Estimating acorn crops using visual surveys

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We describe a visual survey technique for evaluating acorn production. In contrast with previously proposed methods, our technique yields ratio-level data on annual productivity that are analyzable with standard statistics and, by sampling the same trees each year, data on the reproductive patterns of individual trees. We compared this technique with two independent sets of acorn-trap data acquired on oaks of three species at Hastings Reservation in central coastal California. Correlations between acorns counted by the visual surveys and collected from acorn traps under the same trees were significant for all three species. Most scatter in the data appeared to be attributable to three causes: (1) sampling error, especially among trees with very small crops, (2) finite counting speed, leading to a lack of discrimination among trees with very large crops by the visual surveys, and (3) arboreal acorn removal by animals. This latter factor can be particularly large, rendering visual surveys more reliable than the use of traps. Furthermore, only the high efficiency of visual surveys allows for the practical assessment of samples large enough to accommodate high within-population variation and detect widespread geographic variation in acorn production. Visual surveys offer a method of assessing the fruit or cone crops of many hardwood and conifer species that is not only more efficient but also more accurate than the use of traps.

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Une technique visuelle d'étude est décrite afin d'évaluer la production de glands. Comparativement aux méthodes proposées précédemment, cette technique permet d'obtenir des données de proportions sur la productivité annuelle, qui peuvent être analysées à l'aide de méthodes statistiques standards. De plus, cette technique permet d'obtenir des données sur les patrons de reproduction pour chaque arbre, en échantillonnant les mêmes arbres à chaque année. Les données découlant de l'usage de cette technique sont comparées à deux ensembles indépendants de données découlant de la technique de piégeage des glands. Ces comparaisons ont été effectuées à partir de chênes de trois espèces situés à la Réserve de Hastings, au centre de la côte californienne. Pour les trois espèces, les corrélations étaient significatives entre le nombre de glands estimé par l'étude visuelle et celui estimé par l'usage de pièges à glands placés au-dessous des mêmes arbres. La dispersion observée dans les données est apparue attribuable à trois facteurs : (1) l'erreur d'échantillonnage, particulièrement chez les arbres affichant une faible production semencière; (2) la vitesse limite de comptage lors de l'étude visuelle, amenant un manque de discrimination chez les arbres affichant une forte production semencière; et (3) la récolte de glands dans les arbres par les animaux. Ce dernier facteur peut produire un biais particulièrement important, rendant l'évaluation visuelle plus faible que l'usage de pièges. De plus, seule la plus grande efficacité de l'étude visuelle permet l'évaluation pratique d'échantillons assez larges pour tenir compte de la variation intra-population élevée et pour détecter des patrons de variation géographique sur de grandes étendues dans la production de glands. Les études visuelles constituent une méthode d'évaluation de la productivité semencière pour plusieurs espèces feuillues et conifériennes qui est non seulement plus efficace, mais aussi plus précise que l'utilisation de pièges.

[Traduit par la Rédaction]

Introduction

Despite decades of attention from wildlife managers and forest researchers, there is no consensus as to the best method of measuring forest seed production. This is unfortunate, because knowing the patterns of seed production for individual trees and for forest populations as a whole is important for a variety of purposes, including understanding the reproductive strategies of trees, predicting wildlife population sizes, and facilitating forest regeneration. A fast, reliable method for determining the size of forest seed crops would

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greatly aid the acquisition of data needed to solve many of the puzzles presented by the complex fruit-, cone-, and seed-production patterns of many forest trees.

Sampling is particularly challenging for many oak species. Large individual size makes complete seed counts unfeasible, while large within-population variation and among-population differences in acorn production make large samples necessary to estimate overall production. Ground or quadrat counts, used in a few studies, are both labor intensive and subject to considerable error depending on the interval at which quadrats are checked and the presence of ground predators such as deer, cattle, mice, and gophers (Gysel 1956). Traps, used in the majority of studies of acorn production (e.g., Downs 1944; Downs and McQuilkin 1944; Burns et al. 1954; Christisen and Korschgen 1955; Goodrum et al. 1971; Griffin 1976; Feret et al. 1982), are more convenient yet suffer from at least two disadvantages: (1) because several traps must be placed under each tree and traps must be checked frequently during the acorn fall period, they are labor intensive; (2) arboreal acorn removal by animals can be appreciable or even complete depending on the size of the acorn crop produced by both the tree being measured and other trees in the area (Christisen and Korschgen 1955). Thus, although traps may offer a viable means of measuring the number of acorns reaching the ground, they may not yield an accurate measure of overall acorn productivity.

These difficulties have helped spur recent interest in alternative sampling methods, particularly visual surveys. Visual surveys have been proposed by Graves (1980) for oaks and more recently by McDonald (1992), who tested the accuracy of a rating system used primarily for conifers with seed-trap data and found a high correlation between cone production and cone-crop ratings for ponderosa pine (*Pinus ponderosa* Dougl. ex Laws. var. *ponderosa*) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Being based on a rating system, the methods proposed by these authors yield categorical-level data on fruit or cone crop size, thus limiting quantitative analysis and statistical testing. Also, both methods focused on overall production patterns in the population to the exclusion of data on individual trees.

Here we describe a modification of the visual survey method proposed by Graves (1980) that we have used since 1980 to quantify acorn production patterns of individual oak trees at Hastings Reservation in central coastal California. We compared this method with acorn-trap data collected for a small sample of valley oaks (*Quercus lobata* Née) over a 12-year period and a larger number of trees of three species over 2 years. We also determined the sample sizes necessary to accurately estimate overall crop sizes in our population by means of randomization trials.

Study site

The study was conducted between 1980 and 1993 at Hastings Reservation, a 900-ha reserve located in the Santa Lucia Mountains of central coastal California, approximately 42 km inland from Monterey. Elevation at the study site ranges from 460 to 950 m. This area experiences a Mediterranean climate, in which virtually no rain falls between June and October. Annual rainfall ranges from 26.1 to 111.2 cm, with a 50-year mean of 55 cm. In all areas of the study site oaks are the dominant genus. Five species are common, but only three are widespread throughout the site: valley oaks, blue oaks (*Quercus douglasii* Hook. & Arn.), and coast live oaks (*Quercus agrifolia* Née). These are joined locally, mostly at higher elevations, by canyon live oaks (*Quercus chrysolepis* Liebm.) and California black oaks (*Quercus kelloggii* Newb.).

Methods

Visual surveys

Starting in 1980, we tagged 250 individual oaks, including 87 *Q. lobata*, 57 *Q. douglasii*, 63 *Q. agrifolia*, 21 *Q. kelloggii*, 21 *Q. chrysolepis*, and one obvious *Q. lobata* × *Q. douglasii* hybrid. Trees chosen were mature, often large individuals generally located in relatively open stands. Trees were all within 3.5 km of each other but otherwise were arbitrarily chosen.

Each year, between mid-September and early October at the height of the acorn crop just prior to acorn fall, we visually estimated the acorn crop of each tree. The sampling protocol was as follows: two observers stationed near the focal tree sequentially scanned randomly chosen areas of the crown and counted as many apparently viable acorns as possible within 15 s, using either the naked eye (if the section being sampled was close to the ground) or, more commonly, binoculars. Because fruiting may vary with exposure (Lewis 1992), observers chose different sections of the crown. The total number of acorns counted by both observers was added to yield the number of acorns counted per 30 s, which was then log transformed ($\ln[x + 1]$) to reduce the correlation between the mean and variance (see below). At least one of the original observers participated in the counts each year since the study was initiated.

After performing the acorn counts and spending up to several additional minutes visually surveying the tree, the observers negotiated a categorical score between 0 and 4 describing the overall size of the crop for that tree. Categories were modified from the scale proposed by Graves (1980). These categorical measures are highly correlated with the acorn counts (of the 67 species × year data sets with non-zero values through 1993, the Spearman rank correlation coefficient (r_s) between the acorn counts and categorical score was >0.9 for 61 and significant at $P < 0.001$ for all 67). However, although the scores have proved occasionally useful, they do not allow for as wide a range of statistical analyses as the acorn counts and are not considered further here.

Seed traps

We obtained data from two independent sets of acorn traps. The first set (hereafter referred to as acorn traps) was from four large, mature *Q. lobata* (eight trees in 1992 and 1993) and was sampled with plastic garbage bags held in place by hogwire frames. Each trap was 0.25 m^2 in area and permanently located around the tree about halfway between the trunk and the edge of the tree's crown. Four traps per tree were used. Traps were checked at weekly intervals throughout the period of acorn fall, and the total number of acorns caught was summed for all traps for a given tree over the season.

The second acorn-trap data set (hereafter referred to as litter buckets) came from 40 of the sampled trees (39 in 1992) under each of which we placed three 0.2-m^2 plastic litter-fall buckets. Samples included 14 *Q. lobata* (13 in 1992) and 13 each of *Q. douglasii* and *Q. agrifolia*. Trees were chosen so as to encompass the range in quality observed within the population based on our long-term data on the production patterns of trees in the complete sample of trees. Buckets were placed under the crown by dividing the crown into three areas radiating out from the trunk and placing one bucket in each area at a randomly determined distance between the trunk and the drip line. Buckets were collected once a month and the contents were sorted into acorns and acorn caps. We used only material collected between August and December; including acorns collected later than December in the 1992–1993 season did not significantly alter the correlations. Data were log transformed prior to analysis.

To further investigate the relationship between acorns collected in traps and those counted in the visual surveys, we measured the 40 trees sampled by litter buckets in September 1993.

We approximated crown area by assuming that the tree encompassed the area of a circle whose diameter was the average of the length of three cross sections taken at 60° angles from each other directly through the trunk and extended out to the drip line on either side of the tree. We then approximated tree crown volume by assuming that the tree was a cylinder whose base was the area already determined and whose height was the average of three clinometer readings: the first taken in the center directly above the main trunk, the second taken halfway between the center and the left side of the tree, and the third taken halfway between the center and the right side of the tree. Finally, we estimated total wood volume of the tree including bark using the weight equations for the three species provided by Pillsbury (1980).

Estimating minimum sample sizes

We estimated the number of trees necessary to accurately estimate the overall acorn crop for *Q. lobata* as follows. First, we calculated the mean crop for each year by averaging the log-transformed visual survey counts for all 86 trees that survived for the entire 14 years of the study. We then conducted trials by randomly choosing subsamples of N trees for each year, where N ranged from 1 to 50. Subsampling was conducted in two ways: (1) new trees were chosen randomly each year (nonrepeated sampling) and (2) trees were chosen once and data from those trees were used for all years (repeated sampling). Log-transformed visual survey counts were averaged for each year using the subsamples and compared with the values from the complete data set by calculating the Pearson product-moment correlation coefficient between them. For subsamples of each size, we performed 500 trials and then (1) averaged the product-moment correlation coefficients for all trials and (2) determined the proportion of trials yielding r-values that were significantly greater than zero at the $P < 0.01$ level. To determine the effect of having data from different numbers of years, we performed four sets of trials using (1) all 14 years of our data set, (2) the first 10 years of our data set, (3) only 7 years of data, and (4) only 5 years of data. These last two sets of trials were replicated using the first and second sets of 7 years of data (in case 3) and the first and second sets of 5 years of data (in case 4). Results from these replicates were averaged.

Results

Correlation between traps and visual surveys

Using the complete sample of 56 trees (4 trees for each of 12 years and 4 additional trees in 1992 and 1993), there was a strong, highly significant ($P < 0.0001$) relationship between the number of acorns caught in the acorn traps and the visual surveys (Fig. 1*a*). However, there are several sources of nonlinearity, seen more readily in a plot of the standardized residuals (Fig. 1*b*).

We have drawn lines at 0 and ±0.5 standard deviations in Fig. 1*b* to emphasize the areas where values tended to deviate from expected. Note that positive residuals tended to occur when few and when many acorns were counted, whereas negative residuals occurred throughout the observed range of acorn production.

Regressions of the total number of acorns and the number of acorn caps collected in the litter buckets versus the number of acorns counted in the visual surveys for the three different species are graphed in Fig. 2; data for the two years are combined. All were significant; however, the correlations were much better for *Q. lobata* and *Q. douglasii* than for *Q. agrifolia*. Controlling for crown area, crown volume, or total wood volume did not improve correlations between the litter bucket and visual survey data sets for any of the species (Table 1). In all cases, the number of acorns collected in litter buckets was highly correlated with the number of caps collected, although the number of caps was generally greater (Table 2; Fig. 2).

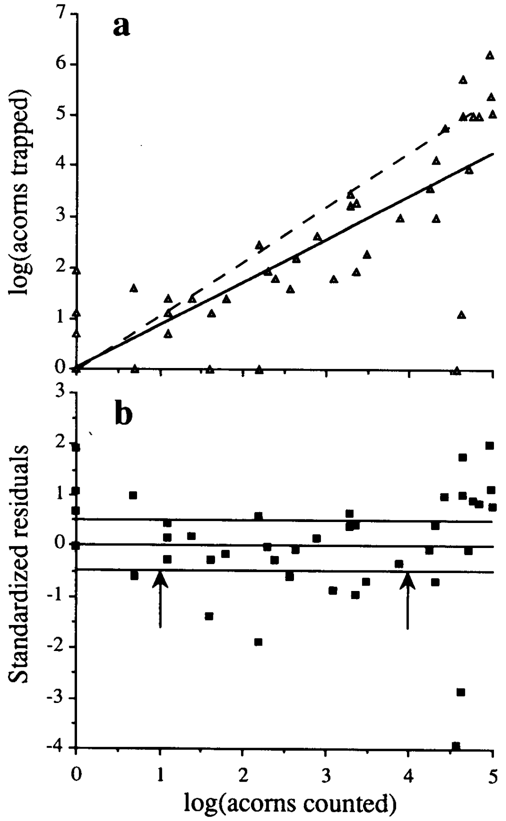

FIG. 1. (*a*) The relationship between the number of acorns caught in traps and the number counted in visual surveys under four individual *Q. lobata* (eight in 1992 and 1993) sampled in 1980–1989 and 1992–1993. Both variables are log transformed. The solid line is for a linear regression ($y = 0.85x + 0.02$; $R^2 = 0.72$, $F_{[1,54]} = 139$, $P < 0.001$), while the broken line estimates the true relationship between the variables (see text). (*b*) Standardized residuals for the regression shown in Fig. 1*a*. Lines are drawn at zero and at ±0.5 SD. Arrows represent arbitrary breaks between trees for which we counted few (less than three), intermediate numbers of, and many (54 or more) acorns during visual surveys.

Estimation of sample sizes

The question addressed by the randomization tests was as follows: Given the variation, both within and among year, in acorn crops observed in our population, how many trees must be sampled to yield a good estimate of overall crop size? Two subquestions were also addressed: (1) How does the necessary sample size vary depending on the number of years of data available? (2) Is it better to sample different trees each year (nonrepeated sampling) or the same trees (repeated sampling)?

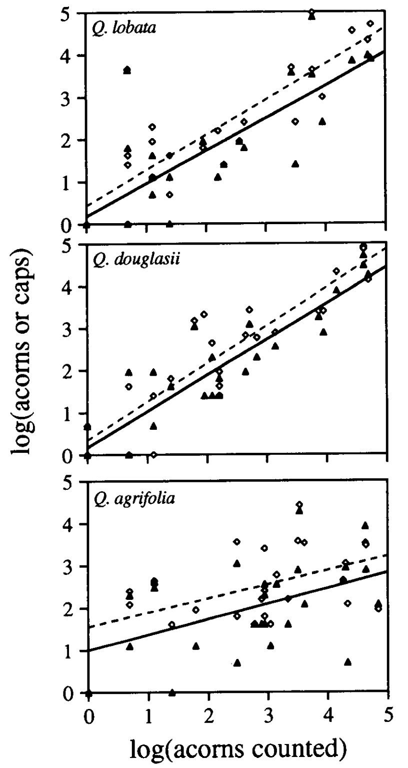

FIG. 2. The relationship between the total number of acorns (solid lines; ▲) and acorn caps (dotted lines; ◇) caught in litterfall traps and the number of acorns counted in visual surveys for three species of oaks. Variables are log transformed. Sample sizes: *Q. lobata*, 13 trees in 1992; 14 in 1993; *Q. douglasii* and *Q. agrifolia*, 13 trees in both 1992 and 1993. Regressions: *Quercus lobata*, $y = 0.77x + 0.18$; $R^2 = 0.63$, $F_{[1,25]} = 42$, $P < 0.001$ (acorns); $y = 0.84x + 0.42$; $R^2 = 0.72$, $F_{[1,25]} = 63$, $P < 0.001$ (caps). *Quercus douglasii*, $y = 0.85x + 0.17$; $R^2 = 0.82$, $F_{[1,24]} = 110$, $P < 0.001$ (acorns); $y = 0.90x + 0.34$; $R^2 = 0.81$, $F_{[1,24]} = 103$, $P < 0.001$ (caps). *Quercus agrifolia*, $y = 0.37x + 1.00$; $R^2 = 0.21$, $F_{[1,24]} = 6.4$, $P < 0.05$ (acorns); $y = 0.33x + 1.56$; $R^2 = 0.21$, $F_{[1,24]} = 7.5$, $P < 0.05$ (caps).

The dependence of sample size on the number of years of data is shown in Fig. 3. The figure graphs data using the nonrepeated sampling scheme, but the results are qualitatively identical if the same trees are used each year. Mean r-values were independent of the number of years of data (Fig. 3*a*), while the percent of trials in which the among-year r-value between the full sample of 86 trees and the subsample was significant at the 0.01 level was highly dependent on the number of years (Fig. 3*b*). To have a 95% chance of obtaining a correlation coefficient significant at the 0.01 level, about 45 trees are needed when there are only 5 years of data, while only 4 trees are needed when there are 14 years of data.

Figure 4 compares the results of the trials using nonrepeated and repeated sampling with 5 years of data; results are similar with increased number of years. Mean r-values are always higher when the same trees are used (repeated sampling) than when different trees are chosen each year (nonrepeated sampling). To be 95% confident that the among-year r-value between the subsample and the complete sample will be significant at the 0.01 level, only about 25 trees are needed if repeated sampling is employed compared with 45 trees if nonrepeated sampling is used.

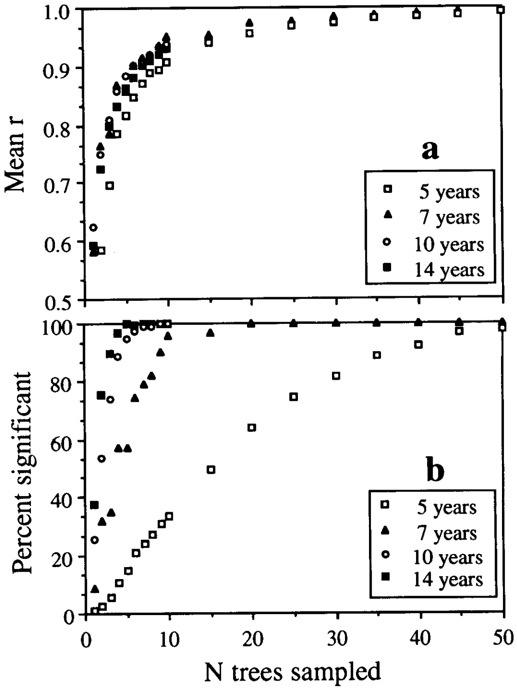

FIG. 3. Results of randomization trials used to estimate the number of trees needed to yield a good among-year correlation between the mean acorn crop of the subsample and the complete sample of 86 *Q. lobata*. Trees were randomly sampled each year (nonrepeated sampling). (*a*) The mean product–moment correlation and (*b*) percent trials significant at $P < 0.01$ for 500 trials in which the number of trees subsampled is given on the x-axis. Subsamples of 5, 7, 10, and 14 years are plotted.

Discussion

We found significantly positive correlations between estimates of acorn crop size for individual trees based on seed-trap data and visual survey data for three species of oaks. Relationships were stronger for *Q. lobata* and *Q. douglasii* than for *Q. agrifolia*. For *Q. lobata*, correlations were highly significant for each of two independent data sets, one involving a small number of trees over many years (Fig. 1) and a second involving a larger number of trees over 2 years (Fig. 2).

What causes the discrepancies between acorn production estimated by seed traps and visual surveys? The acorn traps, covering a large number of years for a few trees, provide

TABLE 1. Product–moment correlations between total number of acorns and acorn caps collected in litter buckets and the number of acorns counted in visual surveys for trees studied in 1992 and 1993

	No controls	Controlling for:		
		crown area	crown vol.	wood vol.
Quercus lobata				
Acorns	0.79***	0.77***	0.75***	0.71***
Caps	0.85***	0.83***	0.81***	0.75***
Quercus douglasii				
Acorns	0.91***	0.81***	0.79***	0.76***
Caps	0.90***	0.83***	0.82***	0.82***
Quercus agrifolia				
Acorns	0.46*	0.40*	0.42*	0.41*
Caps	0.49*	0.42*	0.44*	0.45*

NOTE: Controls were performed by dividing the number of acorns or caps collected by estimated crown area, crown volume, and total wood volume (see text). All variables were log transformed; $N = 26$ trees (13 in each year) for all species except *Q. lobata*, for which $N = 27$ (13 in 1992 and 14 in 1993).

*$P < 0.05$ (two tailed).

***$P < 0.001$ (two tailed).

TABLE 2. Comparison of acorns and acorn caps collected from litter buckets in 1992 and 1993

	Cases in which:			
	no. of acorns < no. of caps	no. of caps < no. of acorns	z-value	r_s between N acorns and N caps
Quercus lobata	18	2	3.4***	0.93***
Quercus douglasii	18	6	2.3*	0.88***
Quercus agrifolia	19	4	2.9**	0.86***

NOTE: z-values are from binomial tests. Sample sizes are as in Table 1.

*$P < 0.05$ (two tailed).

**$P < 0.01$ (two tailed).

***$P < 0.001$ (two tailed).

the clearest clues to an answer. Trees in which relatively few acorns were counted compared with trapped (large positive residuals) were almost always trees for which either no acorns or very many acorns were counted (Fig. 1*b*). Cases in which no acorns were counted but a few were collected in the traps are most likely attributable to minor sampling errors magnified due to the small number of acorns produced. In general we predict that such errors will be smaller for visual surveys than for seed traps, which at most sample only a tiny fraction of the total crown area. For example, we estimated the average crown area to be 200 m^2 for the 14 valley oaks sampled by litter buckets. Given that we used three 0.2-m^2 buckets under each tree, on average only 0.3% of the total crown area was sampled. In contrast, we estimate that we visually inspect at least 25 m^2 of crown in the course of our visual surveys, or about 13% of the total crown area.

The large number of positive residuals among trees for which many acorns were counted is most likely a shortcoming of our visual survey technique. When a tree has a particularly heavy crop, the number of acorns one observer can count in 15 s is limited not by crop size but by counting speed. Consequently, our visual surveys are unable to discriminate among the crop sizes of trees with more acorns than can be counted in this relatively short time, leading to a block of highly productive trees with large positive residuals for the number of acorns trapped (Fig. 1*b*). In most years such trees were uncommon and did not pose a major problem. However, if many trees have large crops and it is important to discriminate among them, a longer counting period might "stretch out" the scale in the very large crop-size region and help to minimize this error. An analogous modification might be needed in order to discriminate among trees with very small crop sizes or those that produce very small fruits that are difficult to see.

In contrast with the positive residuals, large negative residuals occurred throughout the full range of crop sizes as measured by the visual surveys (Fig. 1*b*). The most likely explanation for most of these errors is arboreal acorn removal by animals, particularly scrub jays (*Aphelocoma coerulescens*), American crows (*Corvus brachyrhynchos*), acorn woodpeckers (*Melanerpes formicivorus*), California ground squirrels (*Spermophilus beecheyi*), and dusky-footed woodrats (*Neotoma fuscipes*). All five of these species are common at our study site, and any is capable of removing a large proportion of acorns from a tree. Such depredation could readily result in cases where few or no acorns are collected in traps even though many were counted during the visual survey (Fig. 1*a*).

The litter buckets also yielded significant correlations between acorns counted and trapped for each of three species of oaks (Table 1; Fig. 2). Several results from these analyses are of interest. First, more acorn caps than acorns were collected from most trees, as expected if arboreal predation of acorns is important (Table 2). However, correlations were about the same between the visual surveys and both the

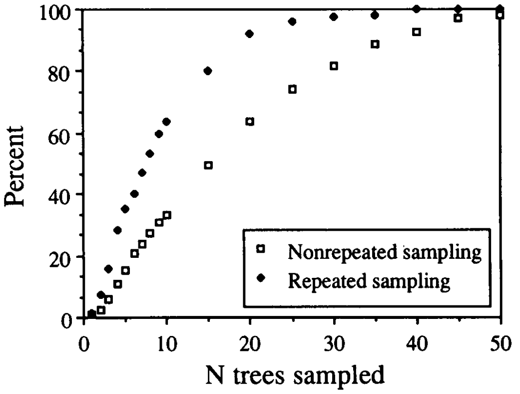

FIG. 4. The percent of trials significant at $P < 0.01$ as a function of the number of trees sampled with 5 years of data, assuming that new trees are sampled each year (nonrepeated sampling) and the same trees are sampled each year (repeated sampling).

number of acorns and the number of acorn caps collected in the buckets (Table 1). Second, controlling for estimated crown area, volume, or total wood volume did not improve the relationships for any of the three species. This suggests that the visual surveys were not biased by tree size and that they measure the relative density of acorns within a tree, as do most of the intensive survey methods such as trapping.

Third, correlations between the visual surveys and acorns trapped were much better for the two deciduous oaks (*Q. lobata* and *Q. douglasii*) than for the evergreen *Q. agrifolia*. There are at least two possible reasons for this. First, *Q. agrifolia* foliage is often very dense and acorns can be hard to see, making visual surveys less reliable than in the other two species. More important is the tendency for *Q. agrifolia* acorns to remain on the tree far longer than in the other two species. In general, both *Q. lobata* and *Q. douglasii* drop all their acorns by early November, while *Q. agrifolia* may continue to retain acorns as late as the following June (Carmen et al. 1987). This phenological difference renders *Q. agrifolia* acorns vulnerable to arboreal predators for a far longer period and ultimately undermines the ability of acorn traps to reliably estimate crop size.

We envision four circumstances in which traps may be comparable or even preferable to visual surveys: (1) if the number of fruits or cones falling to the ground, rather than the number produced by the tree, is of interest; e.g., this would be the case if one wished to measure food availability to ground predators or the number of fruits reaching the ground and potentially germinating; (2) if fruits or cones are hard to see, in which case visual surveys may systematically underestimate crop size; (3) if there is little among-tree variation in fruit production and all trees are good producers, in which case traps, but not visual surveys, might permit discrimination among the crop sizes more readily because of the limitation of counting speed; however, as mentioned above, an alternative solution to this problem might be to extend the time fruits or cones are counted beyond the short time limit used in our protocol; (4) in stands with complete canopy closure where it is difficult to discriminate the crowns of individual trees. Visual surveys can still be performed in at least some closed-canopy forests with minor modifications, such as using spotting scopes, rather than the naked eye or binoculars, to survey trees (W.J. Carmen and J.F. Lynch, personal communication). Thus, under many conditions, the much larger crown volume that can be sampled combined with the possibility of removal by arboreal predators will render visual surveys more accurate than seed traps.

Seasonal timing of visual surveys is important. If performed too early, fruits may be hard to see, while seedfall and arboreal removal by animals make it important not to perform surveys late in the season. Because of annual differences in phenology, the optimal timing of visual surveys may vary from one year to the next, requiring periodic checking of the crop until fruits are nearly ripe. Furthermore, phenological differences among trees and different rates of fruit maturation may make visual surveys difficult. However, our experience suggests that visual surveys are flexible enough to withstand most of the phenological variation observed in central coastal California and still yield good results. Acorns can still be surveyed reasonably well prior to being fully ripe, while fresh caps can be counted along with acorns if surveys are conducted after some seedfall or harvesting has taken place.

Contrary to the visual survey techniques proposed by prior workers (Graves 1980; McDonald 1992), the method described here yields ratio-level data appropriate for many statistical analyses. Although values, like fruit production itself, will rarely be normally distributed, logarithmic transformation significantly reduces the dependence of variance on the mean and will usually result in data that are approximately homoscedastic. For example, when our visual surveys for 86 valley oaks collected over 14 years at Hastings Reservation are divided into two groups (low producers in which 10 or fewer acorns were counted and high producers in which 11 or more were counted), the variances in the counts for the two groups are 6.3 and 1729.5; significantly different ($P < 0.001$) by both Cochran's C and Bartlett–Box F tests for homogeneity of variance (Norusis 1986). Variances of the log-transformed counts for the same two groups are 0.616 and 0.566; not significantly different ($P > 0.25$) by these tests.

Visual surveys do not directly yield data on the absolute (or total) number of fruits produced by a tree or in the habitat, but an approximation of these values can be derived by simultaneously monitoring traps randomly set out under a subset of trees, measuring the number of fruits falling per unit area, and then using the regression between the two measures to estimate the absolute size of the crop (measured as seeds per unit area) of trees based on the visual surveys. However, this procedure is only as accurate as the trap data, and thus is dependent on traps being assiduously collected and on there being little arboreal predation. Counting caps rather than seeds controls for the latter problem, at least in part.

If arboreal removal is common, as was the case in our study, it is necessary to determine two points, one for crop failures and the other for large crops, in order to estimate the true relationship between the number of fruits counted on visual surveys and the number trapped. This is done in Fig. 1*a* for the acorn traps. The first point is easy: both techniques should agree when a tree produces no acorns and thus the *y*-intercept of the regression between these measures must be zero.

The second point is more difficult. As discussed above, arboreal removal should often result in visual survey counts relatively greater than those of the traps, except when the crop is very small (because of sampling error and the impossibility of counting fewer than zero acorns in a tree) and when the crop is very large (because of the limitation in counting speed and the greater likelihood of predator satiation when crops are very large). Thus, if data are available from years of high acorn production, the correlation of acorns counted versus acorns (or caps) trapped should yield a cluster of points in the upper right-hand corner of the plot, as in Fig. 1*a*. A reasonable guess for a point representing the true relationship between acorns counted and trapped for large crop sizes is somewhere near the lower end of this cluster of points. Assuming linearity, the true relationship between these measures of crop size is then estimated by the dotted line in Fig. 1*a*. This line can be used not only to calibrate the visual survey data with absolute crop size but also to estimate the extent to which individual trees suffer arboreal acorn removal by subtracting the observed number of acorns collected from the traps from the number predicted by the dotted line. Points lying on or above the dotted line represent trees for which there was negligible arboreal predation.

The visual survey technique suggested here also differs from those previously proposed by measuring crop size on the same individuals year after year (repeated sampling) rather than arbitrarily choosing new trees each time crops are sampled (nonrepeated sampling). There are at least two advantages to the former method. First, information on the production patterns of individual trees is acquired along with data on overall annual productivity of the site. The recent finding that many oaks produce acorns cyclically at the individual level (Sork et al. 1993; Koenig et al. 1994) proves that such analyses can be illuminating. Second, by using the same individuals each year, the component of among-year variation due to differences in individual quality is reduced, making among-year comparisons more accurate and decreasing the sample size of trees necessary to accurately estimate overall productivity (Fig. 4).

Even if the same trees are not used each year, visual surveys provide a relatively quick and accurate means of assessing crop size within and between sites. As shown in Fig. 3*b*, sample sizes needed to confidently determine relative overall productivity from year to year are small if the study continues for many years (7+), allowing researchers to survey more species or more sites than would be possible using traps. For studies of shorter duration, visual surveys will usually provide the only reasonable means of acquiring samples large enough to confidently estimate overall fruit or cone production.

We estimate the difference in the efficiency of visual surveys compared with traps as follows. In general, two people are able to visually survey 250 oaks at Hastings Reservation in about 15 h, for a total of 30 person-hours of work, or about 0.12 h/tree. In contrast, monitoring three acorn traps set up under eight valley oaks (24 traps total) requires approximately 10 h to set up initially followed by 2 h each year to put the bags in place and a minimum of 1.5 h per week to collect and sort acorns for a period of at least 10 weeks. Thus, in the first year, about 27 h of effort (3.3 h/tree) is required followed by 17 h (2.1 h/tree) each year thereafter. Based on these estimates, visual surveys are on the order of 16 to 25 times faster than acorn traps, even using our conservative protocol involving two observers for the visual surveys. This increased efficiency opens up the possibility of far more thorough monitoring of acorn production on whatever scale, geographic or otherwise, that is of interest.

Our findings, in conjunction with work by McDonald (1992), demonstrate that visual surveys offer a quick and accurate means of estimating the fruit or cone crops of a variety of trees. Counting fruits rather than categorizing the crops of trees is preferable because it allows for greater statistical versatility, while surveying the same trees each year reduces among-year variance and allows for analyses of fruit production patterns by individual trees. Wider use of such techniques offers not only the opportunity to better understand the reproductive strategies of forest trees but also a more accurate means of understanding changes in wildlife populations. Visual surveys of fruit or cone crops deserve to be considered as part of any comprehensive program investigating the ecology or conservation of hardwood and conifer forests.

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Burns, P. Y., Christisen, D.M., and Nichols, J.M. 1954. Acorn production in the Missouri Ozarks. Mo. Agric. Exp. Stn. Bull. 611.

Carmen, W.J., Koenig, W.D., and Mumme, R.L. 1987. Acorn production by five species of oaks over a seven year period at the Hastings Reservation, Carmel Valley, California. *In* Proceedings of the Symposium on Multiple-use Management of California's Hardwood Resources. *Technical Coordinators*: T.R. Plumb and N.H. Pillsbury. USDA For. Serv. Gen. Tech. Rep. PSW-100. pp. 429–434.

Christisen, D.M., and Korschgen, L.J. 1955. Acorn yields and wildlife usage in Missouri. Trans. North Am. Wildl. Conf. **20**: 337–357.

Downs, A.A. 1944. Estimating acorn crops for wild life in the southern Appalachians. J. Wildl. Manage. **8**: 339–340.

Downs, A.A., and McQuilkin, W.E. 1944. Seed production of southern Appalachian oaks. J. For. **42**: 913–920.

Feret, P.P., Kreh, R.E., Merkle, S.A., and Oderwald, R.G. 1982. Flower abundance, premature acorn abscission, and acorn production in *Quercus alba* L. Bot. Gaz. **143**: 216–218.

Goodrum, P.D., Reid, V.H., and Boyd, C. 1971. Acorn yields, characteristics, and management criteria of oaks for wildlife. J. Wildl. Manage. **35**: 520–532.

Graves, W.C. 1980. Annual oak mast yields from visual estimates. *In* Proceedings of the Symposium on the Ecology, Management and Utilization of California Oaks. *Technical Coordinator*: T.R. Plumb. USDA For. Serv. Gen. Tech. Rep. PSW-44. pp. 270–274.

Griffin, J.R. 1976. Regeneration in *Quercus lobata* savannas, Santa Lucia Mountains, California. Am. Midl. Nat. **95**: 422–435.

Gysel, L.W. 1956. Measurement of acorn crops. For. Sci. **2**: 305–313.

Koenig, W.D., Mumme, R.L., Carmen, W.J., and Stanback, M.T. 1994. Acorn production by oaks in central coastal California: variation within and among years. Ecology, **75**: 99–109.

Lewis, V.R. 1992. Within-tree distribution of acorns infested by *Curculio occidentis* (Coleoptera: Curculionidae) and *Cydia latiferreana* (Lepidoptera: Tortricidae) on the coast live oak. Environ. Entomol. **21**: 975–982.

McDonald, P.M. 1992. Estimating seed crops of conifer and hardwood species. Can. J. For. Res. **22**: 832–838.

Norusis, M.J. 1986. SPSS/PC+. SPSS Inc., Chicago, Ill.

Pillsbury, N.H. 1980. Inventory and quantification of central coast hardwood resources in California. *In* Proceedings of the Symposium on the Ecology, Management and Utilization of California Oaks. *Technical Coordinator*: T.R. Plumb. USDA For. Serv. Gen. Tech. Rep. PSW-44. pp. 92–100.

Sork, V.J., Bramble, J., and Sexton, O. 1993. Ecology of mast-fruiting in three species of Missouri oaks, *Quercus alba*, *Quercus rubra*, and *Quercus velutina* (Fagaceae). Ecology, **74**: 528–541.