

Determinants of Acorn Productivity Among Five Species of Oaks in Central Coastal California¹

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Abstract: We measured acorn production of five species of oaks (genus *Quercus*) over a ten year period (1980-1989) at Hastings Reservation in Monterey County, California. Crop production was highly variable and generally asynchronous between species. Variance in crop size decreased directly with increasing species diversity across sub-areas within the study site. Sources of variance in mean annual crop size include annual and interspecific differences and extrinsic factors correlated with different sub-areas of the study site. However, the majority of variance remains unexplained after controlling for these factors and is apparently due to individual variation in crop production. Climatic variables were not found to correlate with mean annual crop productivity in any of the species, with the possible exceptions of *Q. chrysolepis* and *Q. kelloggii*. However, strong autocorrelations were found within the crop sizes of individuals indicating the existence of masting cycles on the order of three years for *Q. douglasii* and *Q. agrifolia*, two to three years for *Q. lobata*, and possibly six years for *Q. chrysolepis* and *Q. kelloggii*. These results indicate distinct reproductive strategies in California oaks; continued studies will be necessary in order to identify the relative importance of the evolutionary factors that have resulted in these patterns.

Acorn crop size is of fundamental importance both to the understanding of oak regeneration problems and to the diverse assemblage of wildlife dependent on acorns as food. However, surprisingly little is known concerning the factors determining acorn crop size or variability. This ignorance is acutely evident in California, where oaks dominate millions of hectares of land area (Griffin and Critchfield 1972, Griffin 1977, Bolsinger 1987), and acorns are a primary food resource for a wide variety of wildlife (Barrett 1980, Verner 1980).

The difficulties of assessing the factors important to crop size are formidable. Acorn crops are notoriously variable, not only at the species level but also at the community, site, and individual tree levels. Moreover, the pattern of spatial heterogeneity in crop sizes is likely to be complex given the diverse geographic and climatic range inhabited by oaks in California. Finally, the logistic problems associated with reliably assessing acorn crop size are considerable. Short-term data collected by

different observers are unlikely to be of value unless carefully coordinated. Acorn traps can provide an accurate estimate of acorn fall for individual trees, but unavoidably miss acorns removed prior to maturity by birds and other animals, require considerable maintenance, and are difficult to put out in sufficient numbers to yield satisfactory sample sizes. Visual estimates (Graves 1980, McKibben and Graves 1987) are subject to considerable variation depending on the observers but have the potential advantage of yielding large sample sizes with reasonable time investment.

With these difficulties and challenges in mind, we began a study in 1980 of the fruiting patterns of five species of sympatric oaks at Hastings Reservation in Monterey County, California. Our goal in this continuing endeavor is to quantify the patterns of intraspecific, interspecific, annual, and spatial variability in acorn production and to determine the environmental and intrinsic factors responsible for the observed variation. Analyses based on the first seven years of data were presented earlier (Carmen et al. 1987). Here we extend our earlier results using data through 1989 (10 years), emphasizing the masting patterns observed at Hastings and the factors, both extrinsic and intrinsic, contributing to individual variation in acorn productivity. We also discuss some of our results concerning local variation in mast production among and within species and the implications of our findings to the understanding of the relationships between acorn producers and their predators.

STUDY AREA AND METHODS

Hastings Reservation is a 900 ha reserve located in the Santa Lucia Mountains of central coast range of California, approximately 42 km inland. Elevation ranges from 467 to 953 m. Mean annual temperature is 17°C. Annual rainfall ranges from 26.1 to 111.2 cm, with a 50-yr mean of about 55 cm. Topography includes relatively narrow valleys amid rugged foothills. Common at the lower elevations are *Quercus lobata*, *Q. douglasii*, and *Q. agrifolia*, while at higher elevations *Q. kelloggii* and *Q. chrysolepis* are also present. These five species include oaks of all three subgenera (*Quercus*: *Q. lobata*, *Q. douglasii*; *Erythrobalanus*: *Q. agrifolia*, *Q. kelloggii*; and *Protobalanus*: *Q. chrysolepis*), both evergreen (*Q. agrifolia* and *Q. chrysolepis*) and deciduous (*Q. lobata*, *Q. douglasii*, and *Q. kelloggii*) species, and species that require one year (*Q. lobata*, *Q. douglasii*, and *Q. agrifolia*) and two years (*Q. kelloggii* and *Q. chrysolepis*) for acorns to mature.

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Beginning in 1980, we established transects in foothill woodland, savanna-grassland, and riparian woodland vegetation types (Griffin 1983). Along these transects we sampled 250 oaks including 87 *Q. lobata*, 63 *Q. agrifolia*, 57 *Q. douglasii*, 21 *Q. kelloggii*, 21 *Q. chrysolepis*, and 1 obvious *Q. lobata* x *Q. douglasii* hybrid. Sample sizes decreased slightly in later years as several trees died and were not replaced. DBH of each tree was measured. Each autumn at the height of the acorn crop and prior to acorn fall, generally between mid-September and early October, we measured the relative abundance of acorns of each of the 250 individual trees using two methods. First, two observers scanned different areas of the tree's canopy and counted as many acorns as possible in 15 s. These counts were added to yield "acorns per 30 s". Second, the two observers agreed on a score between 0 and 4 describing the overall size of the acorn crop for each tree. This score, modified from the visual estimate scale pioneered by Graves (1980), was as follows: 0 (no acorns), 1 (a few seen after close scrutiny), 2 (a fair number, acorns seen readily), 3 (a good crop), and 4 (a bumper crop, acorns just about everywhere on the tree). At least one of the original observers has participated in the annual counts each year since we initiated the study.

Based on elevation and habitat, we divided the 250 trees into four sub-areas: (1) the Arnold, a high-elevation area located in the southern end of the reservation (all five species present, elevation 780 to 878 m), (2) the Road, a low-elevation area traversing the center of the reservation (all but *Q. kelloggii* present in good numbers, a semi-permanent creek running through the area, elevation 470 to 512 m), (3) Big Creek, a low-elevation area running northeast of the Road with a seasonal creek running through it (only *Q. lobata*, *Q. douglasii*, and *Q. agrifolia* present, elevation 488 to 579 m), and Haystack/School Hill, two higher-elevation hills located on either side of Big Creek (only *Q. lobata*, *Q. douglasii*, and *Q. agrifolia* present in good numbers, elevation 579 to 637 m). All four areas are less than a km in diameter and are within 4 km of each other.

Weather data was taken from a station permanently located at the headquarters near the northern edge of the reservation in the "Big Creek" sub-area. Included in the weather station during the study period was a rainfall gauge, a max-min thermometer, and a Campbell Stokes-type sunshine recorder.

STATISTICAL ANALYSES

Using the first year of data (1980), the Spearman rank correlation between the two different measures of acorn productivity is 0.963 ($n=250$, $P<0.001$); thus, the choice between them is largely a matter of taste. In this paper we have used the number of acorns counted in 30 s (henceforth "N30"), which is a continuous, interval measure, in most of our analyses. In order to reduce the dependence of the variance on the mean, N30 was logarithmically transformed ($\ln(N30+1)$) prior to parametric

procedures. The 0 to 4 categorical score was used in the weather and the autocorrelation analyses because we suspect it is less sensitive to tree size, foliage density, acorn color, and acorn size, and thus is probably more comparable across years than N30.

RESULTS AND DISCUSSION

Pattern and Sources of Variation

Acorn production varies considerably both from year to year and from species to species (figure 1). Indeed, there are no significant correlations between the mean yearly crop scores of any of the species except for between the closely related *Q. lobata* and *Q. douglasii* (table 1). There is, however, a tendency for the species requiring a single year to mature acorns to be out of synchrony with those requiring two years: all six correlations of mean crop scores between the one-year species and the two-year species are negative, while all four correlations between species within these categories are positive (Fisher exact test, $P < 0.05$; table 1).

One important consequence of the asynchrony of acorn production across species is that variability in masting patterns are dampened. This is shown by comparing the annual variation of the individual species (figure 1) with the mean acorn crop score of all individuals combined (figure 2). Annual variation measured by the coefficient of variation for the mean annual score of all species combined was considerably less (34 percent) than that for any of the five individual species (range 55 to 128 percent).

This decrease appears to be a direct consequence, at least in part, of increased species number, as indicated by the relationship between the coefficient of variation in the mean annual crop score of all trees within sub-areas of the study site and the number of species of oaks commonly present in those sub-areas (figure 3a). Values decrease from a mean of 63 percent in the sub-areas with three species to 36 percent in the sub-area with five species. For acorn-dependent wildlife, this asynchrony acts to moderate the otherwise potentially disastrous effects of poor acorn years.

These data indicate that annual, local, and interspecific variation in acorn production all contribute importantly to community-wide patterns of crop size. However, all these factors are apparently overshadowed by individual variation. This is shown by a three-way analysis of covariance (ANCOVA) in which year, sub-area, and species were analyzed as main factors and diameter at breast height (DBH) included as a covariate (table 2). Each factor and the covariate are analyzed controlling for all other variables. All variables and their interaction terms are highly significant. However, in total, they account for less than half (46.1 percent) of the variance in crop scores present in the data. Of the individual variables, most important appears to be yearly variation, while sub-area, species, and DBH of individual trees account for only a small proportion of the total variance.

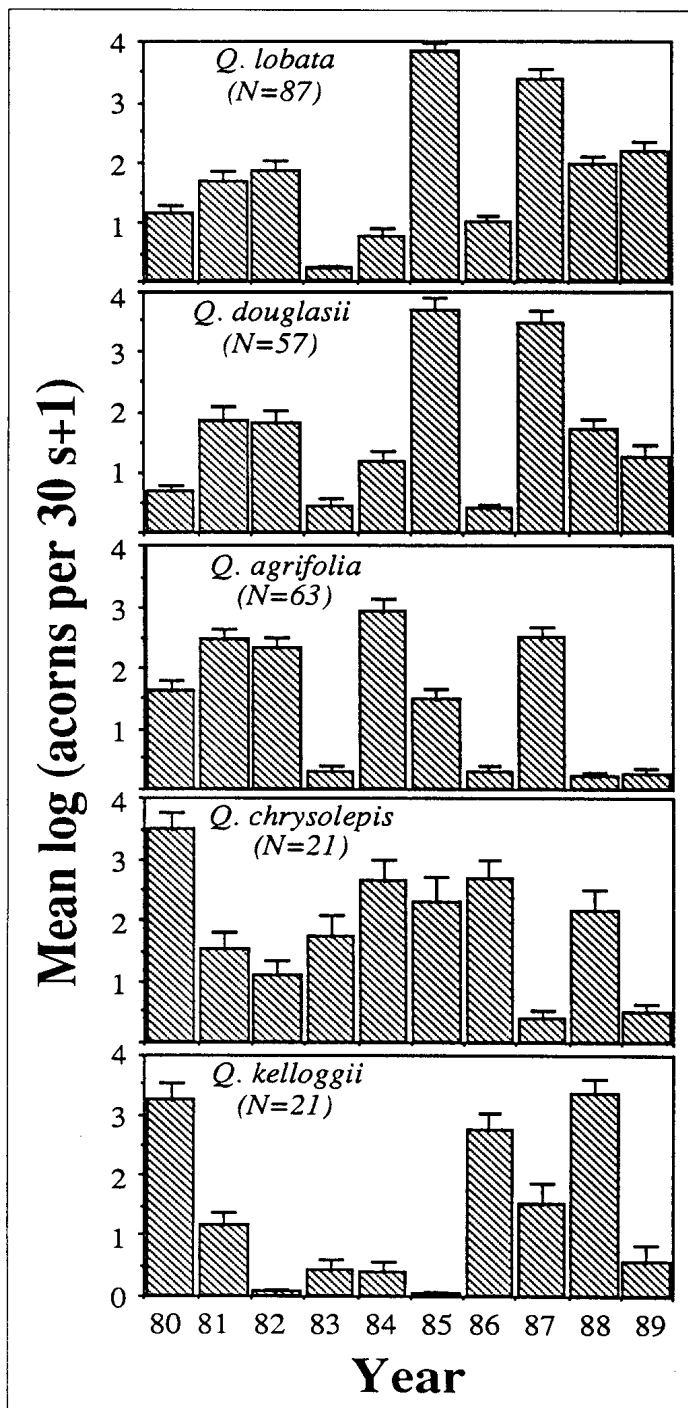


Figure 1—Mean (\pm S.E.) number of acorns counted per 30 s (log transformed) for each of the five oak species at Hastings for the ten years 1980-89.

Table 1—Spearman rank correlations of acorn production by five species oak oaks using mean annual data (mean number of acorns counted per 30 s; see text). $N=10$ years. * = $P < 0.05$.

	<i>Q. lobata</i>	<i>Q. douglasii</i>	<i>Q. agrifolia</i>	<i>Q. chrysolepis</i>
<i>Q. douglasii</i>	0.83*	—	—	—
<i>Q. agrifolia</i>	0.14	0.43	—	—
<i>Q. chrysolepis</i>	-0.42	-0.46	-0.18	—
<i>Q. kelloggii</i>	-0.18	-0.41	-0.39	0.21

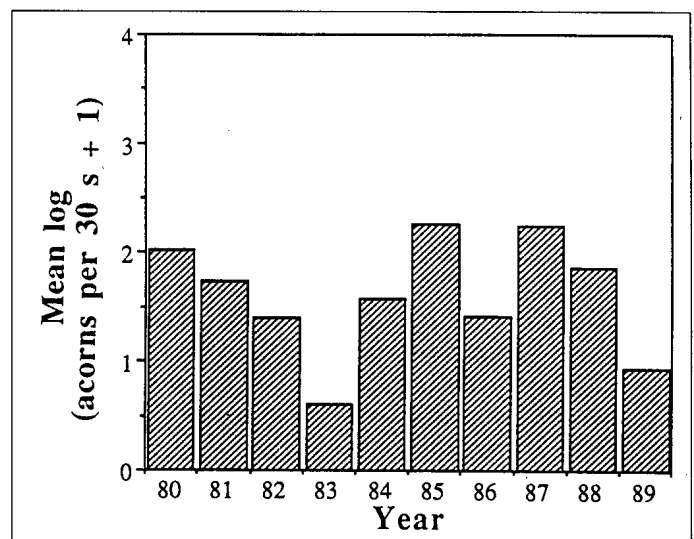


Figure 2—Mean number of acorns counted per 30 s (log transformed) for all five species combined. For each year, values were averaged for the five species to yield a community-wide estimate of overall acorn production.

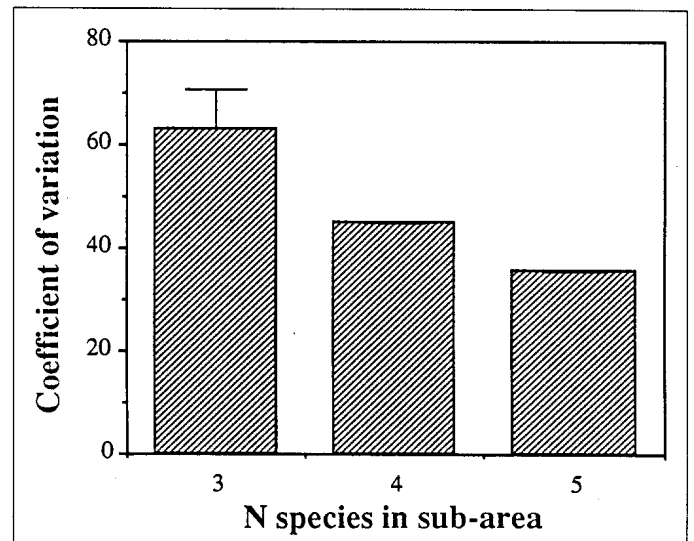


Figure 3—Coefficient of variation in the mean number of acorns counted per 30 s (log transformed) for the four sub-areas of Hastings Reservation, graphed according to the number of species commonly present in those sub-areas. Two sub-areas have three common species while one each have four and five. For the sub-area with three common species, the mean \pm S.E. is plotted.

However, the significant interaction terms make it impossible to determine with confidence the importance of the individual factors, since their effects are not independent of each other. This analysis indicates that individual variation is responsible for a larger proportion of the total variance in crop size than variance associated with different years, species, and sub-areas combined. Only a small part of this individual variation appears to be correlated with tree size.

Table 2—Three-way analysis of covariance of number of acorns counted per 30 s (log transformed) using species, year, and sub-area within the study site as main factors and DBH as a covariate. Each variable is considered controlling for all other variables. * = $P < 0.001$.**

	Sum of squares	Percent of total variance	df	F-value
Main factors				
Year	436.8	—	9	29.3***
Area	120.1	—	3	24.2***
Species	51.7	—	4	7.8***
Interaction				
Species x year	1388.1	—	36	23.3***
Area x year	169.1	—	27	3.8***
Species x area	121.3	—	9	8.1***
Covariate				
DBH	22.5	—	1	14.2***
Explained	3374.1	46.1	89	22.9***
Residual	3950.8	53.9	2383	—
Total	7325.0	100.0	2472	—

Causes of Variation

Possible causes of the considerable variation observed in acorn productivity among individuals include extrinsic factors, such as rainfall, temperature, and correlated factors such as slope and elevation, as well as intrinsic factors such as age, condition, and prior breeding effort. Here we briefly explore the importance of both kinds of factors as causes of variation in the acorn crop at the individual level.

In order to look at the possible effect of climate, we correlated the mean crop score values for each of the five species with a series of 15 weather variables including winter rainfall (1 Sept.-31 May), spring rainfall (1 Mar.-30 April), minutes of spring sunshine, the number of days in spring with <100 min of sunshine, the mean daily sunshine during the winter (1 Dec.-29 Feb.), the number of days in which the temperature dipped below 0°C during March, the mean mean, mean maximum, and mean minimum winter temperatures (1 Dec.-29 Feb.), the mean mean, mean maximum, and mean minimum spring temperatures (1 Mar.-20 April), and the mean mean, mean maximum, and mean minimum summer temperatures (1 June-31 July). In addition, each of these 15 variables was lagged one and two years; that is, mean scores for each species in year x were correlated not only with rainfall in year x , but winter rainfall in years $x-1$ and $x-2$ as well. This analysis yielded a total of 45 climatic variables, each of which was correlated with the mean annual crop scores of each of the five species of oaks.

By chance, 11 to 12 of the 225 correlations can be expected to be significant at the 0.05 level and two to three at the 0.01 level; observed numbers were 12 and three, respectively. Correlations significant at the 0.01 level included inverse correlations between the mean crop score of *Q. douglasii* and spring sunshine two years earlier and between the mean score of *Q. chrysolepis* and both mean winter temperature one year earlier and mean maximum winter temperature one year earlier. Similarly inconclusive results were obtained from a factor analysis. Details are beyond the scope of this paper, but in

essence these analyses extract a small number of uncorrelated variables each of which is made up of different weightings of the large number of often highly correlated climate variables entered into the analysis. The factors can then be treated as new variables and correlated with the mean acorn scores as before. We extracted the first four factors (accounting for an accumulated total of 73.6 percent of the variance in annual climatic differences); by correlating the factors with the mean crop score of each of the five oak species, a total of 20 correlations were obtained. Of these, two (one involving *Q. chrysolepis* and the other *Q. kelloggii*) were significant at the 0.05 level. Both of these involved a factor in which winter temperature one year earlier loaded especially heavily; that is, *Q. chrysolepis* and *Q. kelloggii* tended to produce larger crops one year following particularly cold winters. Although it is possible that these relationships are providing insight about the extrinsic factors influencing acorn production in these species, in general these analyses fail to offer persuasive evidence that the observed correlations between climate and mean acorn production are anything more than the result of chance.

Despite the overall failure of the climate variables to convincingly explain much of the variance in crop production, the significant differences in crop scores among sub-areas demonstrated in the ANCOVA discussed above indicate that extrinsic variables correlated with the four sub-areas significantly influence acorn crop scores (table 2). Thus, extrinsic factors are important, but on a smaller geographic scale than that expected if general climatic trends determined acorn crops from year to year.

Factors intrinsic to individual trees that potentially influence crop production include size, age, genetic differences, condition, and prior reproductive effort. Currently we have little information on any of these factors with the exception of size, measured by DBH, and prior reproductive effort, based on our acorn censuses performed in prior years.

We tested for an effect of DBH by including it as a covariate in three-way analysis of covariance discussed above. In the resulting analysis, DBH was significant and positively associated with N30. However, based on the sum of squares, DBH was of considerably smaller importance than any of the other variables considered, or their interactions. Tree size does appear to be correlated with acorn productivity, but is of relatively small importance compared to annual, interspecific, or micro-geographic variation.

Determining the importance of prior reproductive effort involves calculating autocorrelations of acorn scores for each individual tree with scores for the same tree in prior years. For each year n , the score (s_n) for each tree is correlated with s_{n-1} , s_{n-2} , and so on. Sample sizes decline by one for each successive autocorrelation; for s_n with s_{n-1} , the sample size is the number of years of data (N) minus 1; for s_n with s_{n-2} the sample size is $N-2$, and so on. With only 10 years of data thus far, we were thus able to go back only as far as s_{n-6} and still have enough points for each tree ($N=4$) to obtain a reasonable correlation coefficient.

We calculated all autocorrelation coefficients of s_n with s_{n-1} through s_{n-6} for each of the 250 trees in our sample. We then (1) averaged the autocorrelation coefficients for a given lag time

($n-1$ to $n-6$) for each of the five species and (2) counted the number of times the autocorrelation coefficient was positive and number of times it was negative. We tested the significance of the difference in the resulting number of positive and negative correlations for each of the six lagged intervals for each of the five species of oaks with a 2-tailed binomial test.

The results for the three species requiring one year to mature acorns are shown in figure 4 and for the two species requires two-years to mature acorns in figure 5. For all species except *Q. kelloggii* there is a highly significant inverse correlation between the score in year n and that in the prior year $n-1$. In other words, a good crop in one year generally is followed by a relatively poor crop the next year, and vice-versa. Both *Q. douglasii* and *Q. agrifolia* exhibit a significant three-year masting cycle as indicated by the highly significant autocorrelations of s_n with both s_{n-3} and s_{n-6} . (figure 4). Support for a three-year cycle is further enhanced by the recurrence of the highly significant inverse correlation coefficient of s_n with s_{n-4} as expected given the inverse correlation of s_n with s_{n-1} . Autocorrelations of the intermediate years ($n-2$ and $n-5$) are not significant.

The masting pattern of *Q. lobata* as revealed by the autocorrelation analyses is not clear. The highly significant inverse correlation of s_n with s_{n-1} is followed by a significant positive correlation with s_{n-2} , suggesting a two-year cycle. However, the correlation with s_{n-3} is not significant while that with s_{n-4} is significantly negative, as with *Q. douglasii* and *Q. agrifolia*. This possibly suggests that the masting cycle in *Q. lobata* varies between two and three years. However, it is not strongly cyclic as indicated by the lack of any significant autocorrelations with years $n-5$ and $n-6$.

These patterns contrast with those for the two-year species *Q. chrysolepis* and *Q. kelloggii* shown in Figure 5. The only markedly positive autocorrelations found for either species are with years $n-5$ (for *Q. chrysolepis*) and $n-6$ (for both species); none of these is significant, however. Otherwise, *Q. chrysolepis* exhibits the strong inverse autocorrelation between s_n and s_{n-1} , as

did the one-year species, while *Q. kelloggii* exhibits highly significant inverse autocorrelations with years $n-3$, $n-4$, and $n-5$.

Although not conclusive, these latter results suggest that possibility of a six year cycle for *Q. chrysolepis* and *Q. kelloggii*. To the extent that this is true, examination of figure 1 indicates that the pattern results from opposite strategies in the two species: overall masting of *Q. chrysolepis* was reasonably good in most years, with relatively poor years coming at five- to seven-year intervals (1982 and again in both 1987 and 1989), while malting of *Q. kelloggii* tended to be usually poor with good years occurring at approximately six-year intervals (1980 and again in 1986). Unfortunately, even the 10 years of data we currently have is insufficient to conclusively demonstrate these patterns. However, our results thus far do provide good evidence that several of the species at Hastings have distinct masting cycles and that the cycles are both asynchronous (figure 1) and of different lengths (figures 4 and 5) for the five species.

These findings, although preliminary, have several implications for resource managers and biologists interested in California oak woodlands. First, variation in crop size is considerable. Sources of variation include tree size and interspecific, annual, and local differences among areas even within the relatively small size of our study site. However, none of these factors appears to explain more than a modest amount of the total variance in acorn production; individual variation among trees uncorrelated with size remains the largest source of differences in acorn productivity within the community.

Second, oak species in central coastal California tend to produce crops asynchronously (Carmen et al. 1987). Because of this, the coefficient of variation in annual crop size within a local area decreases with increasing species diversity, as suggested by Bock and Bock (1974). On a community-wide basis, total crop failures are rare. However, on a local geographic scale such as the sub-areas considered here, crop failures can still occur and have significantly detrimental effects on animal populations, forcing local abandonment by species with limited home ranges

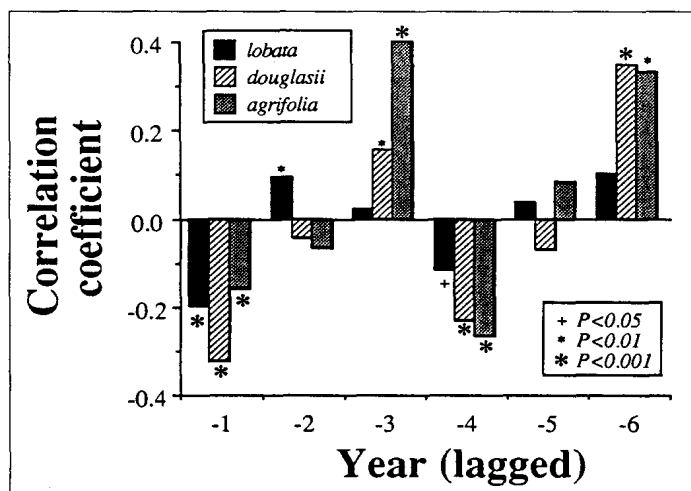


Figure 4—Average autocorrelations of the acorn crop score for each individual of the three species requiring one year to mature acorns with the scores for the same individuals one to six years earlier. Significance values are based on two-tailed binomial tests (see text).

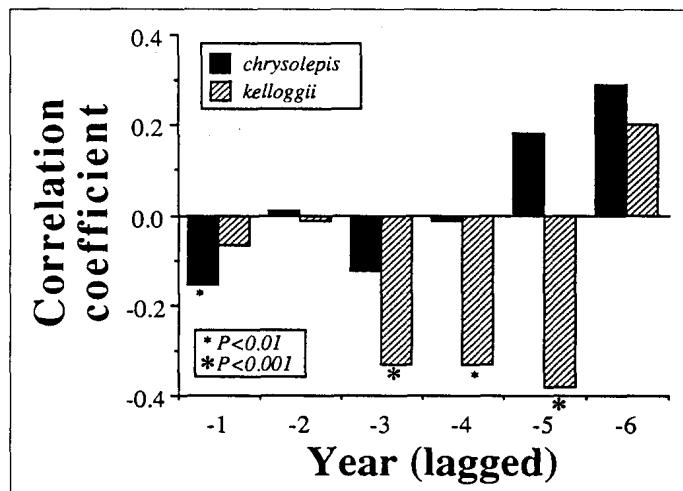


Figure 5—Average autocorrelations of the acorn crop score for each individual of the two species requiring two years to mature acorns with the scores for the same individuals one to six years earlier. Significance values as in figure 4.

such as scrub jays (*Aphelocoma coerulescens*) and acorn woodpeckers (*Melanerpes formicivorus*), both of which are highly dependent on annual acorn crop production (Carmen in press, Hannon et al. 1987). Such disasters are more likely to occur in local areas with fewer species of oaks.

Third, contrary to the findings of Sharp and Sprague (1967) working in eastern oak forests, we found little evidence for an effect of weather on mean acorn productivity for any of the species, with the possible exceptions of *Q. chrysolepis* and *Q. kelloggii*. Extrinsic factors related to differences among sub-areas significantly influenced crop size, but exactly what these factors may be remain to be identified.

Fourth, intrinsic factors, especially those related to prior reproductive effort, are important determinants of crop size within individuals. Significant inverse autocorrelations between the crops in successive years were identified for all species except *Q. kelloggii*. Distinct three-year cycles in acorn production are evident in *Q. douglasii* and *Q. agrifolia*, while possible six-year cycles are present in *Q. chrysolepis* and *Q. kelloggii*. In addition, *Q. lobata* exhibited a possible two- to three-year cycle. Thus, all five species appear to exhibit masting cycles, although not of the same length.

Masting cycles in California oaks have not, to our knowledge, been identified previously, although similar patterns have been found for several eastern species by Sork (1990). Two common hypotheses for the evolution of mast seeding are resource matching and predator satiation (Silvertown 1980). A complete evaluation of these competing hypotheses is beyond the scope of this paper. However, the predator satiation hypothesis predicts high synchrony among species within the population and that good masting should not occur in successive years. The autocorrelation between the acorn crop in year x and that in year $x-1$ is negative for all five species (figure 1), as predicted by the predator satiation hypothesis. Nonetheless, neither of these predictions are strongly upheld in our population: successive masting years do occur, as shown by *Q. agrifolia* in 1980, 1981, and 1982 (figure 1), and asynchrony among species leads to relatively constant availability of acorns on a community-wide level (figure 2). The resource matching hypothesis suggests that annual reproductive investment is proportional to the variable level of available resources, and thus predicts synchrony with some important environmental cue such as rainfall or temperature. Although an exhaustive analysis is yet to be performed, no such correlation appears forthcoming, and the lack of synchrony between species further argues against some common resource influencing crop size in our study site.

Recently, Norton and Kelly (1988) have proposed several alternative hypotheses for masting cycles related to "economies of scale" by which a few large episodes of reproduction are more efficient than many smaller ones. Hypotheses invoking such economies of scale include the predator satiation hypothesis already mentioned and several others, including wind pollination and the attraction of generalist animal seed dispersers. Both are potentially applicable to oaks, which are both wind pollinated and whose seeds are dispersed by generalists such as scrub jays (Grinnell 1936). A full discussion must be left for the future.

Our study is beginning to yield concrete conclusions relevant to the determination of acorn crop size within one area. A variety of questions concerning the reproductive strategies of California oaks remain. Is there a tradeoff between vegetative growth and reproductive effort? Are there genetic differences among individuals correlating with overall reproductive effort or masting patterns? What are the geographic patterns of acorn crop production on a larger scale? We have initiated studies addressing the last of these questions by adding study sites approximately 160 km north (Jasper Ridge, Santa Clara County, California) and 200 km south (Poza, San Luis Obispo County), each of which contain three of the same oak species found at our Hastings Reservation study site. We also hope to acquire data in the future not only extending our crop data but also examining growth patterns of our study trees based on growth rings and genetic correlates based on protein polymorphisms. Considered in concert, these data should eventually allow us to identify the factors determining the reproductive strategies of oaks, thereby yielding more enlightened conservation methods.

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