The Ecology of Blue Oak (*Quercus douglasii*) Acorn Production

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Acorn production by trees of the genus *Quercus* is highly variable from tree to tree, year to year and site to site. Such variability, particularly among years, is so common among temperate-zone trees that it is generally known as "mast fruiting" or simply "masting" after the old English word the seeds of forest trees. Although oaks may be the most widely distributed genus of tree in the world (Critchfield and Little 1966), their patterns of masting are poorly understood. This is nowhere more evident than in California, where nine species of tree oaks dominate over 3.1 million hectares of woodland throughout the foothills of the state. Acorns produced by these oaks provide a major portion of the food supply for a vast array of wildlife from acorn woodpeckers (*Melanerpes formicivorus*) to turkeys (*Meleagris gallopavo*) and from mule deer (*Odocoileus hemionus*) to wild pigs (*Sus scrofa*) (Verner 1980, Barrett 1980). Acorns have also been estimated to have constituted up to half the diet of most tribes of California Native Americans (Pavlik et al. 1991). Thus, understanding patterns of acorn production is likely to lead to insights into the population dynamics of an important fraction of California's wildlife species and prehistoric native peoples.

Here we summarize some of our research on the causes and consequences of variation in acorn production by California oaks, thus updating earlier publications on this project (Koenig et al. 1994a, Koenig et al. 1994b, Koenig et al. 1996, Koenig and Knops 1995, Koenig and Knops 1997). This has been initiated in stages starting with annual surveys of five species at Hastings Reservation in central coastal California. We later became interested in geographic patterns of acorn production and in 1989 began comparable surveys in two other localities in the central coast ranges. Finally, in 1994, we initiated a statewide acorn survey encompassing 34 populations of 6 species located at 14 different sites between Shasta County in the north to San Diego County in the south. With only four years of data for the statewide survey as of this writing, we can only offer preliminary results on this aspect of the study.

One clear finding of our surveys is that there are significant differences between the acorn production pattern of the species (Koenig et al. 1994a). Here we focus on results from the blue oak *Quercus douglasii*, a species of particular economic and conservation interest due to the fact that it appears to be regenerating poorly throughout much of its wide range in California (Pavlik et al. 1991).

Materials and Methods

The blue oak is the most abundant oak species throughout the foothill regions of California, ranging from Shasta County in the north, encircling the Central Valley, and ending in Los Angeles and Santa Barbara Counties in the south (Griffin and Critchfield 1972), a distance of nearly 800 km. Within this range, it covers an estimated 1.2 million hectares of woodland (Bolsinger 1987).

Blue oaks are a member of the "white oak" subgenus *Quercus* and occasionally hybridize with valley oaks, the other major member of this subgenus in California. Both these species are deciduous and require a single year to mature acorns. That is, flowers produced in spring (March and April) are fertilized and grow into mature acorns several months later in the following autumn (September and October).

Our primary study site is Hastings Reservation, a field station run by the University of California, Berkeley, located in the upper Carmel Valley, Monterey County, in central coastal California. Starting in 1980, we surveyed 56 individually marked blue oaks at this site, all within 3.5 km of each other. We used visual acorn surveys (Koenig et al. 1994b) modified from the original method proposed by Graves (1980). Briefly, each tree is visited in September prior to acorn fall. Two individuals visually survey different parts of the tree and count as many acorns as they can in 15 seconds. These counts are then added to yield "N30," the number of acorns counted in 30 seconds. We also give each tree a score of between 0 (no acorns seen) and 4 (a bumper crop). For statistical analysis, N30 values are generally log-transformed [log(N30+1)]; these values will be referred to as "LN30." Log-transformation compensates for the fact that differences between large N30 values (i.e., between 100 and 110) are intuitively much less than differences between small N30 values (i.e., between 0 and 10). LN30 values are averaged across all individuals to obtain an estimate of the mean annual crop.

For study of geographic synchrony in acorn production, we obtained data from eight additional sites throughout California (see Fig. 6). Two of these (Jasper Ridge and Pozo) were first surveyed in, while the other six were first surveyed in 1994. Methods used were identical to those used at Hastings Reservation.

Results

Annual variation

Acorn production by blue oaks shows considerable variation from year to year (Fig. 1). At Hastings Reservation, the mean number of acorns counted per tree has ranged from less than 1 in 1986 to just over 70 in 1985. Effectively, these correspond to years when it is very difficult to find an acorn and years when almost every blue oak tree produces a bumper crop.

These data raise several issues of interest. First, do these data correspond to what we would expect if acorn crops occur primarily as "boom"

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and "bust" crops? That is, are most years either excellent or poor years for blue oak acorns, with relatively few intermediate years? One way to examine this hypothesis is to compare the frequency distribution of the mean acorn crops against that expected by a normal distribution. If we are unable to reject the hypothesis that the distribution of mean acorn crops is normally distributed, then the data fail to support a bimodal pattern in which most years are either very good or very poor. This is done in Fig. 2 by plotting the actual values versus those expected if mean acorn crop size follows a normal distribution. The observed values match the expected distribution very closely and is not significantly non-normal by a Kolmogorov-Smirnov one-sample test ($z = 0.5$, $P > 0.9$). Thus, the distribution of acorn crop size across years is not strongly bimodal, but rather corresponds to that expected under a (log-) normal distribution, with most years being intermediate in size and relatively few years being either very good or very poor.

What determines the mean acorn crop in any particular year? Previous work has suggested three potentially important variables: (1) rainfall, (2) conditions during flowering and pollination in the spring, and (3) the acorn crop in the prior year. The first pair of these variables tests for correlation between weather conditions and the subsequent acorn crop, while the last postulates significant autocorrelation between the acorn crop in one year and that in the subsequent year.

Pearson correlation coefficients between each of these three variables and the blue oak acorn crop are all significant or nearly so (rainfall during the prior year: $r = -0.52$, $n=18$ years, $P = 0.026$; mean April temperature: $r = 0.75$, n = 18 years, $P < 0.001$; prior year's acorn crop: $r = -0.45$, $n = 17$ years; $P = 0.07$). That is, blue oak acorn crops at Hastings tend to be larger in years when April temperatures are warm and smaller when the prior winter was wet or the prior year's acorn crop was large. However, in a multiple regression including all three of these variables as predictors, only mean April temperature is significant ($F_{1,15} = 3.45$, $P < 0.005$). Using only this variable, we are able to explain 56 percent of the variance in mean annual acorn production by blue oaks at Hastings Reservation. Examination of data suggests that

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Quercus douglasii *Hook and Arn. woodland in the foothills of the Tehachapi Mountains in southern California.*

the main predictive power of this relationship is at the extremes of the spectrum. That is, when mean spring temperatures are very low (<10ºC) or very high (>13.5ºC), we can confidently predict that the subsequent acorn crop will be correspondingly poor or very good. However, when spring temperatures are intermediate, it is more difficult to be certain what the subsequent acorn crop will be other than that it is unlikely to be unusually large.

One further descriptive issue of interest is the extent to which mean annual acorn production cycles in a predictable way. We have already mentioned that there is a nearly significant negative autocorrelation between the acorn crop one year (year x) and the next year (year $x+1$). However, there is no significant correlation between the acorn crop in year x and in any other subsequent year (Pearson r values for x with $x+2$ through $x+9$ all yield P-values > 0.05). A more precise way to search for cyclicity is to perform time-series analysis. Based on results using the spectral density indicating the relative strength of cycles of the length shown along the x-axis, there is a statistically significant tendency for a cycle of between 2 and 4 years in length with a peak at a period of 2.25 years. Thus, there is significant cyclicity to the mean acorn crop data, but it tends to be obscured by the fact that it is not an integral number of years in length. Data from this testing can only be considered preliminary due to the relatively short (18 year) length of the data set,

Individual variation

Mean annual acorn productivity is a standard measure but sidesteps the considerable variation among individual trees that occurs within the population. For example, one of the 56 trees at Hastings never produced a single acorn as far as we know, while another never had a year in which it did *not* produce at least a detectable. Conversely, 11 trees never produced a "very good" crop defined as having a score of 3 or 4, while the most productive tree in the study was classified as having a very good crop in 13 of the 18 years.

Averaging the LN30 values across all years for each tree, the distribution of the mean productivity of the 56 trees in the Hastings study site can be graphed overlaid with the expected distribution under the null hypothesis that the distribution is (log-) normal across trees. And again, as before, there is no significant difference in the distributions (Kolmogorov-Smirnov test, $z = 0.8$, $P > 0.4$), indicating that, like mean annual productivity, mean individual productivity of blue oaks at Hastings is normally distributed. That is, there are a few extremely productive trees and a few very unproductive trees, but on average, most trees produce, over time, an intermediate number of acorns.

Prior analyses have demonstrated that among-year patterns of acorn production are similar within species (Koenig et al. 1994a). In other words, although individual trees vary widely in their productivity, they are synchronized in their relative productivity; in good years virtually all trees do relatively well and in poor years virtually all trees do relatively poorly. For example, of the 56 trees in our sample, 41 (73%) produced as many acorns as they did during any year of the study in 1985 or 1987, the two best years overall. Conversely, 48 (86%) experienced their worst year in either 1983 or 1986, the two poorest years overall during the study.

What causes individual variation in long-term productivity of individual trees? To address this issue, we measured several variables characteristic of individual trees, including size (DBH), elevation, slope, xylem water potential (Knops and Koenig 1994), leaf nutrient concentrations, and soil nutrient concentrations (Knops and Koenig 1997). Xylem water potential was measured in September and October 1991. Leaves were collected in summer and fall of 1992. Available soil nitrogen and phosphorus were measured using ion exchange

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resin bags buried in the soil around each tree during the winter of 1992-1993, while total soil nitrogen and phosphorus were measured in the summer of 1992. Additional analyses are forthcoming; in particular, we have not yet completed an analysis of monthly nutrient flux and litterfall underneath a subsample of our trees that we conducted over a five-year period. However, results based on this preliminary data set yield no significant correlation between long-term mean acorn production by individual blue oaks at Hastings and the majority of variables we have measured, including DBH, elevation, and slope. Variables that correlate significantly with mean long-term acorn productivity include predawn xylem water potential, total soil nitrogen, and specific leaf mass, the latter both measured in July 1992. These relationships suggest the following correlates of good long-term acorn production:

(1) *Predawn xylem water potential.* —Trees with better access to ground water have higher predawn xylem water potential values and greater long-term acorn productivity.
(2) *Total soil nitrogen.* —Trees growing in soil containing greater concentrations of nitrogen produced more acorns over the long term.
(3) *Specific leaf mass.* —Trees with tougher, more sclerophyllous leaves tend to produce more acorns, possibly because these trees are also better at conserving water.

How well can we predict long-term acorn productivity based on these values? Including all three of the significant variables in a multiple regression, only predawn xylem water potential variables come out to be significant ($P < 0.05$), explaining 20% of the variance, compared to the 56 percent of the variance in mean among-years productivity we are able to explain with April temperatures. Thus, we are currently able to explain only a relatively small proportion of the variance in productivity among individual trees.

Geographic variation

Masting fruiting is a population phenomenon (Kelly 1994). That is, an individual tree may produce a variable number of seeds from year to year, but masting only occurs when a group or population of many trees together produce (or fail to produce) seeds synchronously from one year to the next. How large is the population of trees that produce acorns synchronously? Most studies of seed production have focused on relatively small areas and there are few data with which to examine this important question.

We now have data on blue oak acorn production over a period of four years by 20 or more individual trees at nine sites throughout California. Although preliminary, the results appear clear. First, the overall trend is for correlation between the mean acorn crops of the various sites to be very high; of the 36 pairwise correlation coefficients, all but one (97 percent) is >0.70. There is also no apparent decrease in synchrony with distance; in fact, using a Mantel test, which tests for a relationship between mean r values and distance, the correlation increases with distance (overall z-value = 0.3, P = 0.04).

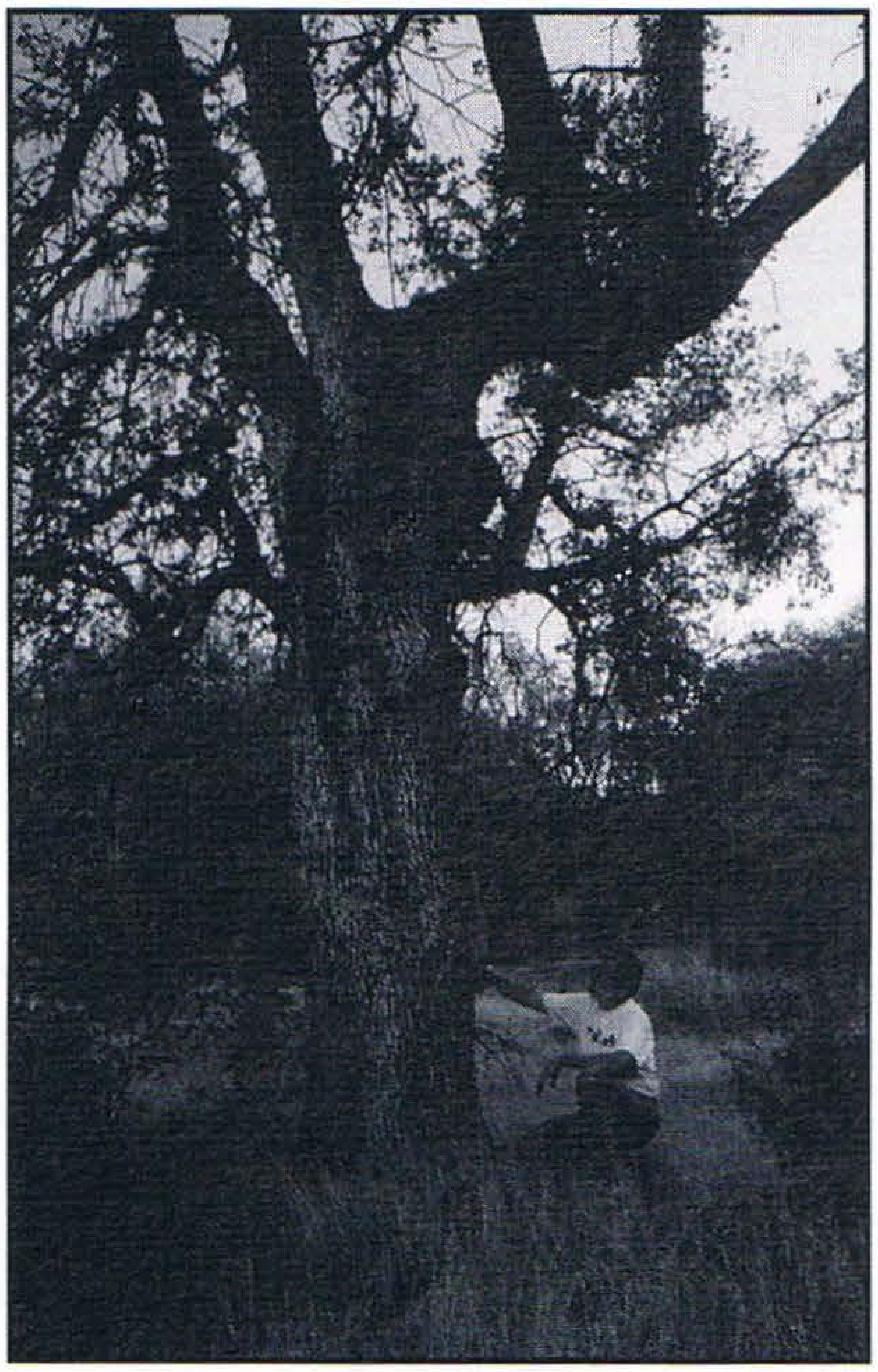
Many of the correlations are high due to the fortunate circumstance that the first year of the survey (1994) was an extremely good year throughout the state whereas the second year (1995) was extremely poor (Koenig and Knops

1997). Values are likely to decrease as we accumulate more data, as suggested by the single relatively small value (0.42) which is the correlation between Jasper Ridge and Pozo based on nine years (1989 - 1997) rather than only four years of data. In any case, it appears that blue oaks are clearly synchronized, at least to some extent, in their annual acorn production throughout their range.

Discussion

Our results suggest several important conclusions about acorn production patterns by blue oaks. First, annual crop size correlates strongly with conditions during the spring pollination and fertilization period: relatively dry, warm conditions are presumably favorable for fertilization and are generally followed by larger autumn acorn crops. Second, the distribution of mean annual acorn crops is normally distributed, with most years experiencing intermediate acorn crops rather than "boom" or "bust" crops. Third, there is a significant cyclic period in mean annual acorn production of between 2 and 4 years with a peak at 2.25 years.

As with mean annual productivity, the productivity of individual blue oak trees is normally distributed; most trees produce an intermediate number of acorns over the long term. Several variables correlate with long-term productivity of individual trees, including their access to ground water (as indicated by xylem water potential), total soil nitrogen where they are growing, and the specific leaf mass of their leaves during the summer. However, even in combination, these variables are able to explain only a relatively small proportion of the variance among trees. Currently we have a good idea of what makes for a good and a bad blue oak acorn year, but we know very little about what makes for a good and a bad blue oak acorn tree, other than that differences in productivity are consistent across years.



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Guy Sternberg examining an old Quercus douglasii *Hook and Arn. in the Los Padres National Forest during the Ventura County field trip of the Second International Oak Conference.*

Although results are preliminary, thus far our statewide acorn surveys suggest that the mean annual blue oak acorn crop is geographically synchronous throughout their range, which extends over nearly 800 km. Apparently the population involved in mast fruiting by blue oaks is very large, covering most, if not all, of the range of the species. Even more extensive geographic synchrony in seed production has been found in boreal trees (Koenig and Knops 1998).

Why do blue oaks exhibit variable acorn production? Like most evolutionary questions, this must be addressed at several levels. Proximately, varying acorn crops by individual trees are the products of ecological differences between trees, including their access to ground water and the nutrient conditions of the soil in which they are growing. Virtually nothing is known con-

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cerning the possible effects of genetic differences between trees or of the role that parasites, predators, or other organisms may play in the long-term success of individual trees in producing acorns. Even less is known about how differences between individual trees in their acorn production patterns may translate into subsequent fitness differences in terms of the probability (which is always very low) that acorns produced by a tree may ultimately survive to grow into a reproductive adult.
Between years, the size of the crop produced by trees within the population at large is correlated with weather conditions during the spring; warm, dry springs are apparently more conducive for pollination and fertilization of flowers. At this point, however, relatively little is known about this important aspect of the life history of blue oaks, or any species of California oak.

Ultimately, the question is one of the fitness consequences of variable acorn production: presumably, trees that produced many acorns some years and few acorns in other years are more successful at leaving progeny than trees that do not vary their acorn production from year to year. Furthermore, trees that vary their patterns of acorn production in synchrony with other trees in the population are also more successful, leading to the pattern of relatively synchronous mast fruiting over the entire range of the species.

Data from our surveys at Hastings Reservation also indicate that species requiring the same number of years to mature acorns produce crops are positively correlated, while those that require different numbers of years to mature acorns are not. For blue oaks, this shows up as a significant positive correlation with both valley and coast live oaks and negative (but non-significant) correlation with both canyon live and California black oaks. This means that acorn availability within many sites throughout California are moderately synchronized, since valley, blue, and coast live oaks are the three common constituents of many coast range communities throughout the state. However, most sites in California are topographically quite diverse and species requiring two years to mature acorns are frequently either present or growing less than a few miles away. Thus, in general, it is rare in California for acorn production by all species of oaks at a site to fail simultaneously.

This puzzling aspect of oak biology may be partially explained by the curious fact that some of the major vertebrate predators of acorns, particularly California scrub-jays (*Aphelocoma californica*), are simultaneously the primary dispersers of acorns throughout much of California, caching large numbers of acorns in the ground where they are offered a relatively good chance of surviving and germinating (Grinnell 1936). From an evolutionary standpoint, this places many species of California oaks in something of a dilemma. From a pure standpoint of predator satiation, the more synchronized all trees in the community are the better. However, to maximize dispersal of acorns, trees probably benefit by maintaining a moderately large, healthy population of scrub-jays. Perhaps the observed result, which is a population of predators sustained sufficiently by acorns that they are able to harvest the entire crop in most years but are overwhelmed in very good years, is exactly the compromise we would expect given the conflicting roles of many of these major acorn predators.

Conclusion

The acorns produced by California oaks offer both a vast wealth of food for wildlife and a nearly limitless source of variation begging to be explained. We are just now beginning to describe and understand the complex patterns of acorn production, both across individuals, species, years, and sites. Yet many questions remain. We still know very little about what goes on prior to the maturation of a particular year's acorn crop. The extent to which the production of female flowers or varies in synchrony with subsequent acorn production is largely unknown, in part because of the relative difficulty of censusing female flowers. We know surprisingly little about the effects of predators on patterns of acorn production and even less about the causes of variation in the life-history strategies of individual trees. We are able to explain a high proportion of annual variation in some species but relatively little in others (Koenig et al. 1996).

Particularly notable is the all but complete absence of information on catkins production or on pollen dispersal by oaks; only recently with the development of molecular DNA markers has it become possible to determine paternity of acorns (Dow and Ashley 1996). Although few data are available spatial patterns of acorn production, ongoing work promises to make a significant inroads in this field as well. Ultimately, we look forward to a day when we are able to explain a much higher proportion of the variation in acorn production by California oaks at all levels than is currently within our grasp.

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