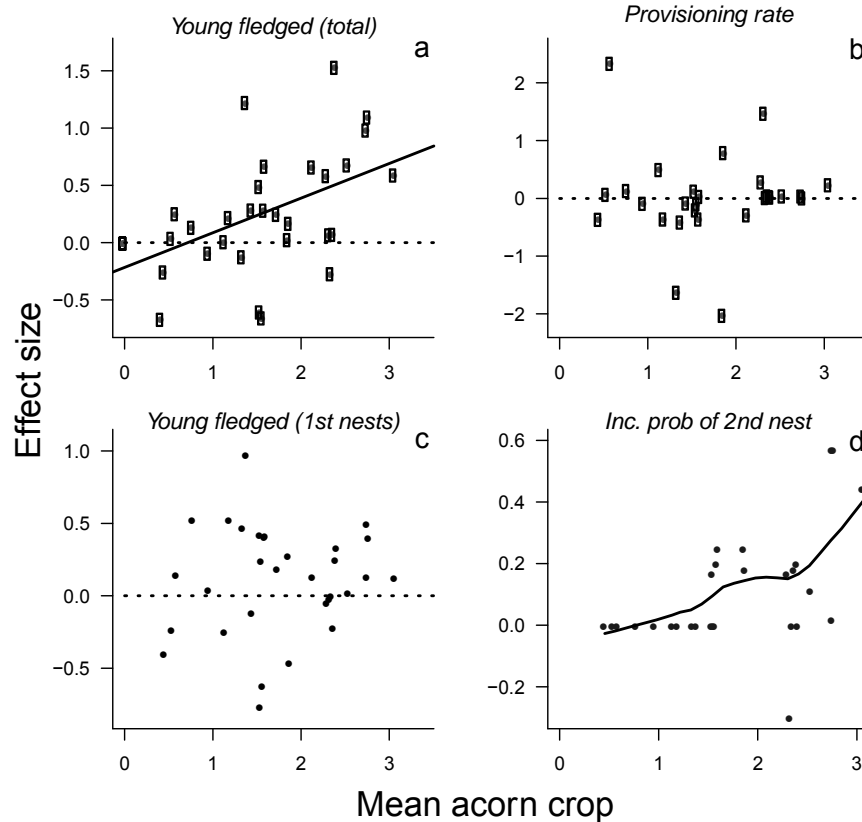


Figure 5—Mean effect size attributable to a single helper male plotted against the mean acorn crop size; 1981 to 2012; each point is a year. (a) Total young fledged ($r = 0.50$, $P = 0.003$); (b) provisioning rate ($r = -0.02$, $P = 0.9$); (c) young fledged at first nests only ($r = 0.10$, $P = 0.6$); (d) increased probability of breeding pairs having a second successful nest when they have a helper male ($r = 0.50$, $P = 0.007$).

Discussion

Acorns, which can be high in lipids but are generally low in available protein, are in general a supplementary food resource for acorn woodpeckers that provide a relatively small, but still extremely important, fraction of the energetic requirements of their populations in central coastal California (Koenig 1991, Koenig and Mumme 1987). Acorn availability allows acorn woodpeckers to remain resident in all but the worst acorn years (Hannon and others 1987) and provides them with the flexibility to feed more nutritionally valuable insects to their nestlings (Koenig and others 2008b). It is thus not surprising that acorn woodpecker dependence on this resource is manifested in a variety of ways, both demographically and behaviorally.

When the acorn crop fails, the effects are immediately evident in terms of the breakdown of group structure and the disintegration of many woodpecker groups (Hannon and others 1987). Conversely, when the acorn crop in the fall is good, birds can have fall nests (Koenig and Stahl 2007). Because the acorn crop of different species of oaks are to some extent asynchronous, the probability of territory abandonment in a poor year is mitigated by oak richness, especially in areas of sympatry between ‘1-year’ and ‘2-year’ species that mature acorns in different years. Such effects are manifested in acorn woodpecker populations along the Pacific Coast by reduced annual population variability in sites with greater oak species richness,

but are even expressed on a smaller scale within our study site by groups with access to more species of oaks exhibiting higher mean group size and lower annual variability.

The size of the acorn crop has longer-term effects by driving high woodpecker productivity the following spring and resulting in relatively large groups 2 years later. Because of the correlation between mean maximum temperatures in the spring and the subsequent acorn crop, apparently driven by effects on phenology and pollen availability, it is possible to predict, at least to some extent, not only the acorn crop but the reproductive success and subsequent group size of acorn woodpeckers in the population 2 years later based on environmental conditions during the spring.

The acorn crop also affects the competitive environment faced by acorn woodpecker helpers and thus the probability that they will obtain a reproductive vacancy rather than remain as nonbreeders in their natal group. More dramatically, the presence of helper males, but not helper females, enhances the reproductive success of groups, not by their provisioning behavior, but by increasing the probability that the group will successfully fledge more than one nest in a season. What helper males are doing to cause this result is currently under study, as is the even more perplexing reason for why helper males, but not helper females, exhibit these effects.

In contrast to some superficially comparable systems, such as that of Clark's nutcrackers (*Nucifraga columbiana*) and piñon pines (*Pinus edulis*) (Vander Wall and Balda 1977), the evolutionary dependence of the acorn woodpecker—oak system is apparently mostly one-way. That is, although acorn woodpeckers are highly dependent on acorns and oaks, no species of oak is dependent, as far as is known, on acorn woodpeckers for dispersal or regeneration. Indeed, given the relative efficiency with which acorn woodpeckers are able to recover acorns stored above ground in their granaries as opposed to western scrub-jays (*Aphelocoma californica*) that store acorns in the ground where subsequent germination is potentially enhanced (Carmen 2004), it is unsurprising that oaks exhibit no obvious adaptation facilitating their use or harvesting by acorn woodpeckers. Acorn woodpeckers are, nonetheless, one of the most characteristic denizens of California oak woodlands, and continue to provide endless surprises with their unique and surprising behavior.

Acknowledgments

We thank our colleagues who have helped with the acorn woodpecker and oak studies over the years and the many field assistants who collected much of the data. We particularly thank Vince Voegeli and the Museum of Vertebrate Zoology, University of California, Berkeley, for their assistance. Our work has been supported by the National Science Foundation, most recently by grants IOS-0918944 and DEB-1256394, and the UC Integrated Hardwood Range Management Program.

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