Arboreal Seed Removal and Insect Damage in Three California Oaks[1]

Walter D. Koenig,[2] Johannes M. H. Knops,[3] and William J. Carmen[4]

Abstract

We investigated arboreal removal and insect damage to acorns in an undisturbed oak woodland in central coastal California. Arboreal seed removal was determined for four to eight individual *Quercus lobata* trees over a period of 14 years by comparing visual estimates of the acorn crop with the number of acorns caught in seed traps. Insect damage was assessed by sampling acorns from trees of all three species of oaks common in the study site (*Quercus lobata, Q. douglasii,* and *Q. agrifolia*). Patterns were generally similar for both sets of data: more acorns, but a smaller proportion of the crop, were removed or damaged as the productivity of an individual tree increased. However, we found no evidence that trees outproducing local conspecifics attracted a disproportionate number of arboreal seed or insect predators. Acorn removal was not significantly correlated with population sizes of either California scrub-jays (*Aphelocoma coerulescens*) or acorn woodpeckers (*Melanerpes formicivorus*), two common arboreal seed removers that are also potentially important dispersal agents. These patterns are partially in accord with predator satiation, but not the attraction of seed dispersers, being an important factor potentially influencing the reproductive strategies of oaks in central coastal California.

Introduction

Patterns of seed production, including reproductive synchrony on a geographically large scale or masting (Kelly and Sork [In press]), Silvertown 1980), may be explained by two general hypotheses. First is resource matching, which proposes that masting is associated with years in which resources are more available, and second are economies of scale, which propose that synchrony arises from the potential energetic advantages to individuals within a population of investing more into reproduction synchronously every few years rather than less each year, given an overall constraint to the total level of reproductive effort (Norton and Kelly 1988).

Economies of scale include energetic advantages related to wind pollination (Norton and Kelly 1988, Smith and others 1990), predator satiation (Ims 1990a, 1990b; Janzen 1971), and the attraction of seed dispersers (Givnish 1980, Sork and others 1983). As traditionally envisioned, the importance of predator satiation is

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[2] Research Zoologist, Hastings Reservation and Museum of Vertebrate Zoology, University of California, Berkeley, 38601 E. Carmel Valley Road, Carmel Valley, CA 93924 (e-mail: wicker@uclink4.berkeley.edu)

[3] Assistant Professor, Department of Biological Sciences, University of Nebraska, 348 Manter Hall, Lincoln, NE 68588.

[4] Principal, 145 Eldridge Ave., Mill Valley, California 94941.

dependent on the ability of highly productive trees to overwhelm seed predators, thereby resulting in a negative correlation between the size of the seed crop and the proportion of seeds depredated (Norton and Kelly 1988). Selection for reproductive synchrony should be particularly intense depending on neighborhood effects, that is, the crop of a particular tree relative to the area as a whole (Sargent 1990). Trees outproducing the local area should suffer increased seed predation and there will be selection to synchronize reproductive effort within the population.

Alternatively, if the attraction of seed dispersers is important, trees should produce fruit in ways which differentially attract potential seed dispersers and lead to a relatively high proportion of seeds removed being cached rather than eaten. Thus, the optimal pattern of seed production for an individual tree depends on the potentially complex and generally unknown relationship between the proportion of seeds cached by animals, the efficiency with which cached seeds are recovered, the reproductive effort of an individual tree, and overall seed availability in a particular year. If neighborhood effects are strong, some trees should invest heavily in reproduction each year in order to outcompete other conspecifics and ensure the attraction of potential dispersal agents. On the other hand, an individual tree producing a large crop in a year when all other trees fail will presumably suffer heavy predation as animals attracted to the tree eat rather than cache most of the acorns they remove.

The expected result of these conflicting selection pressures is not likely to be straightforward (Ims 1990a). Presumably these competing considerations are likely to result in moderate to low reproductive synchrony (Koenig and others 1994a). With respect to the size of the acorn crop per se, we can expect a positive correlation between a tree’s seed crop and not only the number but also the proportion of acorns removed if productive trees successfully attract proportionately more dispersers than unproductive trees.

A third possibility is that primary seed predators are generalists switching from alternative food resources, in which case Ims (1990a, 1990b) has shown that the expected pattern of reproduction is one of asynchrony rather than synchrony. Given the vast array of both vertebrate and invertebrate acorn predators, it is thus not possible to confidently predict the optimal pattern of reproduction in response to predation in this system (Koenig and others 1994a). Consequently, we restrict ourselves to the more traditional form of predator satiation discussed above.

Invertebrate users of oaks (genus *Quercus*, family Fagaceae) are particularly extensive: as many as 5,000 insect species are associated with oaks in California, of which approximately 800 use some portion for food (Pavlik and others 1991). In addition, over 170 species of birds and mammals are dependent on oak habitats in California and nearly 100 species are known to feed on acorns in the United States, making *Quercus* one of the most important genera of woody plants to wildlife in North America (Barrett 1980, Christisen and Korschgen 1955, Martin and others 1951, Van Dersal 1940, Verner 1980). Given this impressive assemblage of animals, it is likely that predation is important to reproductive patterns of oaks. In return, oaks disperse their seeds largely by taking advantage of animals that fail to remove some proportion of acorns that they have moved and cached (Smith and Folmer 1972, Sork and others 1983). Particularly significant in this respect are jays (family Corvidae); birds of this family are common seed removers (Darley-Hill and Johnson 1981) and, since they store acorns in the ground, are excellent dispersal agents (Carmen [In press], Grinnell 1936, Vander Wall 1990).

This paper is one of a series devoted to understanding acorn production patterns of California oaks. Here we discuss the factors influencing arboreal acorn removal, primarily by birds, and predation on acorns, again prior to acorn fall, by insects; we do not discuss seed predation on sound acorns after they have fallen from the tree. We focus on three questions. First, what is the intensity of arboreal acorn removal and and of insect predation? Second, what factors influence the extent of these phenomena? Third, does the pattern of acorn removal and insect damage suggest an important role for either predator satiation or the attraction of seed dispersers in the evolution of oak reproductive patterns?

Methods

The study was conducted 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 during the summer and early fall (June-September). Annual rainfall ranges from 26.1 to 111.2 cm, with a 50-yr mean of 55 cm. In all areas of the study site oak (*Quercus*) is the dominant genus of tree. Five species are common, but only three are widespread throughout the site: *Quercus lobata* (valley oak), *Q. douglasii* (blue oak), and *Q. agrifolia* (coast live oak). These are joined locally, mostly at higher elevations, by *Q. chrysolepis* (canyon live oak) and *Q. kelloggii* (California black oak).

Arboreal Seed Removal

Eight large, mature *Quercus lobata* trees were used. Four, sampled from 1980-1989 and 1992-1996, were located on level ground in the floodplain about 0.5 km from the reserve headquarters, while the other four, sampled from 1992-1996 only, were located in an old field on a hill 0.75 km from headquarters.

For each tree, we estimated the extent of arboreal seed removal by comparing visual estimates of the acorn crop made prior to acorn fall with the number of acorns collected from seed traps. Visual estimates involved having two experienced observers scan different areas of each tree's canopy and count as many apparently viable acorns as possible in 15 seconds. Counts were made each autumn in September or early October at the height of the acorn crop prior to acorn fall. The total number of acorns counted by both observers was added to yield acorns counted per 30 seconds and then log-transformed to reduce the correlation between the mean and variance (Sokal and Rolf 1969). For further details on this survey method, see Koenig and others (1994b). Log-transformed values for the four (or eight) trees were averaged to estimate the mean crop of the focal trees for each year.

Acorn fall under each of the focal trees was sampled using seed traps consisting of plastic garbage bags held in place by hogwire frames. Each trap was approximately 0.25 m^{-2} in area and permanently located around the tree about half-way between the trunk to the edge of the tree's canopy. Each trap was assumed to sample an approximately equal volume of canopy. 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 summed for all traps for a given tree throughout the season.

Arboreal seed removal was estimated as follows. First, we plotted the relationship between the two measures of the acorn crop for the individual trees (figure 1). The expected number of acorns trapped was estimated from a line drawn from the origin to the point yielding a line of maximum slope (point A); the formula for this line is $y = 1.259\ x$, where y is the number of acorns trapped and x is the number of acorns counted (both log-transformed). This conservatively assumes that point A represents no seed removal and, given this assumption, the deviation of the other points from the line provides an estimate of the extent of arboreal seed removal. Values for the expected and observed numbers of acorns trapped were then back-transformed (to acorns m^{-2}), from which we estimated both the total number of acorns (per trap) that were apparently removed by arboreal seed predators (the "total" number of acorns removed) and the proportion of acorns produced that were removed by arboreal seed predators (the "relative proportion" of acorns removed). Values were then averaged within years to derive mean annual values. Trees and years in which no acorns were produced were excluded, since the number and proportion of acorns removed in such cases were indeterminate. This left samples for 61 trees over a period of 14 years (none of the trees sampled produced any acorns in 1983).

In addition to the focal trees, an additional 37 *Q. lobata* trees within 1 km of the focal trees were visually sampled at Hastings each autumn in order to assess the overall acorn crop. The average number of (log-transformed) acorns counted in these trees was used as a measure of the overall acorn crop. Results were not substantively changed if all sampled trees (including 25 *Q. douglasii* and 27 *Q. agrifolia*) within 1 km were used instead. Neighborhood effects, that is, the effect of local seed density on removal from individual trees (Sargent 1990) were investigated by comparing the estimated proportion of acorns removed from trees that outproduced an average tree in the full *Q. lobata* sample with those that produced fewer acorns than the full sample, based on the number of acorns counted per 30 seconds.

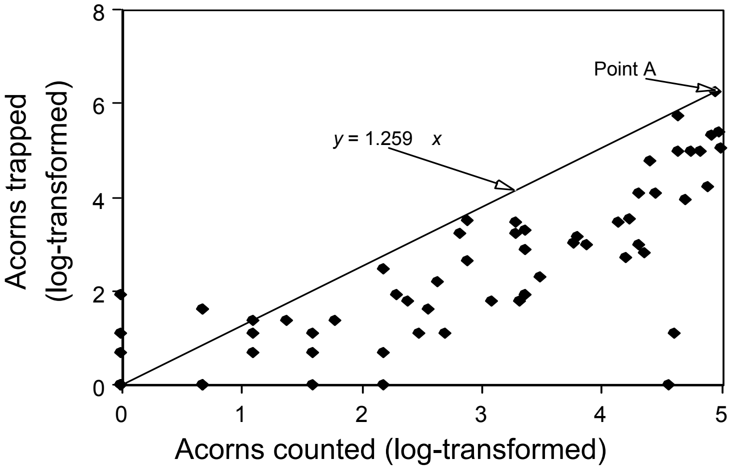

Figure 1—Relationship between the number of acorns counted by visual censusing per tree and the number caught in four 0.25-m^2 acorn traps; both variables are log transformed. Four *Quercus lobata* trees were measured for each of 10 years (1980-1989) and the same four plus four additional trees were measured for an additional four years (1992-1995); each point represents an individual tree. The formula is for the line drawn from the origin to point A, the point highest in the quadrant and therefore yielding the greatest slope. This assumes a linear expected relationship between the variables and no seed removal between the acorn census and acorn fall for point A.

Population densities of acorn woodpeckers (*Melanerpes formicivorus*) and California scrub-jays (*Aphelocoma californica*), two of the major arboreal seed predators on the study site, were estimated based on concurrent long-term studies of marked individuals of these species (Koenig and Mumme 1987, Carmen in press). Densities of acorn woodpeckers were known for all 15 years of the study, while those for California scrub-jays were known from 1981 to 1986. For the latter species, the number of residents, plus the estimated number of floaters present in the fall, were added together. Densities used were the number of individuals present within 1 km of the focal trees during October.

Insect Predation

Each year between 1984 and 1995 we collected 20 to 25 acorns from as many trees as possible during the acorn survey in the autumn. Acorns were dried at room temperature and later shelled, at which time insect damage was assessed and the relative proportion of acorns suffering damage determined. This proportion was multiplied times the number of acorns counted to yield an index of the total number of acorns damaged by insects in the tree. These values were correlated with the acorn production of individual trees and the mean overall acorn crop of trees for each species for each year. We included only the three most widespread species (*Q. lobata, Q. douglasii*, and *Q. agrifolia*) for which we had the largest sample sizes.

Neighborhood effects were investigated by calculating the correlation between the amount of insect damage for each sampled tree and the difference between its acorn crop and the mean crop of other conspecifics surveyed within 100 m, 250 m, and 1 km that year.

Two-tailed probability values for statistical tests are reported when possible; P-values < 0.05 are considered significant.

Results

Arboreal Seed Removal

There was a significant correlation between the acorn crop as determined from the visual survey and from the seed traps of the four (or eight) focal *Q. lobata* trees ($r_s = 0.86$; $N = 72$, $P < 0.001$; *fig. 1).* At very low crop sizes, acorns were sometimes caught in the traps even though none was counted. At larger crop sizes, arboreal seed removal usually resulted in fewer acorns being trapped than expected from the visual counts. In one case, no acorns were trapped even though 96 were counted in the 30 second visual survey.

We calculated both the total number and relative proportion of acorns removed prior to seed fall each year *(table 1).* These values were not significantly correlated using either the mean annual ($r_s = -0.23$, $N = 14$ years, $P = 0.42$) or individual tree data ($r_s = 0.19$, $N = 57$ trees, $P = 0.16$).

Correlations of the measures of arboreal seed removal with variables related to the acorn crop and the population sizes of the two avian acorn specialists are given in table 2. In general, as acorn productivity of either the focal trees or the overall area increases, the total number of acorns removed increases, while the relative proportion of acorns removed decreases, albeit only slightly *(fig. 2).* Relationships with the population sizes of both acorn woodpeckers and California scrub-jays were in the same direction. That is, when population size of either of these species was greater, they were apparently able to harvest more acorns but a smaller proportion of the overall crop from the focal trees. However, these correlations were not significant.

Table 1—*Acorn production and population size of potential predators. Acorn production values are means of log-transformed number of acorns counted per 30 seconds for the four (1980-1989) or eight (1992-1995) focal* Q. lobata *trees. Overall mean acorn crop values average counts for 34* Q. lobata *trees sampled within 1 km (but excluding) of the focal trees.*

Year	Overall mean acorn crop	Focal tree			Population size	
		Acorns counted	Number removed (m^{-2})	Pct removed	Acorn woodpeckers	California scrub-jays
1980	0.92	1.68	20.8	83.8	43	
1981	1.79	2.24	183.9	66.0	41	97
1982	1.54	2.86	62.4	93.5	43	74
1983	0.22	0.00	—	—	8	14
1984	0.71	0.17	1.4	100.0	41	29
1985	4.01	3.70	226.3	38.5	66	40
1986	1.25	0.40	6.6	100.0	49	47
1987	3.58	4.13	143.1	61.3	61	—
1988	2.09	0.62	1.4	34.8	74	—
1989	1.83	3.62	176.2	99.0	64	—
1992	3.02	3.42	120.4	56.1	46	—
1993	1.20	1.69	9.8	48.0	63	—
1994	2.56	3.68	150.9	82.8	83	—
1995	0.46	0.37	2.8	98.2	47	—
1996	2.07	3.20	77.0	57.8	41	—

We looked for a neighborhood effect by comparing the estimated proportion of the acorn crop removed for trees that outproduced the overall mean acorn crop (N = 44) with those producing fewer acorns than the mean overall acorn crop (N = 13), excluding trees for which we counted no acorns (N = 15). There was no significant difference between these two categories of trees (Mann-Whitney U-test, z = 0.9, P = 0.35). As an additional test, we restricted analysis to within years and compared the proportion of acorns removed from the tree producing the largest crop with the one producing the smallest (non-zero) crop. In only seven out of 12 (58 percent) years with two trees producing different-sized crops, the tree with the smaller crop had the higher proportion of acorns removed. Thus, neither test provides strong evidence that a larger proportion of the acorn crop is removed arboreally by animals when a tree produces more acorns than the average tree in the study area.

Table 2—*Spearman rank correlations between annual mean values of variables potentially related to the extent of arboreal seed removal. Overall mean acorn crop values as in Table 1.* * P *<0 .05,* *** P *<0.001 (two-tailed); other* P *>0.05.*

	Pct acorns removed	Total number of acorns removed	*N* years
Mean crop of focal trees	-0.41	0.85***	14
Overall mean acorn crop	-0.62*	0.65*	14
Acorn woodpecker population size	-0.34	0.16	14
California scrub-jay population size	-0.31	0.40	5

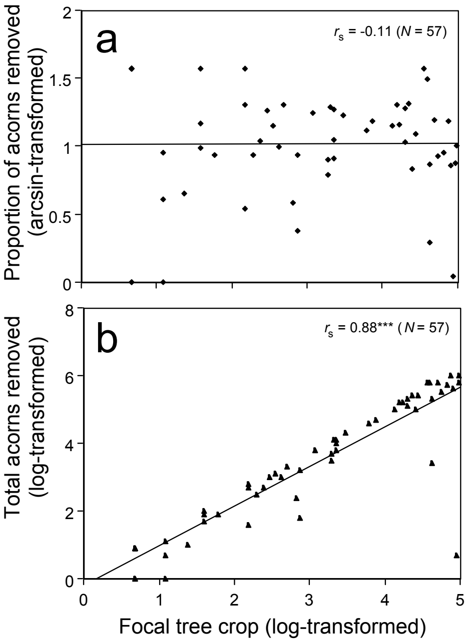

Figure 2—Relationships between relative (a) and total (b) extent of acorns removed arboreally from four (eight in four years) *Quercus lobata* trees measured over 14 years and the acorn crop of the focal tree based on visual censuses. Trees failing to produce any acorns are excluded. Values are estimated from the difference between the observed and expected acorns captured in traps given the number counted visually.

Insect Predation

Correlations were significantly positive between the relative proportion and total amount of insect damage to acorns (r_s= 0.43 [N = 157 trees], 0.36 [N = 141], and 0.82 [N = 131] for *Q. lobata*, *Q. douglasii*, and *Q. agrifolia*, respectively; all $P < 0.001$). With the exception of a slight increase in the proportion of *Q. agrifolia* acorns damaged as productivity increased, the proportion of acorns damaged decreased and the total number of acorns damaged increased with focal tree productivity (figure 3). This pattern was also evident in an ANCOVA combining all trees and years (table 3). Using annual means, correlations were mostly nonsignificant, but the trends were the same, and larger acorn crops correlated with significantly higher total insect damage in *Q. agrifolia (table 4).*

Table 3—*Analysis of covariance of relative proportion and total insect damage to acorns for three species of California oaks. Analyses first control for the main factors and then for the covariate. Presented are the partial* F-*values for the variables and whether they are significant. For the covariate, the direction of the regression line (positive or negative) is in parentheses. Degrees of freedom are (. , 397), where the numerator is the number in parentheses after the variable.* * P *<0.05,* *** P *<0.001.*

		Pct insect damage	**Total insect damage**
Main factors	Species (2)	1.6	1.3
	Year (10)	7.8***	14.8***
Interaction	Species x year (18)	1.7*	1.7*
Covariate	Focal tree crop (1)	2.6 (-)	276.5*** (+)
Explained (31)		4.8***	16.5***

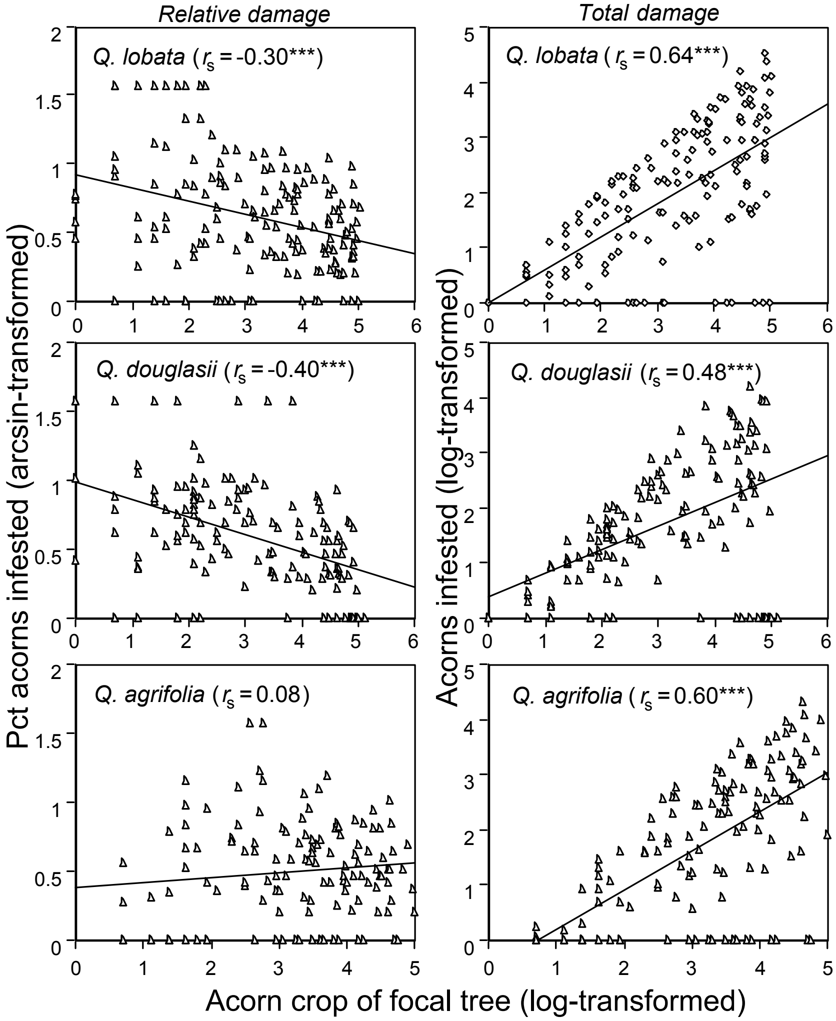

Figure 3—Relationships between relative (left side) and total (right side) extent of insect damage to acorns from three species of oaks and the acorn crop of the focal tree based on visual censuses.

Neighborhood effects were investigated by examining the degree of insect damage vis-à-vis the degree to which focal trees outproduced or underproduced acorns compared to nearby conspecifics. In general, correlations were not significant, with the exceptions of *Q. lobata* and *Q. douglasii* compared to conspecifics within 1 km *(table 5)*. In both these cases, trees that outproduced conspecifics tended to suffer less relative insect predation than trees underproducing conspecifics.

Table 4—*Spearman rank correlations between the mean overall acorn productivity of three species of oaks and the mean relative and total extent of insect damage. Samples sizes are years.* * P *<0.05 (two-tailed); other* P *>0.05.*

	Mean pct acorns damaged	Mean total number of acorns damaged	*N* years
Quercus lobata	-0.26	0.35	11
Quercus douglasii	-0.55	0.35	10
Quercus agrifolia	0.36	0.73*	10

Table 5—*Spearman rank correlations (N trees) between the proportion of insect damaged acorns and the difference between the acorn crop of the focal tree and the mean acorn crops of conspecific trees within 100 m, 250 m, and 1 km. Positive correlations indicate that trees with relatively large acorn crops suffer relatively greater insect damage, whereas negative correlations indicate the converse.* * P *<0.05; other* P *>0.05.*

	Comparison population: conspecifics within		
	100 m	**250 m**	**1 km**
Quercus lobata	-0.09 (147)	-0.06 (157)	-0.19* (157)
Quercus douglasii	-0.13 (125)	-0.13 (141)	-0.21* (141)
Quercus agrifolia	0.13 (104)	0.02 (131)	-0.10 (131)

Discussion

Implications for Masting

A primary prediction of the predator satiation hypothesis as traditionally viewed is that there should be an inverse correlation between productivity and the proportion of seeds depredated. This prediction was upheld in two of the three species for insect damage *(fig. 3)* and was also true, albeit only weakly, for arboreal seed removal *(fig. 2)*. In all cases, the total number of acorns damaged or removed increased with larger seed crops. In the case of insect predation, this was true to some extent even after controlling for year and species differences *(table 3).* This suggests that seed predators may be an important influence synchronizing acorn production among California oaks.

Crop size of an individual tree is not the only factor potentially influencing the extent of acorn removal: local seed density may be important as well. Such neighborhood effects were not detected for arboreal seed removal, which was apparently independent of the size of the overall acorn crop. Evidence for neighborhood effects was also weak with respect to insect damage, where the only significant results indicated that trees producing more acorns than local conspecifics suffered relatively less insect damage than trees producing fewer acorns *(table 5).* These results are in the opposite direction from those predicted by the hypothesis that synchrony is reinforced by the inordinate attractiveness of trees outproducing neighbors. Instead, trees with larger acorn crops than local conspecifics suffer relatively less, rather than more, insect damage.

What is the selective effect of these patterns on the reproductive effort of oaks at Hastings Reservation? To the extent that the proportion of acorns removed and the incidence of insect damage decreases as the acorn crop of a tree increases, it suggests that predator satiation occurs at both these levels. These relationships should select for masting, at least once year-to-year variation in weather-mediated resource availability initiates some degree of synchronization in acorn crop size (Lalonde and Roitberg 1992). However, we found no detectable disadvantage to individual trees that outproduced conspecifics in terms of either increased arboreal seed removal or increased incidence of insect damage to their acorns. Thus, the synchronizing effects of these phenomena at the neighborhood level do not appear to be strong.

Which is more important to the masting patterns of oaks: arboreal seed removal or insect predation? The estimated percent of acorns removed prior to acorn fall ranged between 34.8 and 100 percent *(table 1),* whereas the mean annual proportion of acorns infested with insects varied from 0 to 63 percent, suggesting that arboreal seed removal may be greater. However, these figures may be misleading for at least two reasons. First, insect damage could only be assessed in trees with relatively large acorn crops, since adequate samples could not be obtained from trees with small crops. Because the proportion of acorns damaged decreases with crop size *(fig. 2),* our samples are biased toward trees that are likely to have relatively low insect predation. Second, arboreal seed removers, in contrast to insects, are both predators and important dispersal agents. California scrub-jays, for example, store acorns extensively in the ground where many may eventually sprout (Carmen [In press], Grinnell 1936), and even acorn woodpeckers, which store acorns in granaries from which relatively few acorns eventually escape destruction (Koenig and Mumme 1987), inadvertently drop some acorns in while caching them. Consequently, it is likely that trees may ultimately benefit by attracting individuals of these two species, despite the fact that many of the acorns they remove are destroyed rather than dispersed. Fruiting strategies of individual oaks should be designed to reduce the extent of insect damage to acorns, but may benefit by attracting, rather than evading, arboreal seed removers, at least when conditions are such that some of the seeds removed are cached rather than eaten immediately.

Although acorn dispersal by arboreal seed removers such as scrub-jays is certainly important to the long-term survival of oaks, to what extent does the attraction of such dispersal agents appear to have influenced masting strategies? Two predictions can be made by this hypothesis: (1) in years when population sizes of arboreal seed removers are greater, more acorns, both proportionately and in total, should be dispersed, and (2) there should be a significant neighborhood effect in that trees outproducing the overall mean acorn crop should attract relatively many arboreal seed removers, potentially leading to a higher proportion of acorns dispersed. Our data are not definitive since we examined only acorn removal and not the probability of dispersal per se. However, to the extent that arboreal acorn removal is an index of caching, neither of these predictions was upheld. First, the correlation between population sizes of California scrub-jays and acorn woodpeckers, two major seed removers, and both the relative and total number of acorns removed were not significant *(table 2),* and second, no significant neighborhood effect was found with respect to arboreal acorn removal. These results fail to support the hypothesis that the attraction of seed dispersers is a major influence on seed production patterns in this population.

In contrast, the observed patterns of reproduction are generally consistent with both predator satiation as traditionally envisioned or an alternative hypothesis, that of increased pollination efficiency due to wind pollination, being important factors leading to masting. Both these hypotheses successfully predict relatively low variation in acorn production within years, high variation in acorn production among years, and the existence of crop failures (Koenig and others 1994). Thus, the satiation of predators, both arboreal and insect, may be an important factor tending to synchronize reproduction by oaks in central coastal California. Acorn dispersal by arboreal seed removers does not appear to be the dominant factor influencing the reproductive strategies of oaks in our population, although it may still be a factor countering the within-population synchrony observed in the population.

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