University of Nebraska - Lincoln
DigitalCommons@University of Nebraska - Lincoln

Faculty Publications in the Biological Sciences | Papers in the Biological Sciences

1-1-2009

Natural History Note No Trade-Off between Seed Size and Number in the Valley Oak *Quercus lobata*

Walter D. Koenig
Cornell University

Johannes M. N. Knops
University of Nebraska - Lincoln, jknops2@unl.edu

William J. Carmen

Richard D. Sage
University of California - Berkeley

Follow this and additional works at: http://digitalcommons.unl.edu/bioscifacpub

Part of the Life Sciences Commons

Koenig, Walter D.; Knops, Johannes M. N.; Carmen, William J.; and Sage, Richard D., "Natural History Note No Trade-Off between Seed Size and Number in the Valley Oak *Quercus lobata*" (2009). *Faculty Publications in the Biological Sciences.* Paper 131.
http://digitalcommons.unl.edu/bioscifacpub/131

This Article is brought to you for free and open access by the Papers in the Biological Sciences at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Faculty Publications in the Biological Sciences by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

Natural History Note

No Trade-Off between Seed Size and Number in the Valley Oak *Quercus lobata*

Walter D. Koenig,[1,2,*] Johannes M. H. Knops,[3] William J. Carmen,[4] and Richard D. Sage[2]

1. Laboratory of Ornithology and Department of Neurobiology and Behavior, Cornell University, Ithaca, New York 14850; 2. Museum of Vertebrate Zoology, University of California, Berkeley, California 94720; 3. School of Biological Sciences, University of Nebraska, Lincoln, Nebraska 68588; 4. 145 Eldridge Avenue, Mill Valley, California 94941

Submitted August 22, 2008; Accepted November 25, 2008; Electronically published March 20, 2009

abstract: We examined the relationship between acorn mass and number in valley oaks (*Quercus lobata*) over 4 years in central coastal California. Despite considerable variation in acorn size among both trees and years, trees produced acorns of the same size relative to other trees in different years. Across years, the relationship between acorn mass and acorn crop size was generally positive, even after controlling for environmental conditions and differences in individual tree size and quality. Life-history trade-offs in valley oaks are primarily between current and future reproduction and indirectly between concurrent growth and reproduction, not between seed size and number, and are probably related to this species' mast-seeding behavior. Phenotypic trade-offs in long-lived plants such as oaks exhibit complex patterns of life-history covariation and deserve greater attention, both theoretically and empirically.

Keywords: acorns, life-history trade-offs, mast fruiting, oaks, seed size, *Quercus lobata*, valley oak.

Introduction

A trade-off between offspring size and number has been a foundation for much of the theoretical work on life-history patterns for over 30 years (Smith and Fretwell 1974; Wilbur 1977). There has been considerable empirical work examining this relationship at the interspecific and interpopulation levels, leading to the conclusion that an inverse relationship between size and number is widespread among plants (Westoby et al. 1992; Greene and Johnson 1994; Jakobsson and Eriksson 2000; Leishman 2001; Abrahamson and Layne 2002; Parciak 2002) as well as other taxa (Warne and Charnov 2008), at least after controlling for potentially confounding effects of adult size (Aarssen and Jordan 2001; Henery and Westoby 2001). Within populations of plants, however, the growth form of species studied has been limited—most studies have been conducted on forbs, with a small number on shrubs or small trees—and results have been mixed. For example, inverse relationships between seed size and seed number within individual plants have been reported in *Ipomopsis aggregata* (Wolf et al. 1986), *Lupinus polyphyllus* (Aniszewski et al. 2001), and the shrub *Banksia marginata* (Vaughton and Ramsey 1998). However, a comparative study of six species of *Asclepias* yielded correlations between seed size and number ranging from significantly negative to significantly positive (Wilbur 1977), and work on *Claytonia virginica* (Morgan 1998), *Lupinus texensis* (Schaal 1980), *Desmodium paniculatum* (Wulff 1986), and the small tree *Prunus virginiana* (Parciak 2002) yielded no consistent relationship between seed size and number.

The interpretation of these results is complicated by at least two well-recognized difficulties. First, correlation is not causation, and even apparently strong life-history correlations can be due to confounding variables rather than trade-offs (Knops et al. 2007). Second, variation in resource availability can confound the relationship between seed size and number: if resources vary greatly from year to year or individuals vary in quality, underlying trade-offs between seed size and number can be obscured by variation in resources (van Noordwijk and de Jong 1986; Pease and Bull 1988; Venable 1992). To the extent this is occurring, there should be more of a trade-off (i.e., a stronger negative correlation) in poor years and among low-quality individuals for which resources are more likely to be limiting than in good years and among high-quality individuals, resulting in a positive correlation between resources (or individual quality) and the correlation coefficient between the life-history characters of interest.

Given these issues, studies controlling for resources, focusing on individual variation across years, and extending the growth form of species that have been studied to date are clearly desirable. Here we investigate the seed size/number trade-off in a population of valley oaks (*Quercus lobata*) in central coastal California. Apart from being by far the largest and longest-lived species in which this relationship has been studied to date—valley oaks can grow

* Corresponding author; e-mail: wdk4@cornell.edu.

Am. Nat. 2009. Vol. 173, pp. 000–000. © 2009 by The University of Chicago. 0003-0147/2009/17305-50697$15.00. All rights reserved.
DOI: 10.1086/597605

Table 1: Sample sizes, mean, and coefficient of variation (CV) of acorn mass among trees and the mean acorn crop (acorns counted per tree in 30 s) in the 4 years of the study

Year	*N* trees	*N* acorns	Dry mass (individual tree means) Mean ± SD (g)	Mean CV (%)	Mean ± SD acorn crop (acorns counted in 30 s)
2004	74	809	2.20 ± .97	39.8	46.7 ± 40.9
2005	28	136	1.07 ± .91	44.1	2.0 ± 4.4
2006	43	333	1.75 ± .82	38.3	11.4 ± 22.9
2007	75	1,263	2.08 ± .76	37.1	61.9 ± 43.5

to be over 2.5 m in diameter and live over 500 years (Pavlik et al. 1991)—they are well suited to such a study as a consequence of their relatively large seed size and mast-fruiting habits (Koenig et al. 1994*a*), the latter ensuring that seed numbers vary widely from year to year. As in many other taxa, including other species of oaks (McComb 1934; Tripathi and Khan 1990; Westoby et al. 1992; Kennedy et al. 2004), larger valley oak acorns accrue a clear fitness advantage in terms of increased growth (R. D. Sage, unpublished data), thus fulfilling one of Smith and Fretwell's (1974) "intuitively obvious" relationships linking patterns of energy expenditure by parents and their offspring. Here we investigate the extent to which the second of these relationships, that between energy expended per offspring (i.e., size) and number of offspring, follows the expected inverse relationship in this species.

Methods

Study Site and Data Collection

We studied acorn size variation in valley oaks at Hastings Reservation in Monterey County, central coastal California, which were tagged in 1980 as part of a long-term study of acorn production. A total of 88 trees were sampled, ranging in size from 31 to 193 cm diameter at breast height (DBH). Focal trees grew over a 900-ha area ranging in elevation from 475 to 875 m. Over the course of the study, three of the trees died, leaving a sample of 85. Not all data were available for all trees, however, and sample sizes for individual analyses are generally smaller. This was particularly true for the poor acorn crop in 2005, when many trees produced no or so few acorns that samples could not be obtained.

Each year, we estimated acorn production by visual surveys in which two observers, each counting for 15 s (30 s total), counted as many acorns as possible on each tree, a method that provides a good index of relative acorn production in this population (Koenig et al. 1994*b*). Counts were then added and log transformed ($\log(x+1)$) to reduce the correlation between the mean and variance (Sokal and Rohlf 1981). Counts were made for all trees in the study for 28 years from 1980 to 2007, inclusive.

Acorn size was obtained in 2004–2007 from as many individual trees as possible. In each year, acorns were collected from the tree or, when the tree they came from was unambiguous, directly under the tree. The latter was only possible in very good acorn years when predation was relatively low, ensuring that the acorns collected were a reasonably random sample of those produced. Acorns were dried, shelled to extract the endosperm from the husk, and weighed to the nearest 0.01 g. Only acorns that were easily extracted from their caps without damaging the husk were used, and any that were noticeably insect damaged or abnormal were excluded. On average (±SD), we measured 11.6 ± 7.6 (range 1–42) acorns from each tree × year combination sampled (table 1).

Size of trees was measured by their DBH in September 2008. As indexes of individual tree quality, we used (1) the mean acorn production of trees over the entire 28 years that acorns were counted and (2) access to groundwater, a key limiting factor in this habitat, estimated by xylem water potential using the pressure chamber technique (Waring and Cleary 1967) measured at predawn September 20–October 5, 1991 (Knops and Koenig 1994). Subsequent measurements confirmed that although xylem water potential differs from year to year, predawn values for individual trees are concordant across years (Knops and Koenig 2000). Thus, values used provide a good index of relative water availability, despite having been obtained over a decade before the study. To capture an additional life-history trait potentially involved in trade-offs with reproduction, each autumn at the time acorns were counted, we measured radial growth of trees using dendrometers (Cattelino et al. 1986) placed on the trees in 1992. Values used were the radial growth during the year before acorns were collected, relative to the mean annual growth for the same tree for 1993–2007.

Statistics

Neither mean acorn mass nor mean log-transformed acorn mass of individual trees was normally distributed (Shapiro-Wilks normality test using all tree × year means; both $P < .005$). However, normality was achieved by square-root transformation (Shapiro-Wilks normality test: $W = 0.99$, $P = .26$), and consequently this transforma-

tion was used on mean acorn mass in all parametric analyses. However, untransformed values were used for calculating descriptive statistics in order to render results easier to visualize and more directly comparable to the acorn crop data.

Although the relationship between acorn mass and acorn crop size can be estimated several ways, it only potentially involves a phenotypic trade-off when measured across years within individual trees. Thus, only this level is analyzed here.

We performed two tests. First, we tested pairs of years using Wilcoxon signed-ranks tests that compared the mean mass of acorns produced in the year when a tree had a larger acorn crop based on the acorn survey versus the mean mass of acorns produced by the same tree during the year it had a smaller acorn crop. With 4 years of data, six pairs of years could be tested (although not all six pairs of years were available for all trees). The overall relationship was examined visually by plotting the difference between the acorn crops of individual trees in each pair of years (calculated by subtracting the smaller crop from the larger crop) versus the difference in the mean mass of acorns collected from the tree in the same pair of years. The relationship was tested statistically by conducting trials in which we randomly chose one pair of years for each tree and compared the number of cases in which acorn size was larger in the year with the larger acorn crop ("positive" trees) with the number of cases in which acorns were smaller in the year with the larger acorn crop ("negative" trees). Significance was based on the proportion of 1,000 trials in which the number of positive trees exceeded the number of negative trees.

As a second test, we calculated the correlations between mean square-root-transformed acorn size and the log-transformed acorn crop size for the 53 individual trees for which acorns were collected in at least 3 of the 4 years and tested the significance of the resulting values using a binomial test to determine whether the proportion of correlations greater/less than zero was more or less than expected by chance. In order to control for variation in resource availability and individual quality, we controlled for total available resources as estimated by annual rainfall, mean annual temperature, and annual net primary productivity (NPP), calculated from annual rainfall and mean annual temperature at Hastings Reservation headquarters using the Miami model (Leith 1975). However, NPP in this Mediterranean climate is closely correlated with annual rainfall, and so only results for annual rainfall and mean annual temperature are presented. Since acorns mature in September and October, calculations were made from September 1 to August 31.

The relationship between individual tree size/quality and its seed size/number was investigated using the relationships between (1) the correlation coefficients between mean acorn mass and acorn crop size for trees for which we had at least 3 years of data and (2) three measures of tree size/quality, including DBH, the mean long-term acorn productivity of the tree, and access to groundwater measured by predawn xylem water potential. If a trade-off between mean acorn mass and acorn crop size exists, a positive relationship in these analyses would indicate that trade-offs were stronger (i.e., more negative) in years when resources were more limiting.

Statistics were performed using SPSS (ver. 8.0) and R (ver. 2.6.2). Values are means ± SE, except where noted; $P < .05$ is considered significant.

Results

Individual and Annual Variation in Seed Mass

Mean mass of acorns produced by individual trees ranged from 0.11 to 4.65 g. Combining data from all trees, mean acorn mass among years varied from 1.06 to 2.20 g, with moderate coefficient of variation (CV) among trees within years ranging from 37.1% to 44.1% (table 1). Using untransformed values, the CV among years of mean acorn size was 28%, compared to 93% for the mean acorn crop.

Acorn mass varied significantly both among individuals and across years (repeated-measures generalized linear model using mean acorn mass for 18 individuals with data for all 4 years, within-subjects effects [i.e., differences among years] were $F_{3,15} = 14.9$, $P < .001$, and between-subjects effects [i.e., differences among trees] were $F_{1,17} = 82.7$, $P < .001$). Despite this variation, there was high concordance between the relative size of acorns produced by trees across years, as indicated by positive correlations between the size of acorns produced by individual trees considering each pair of years separately (six correlations; mean $r = 0.61$; range 0.47–0.70; $N = 18$–72 trees; all six $P < .01$), and high concordance of mean acorn mass among the 18 trees for which we collected acorns in all 4 years (Kendall's coefficient of concordance = 0.73; $\chi^2 = 50$, df = 17, $P < .001$).

Using trees with at least 3 years of data, the mean correlation between mean acorn size and radial growth was -0.30 ± 0.09 ($N = 52$). Thirty-nine (75%) of the correlations were negative, significantly greater than expected by chance (binomial test, $P < .001$).

Relationship between Acorn Mass and Crop Size

We first used Wilcoxon signed-ranks tests to compare, for individual trees, the mean mass of acorns produced in a year when the tree had a larger acorn crop versus the mean mass produced by the same tree during a year in which it had a smaller acorn crop. Of the six pairs of years, four

were significant, all in the direction of acorns being larger in years when trees produced larger crops (table 2). We then examined this relationship by plotting, for all trees and all pairs of years combined, the difference between the acorn crops in the 2 years (subtracting the smaller crop from the larger crop) versus the difference in the mean mass of acorns collected from trees in the same pair of years. The results (fig. 1) demonstrate a strong overall positive relationship between the magnitude of the difference in size of the acorn crop and the size of acorns produced by trees in different years.

Second, we calculated the correlations between mean acorn mass and the acorn crops for the 53 trees sampled in 3 (35) or 4 (18) years. The mean correlation was 0.51 ± 0.12; 41 (77%) of the correlations were positive (binomial test, $P < .001$). In partial correlations controlling for environmental conditions, the mean partial correlation coefficient remained positive, although not significantly so (mean annual temperature: $r = 0.03 \pm 0.09$, 26 of 53 trees positive, $P = .9$; annual rainfall: $r = 0.12 \pm 0.09$, 30 of 53 trees positive, $P = .4$).

The relationships between the three tree characteristics considered (DBH, xylem water potential, and overall productivity) and the correlations between seed size and number were all nonsignificant (fig. 2). These results were confirmed by a multiple regression of the correlation coefficients on the three independent variables, the results of which indicated that neither the individual variables nor the overall regression were significant (P values of the independent variables all $> .1$; overall $F_{3,49} = 1.2$, $P = .3$). In all cases, the regression lines depicting the relationship for a given size or amount of resources were positive over the observed range of trees (fig. 2). Thus, in no case did the relationship correspond to that expected if more limited resources result in stronger trade-offs between seed size and number or, for that matter, any trade-off whatsoever.

Table 2: Pairwise comparisons of mean acorn mass and mean acorn crop produced by individual trees tested using Wilcoxon signed-ranks tests

Years compared	N positive trees	N negative trees	z	P
2004 vs. 2005	26	1	4.5	<.001
2004 vs. 2006	28	15	3.0	.003
2004 vs. 2007	32	41	−.8	.440
2005 vs. 2006	13	5	1.6	.110
2005 vs. 2007	26	2	4.1	<.001
2006 vs. 2007	33	10	2.6	.008
All years combined	158	74	6.2	<.001

Note: Positive trees produced larger acorns in the year in which they had a larger acorn crop, while negative trees produced smaller acorns in the year in which they had a larger acorn crop.

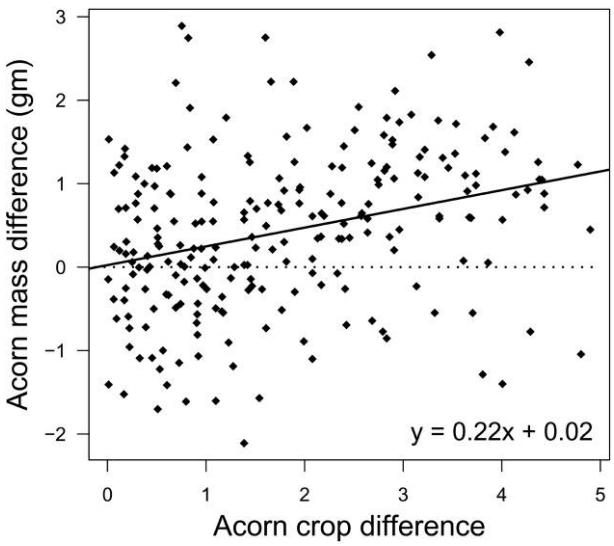

Figure 1: All 158 comparisons of mean acorn mass for the same tree in 2 years plotted against the acorn crop difference for the tree in the same 2 years, the latter calculated such that the smaller value is always subtracted from the larger value. Regression line (drawn) above zero over the entire range of the X-axis indicates that trees produced larger acorns in years when they had larger acorn crops, and the positive slope of the regression indicates that the difference in acorn size became greater as the difference in crop size between the 2 years increased. Regression line is significant ($P = .003$, determined by randomization).

Discussion

Valley oak acorns vary considerably in size among both individuals and years. Nonetheless, there is significant concordance among trees in the relative size of their acorns from one year to the next.

We tested for an inverse relationship between acorn size and acorn number at the level of individual trees, where phenotypic trade-offs are potentially taking place through differential allocation of resources. Contrary to the trade-offs hypothesis, trees produced larger acorns in years when they produced larger acorn crops, with larger differentials occurring in years when the difference between the crops was larger. We found no evidence that this result was an artifact of environmental conditions or differences in individual quality: correlations between acorn size and number remained positive controlling for rainfall or temperature and across trees regardless of their size, access to groundwater, or overall fecundity.

Given that valley oaks produce acorns that are neither as large or numerous as is apparently physiologically possible, trade-offs involving these characters must exist at some level (Stearns 1989). However, our analyses indicate that neither resources nor individual quality is confounding our failure to detect phenotypic trade-offs. More likely

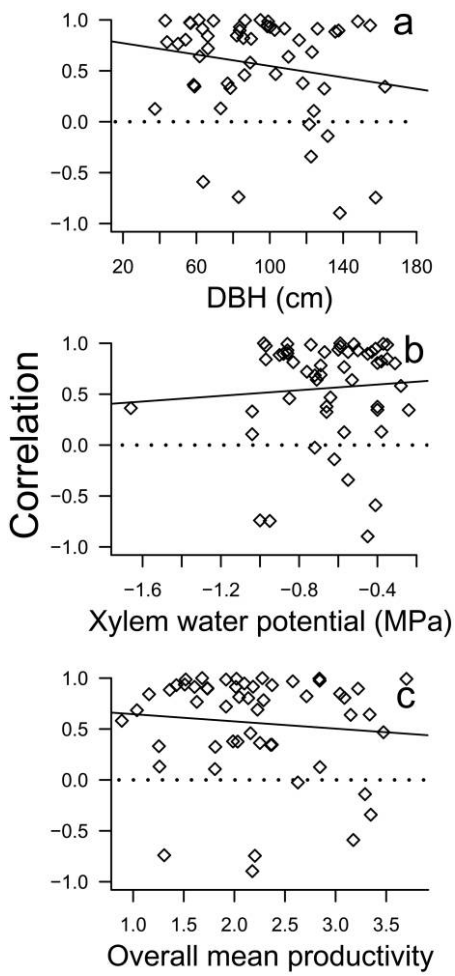

Figure 2: Relationships between acorn size/number and individual differences among trees. Correlation coefficients between acorn size and acorn crop size measured across years for the 53 trees sampled at least 3 years (*Y*-axis) plotted against the variable measuring individual size or quality (*X*-axis). The three variables and statistics are (*a*) diameter at breast height (DBH; $r = -0.2$, $t_{51} = -1.4$, $P = .16$), (*b*) predawn xylem water potential ($r = 0.07$, $t_{51} = 0.5$, $P = .6$), and (*c*) overall long-term acorn productivity ($r = -0.10$, $t_{51} = -0.7$, $P = .5$). Solid lines are linear regressions. Dotted lines, at $y = 0$, separate negative correlations, indicating a potential trade-off between acorn size and acorn number, from positive correlations. In *b*, the correlation excluding the single outlier is $r = 0.05$, $t_{50} = 0.4$, $P = .7$.

is that, as only two among a series of reproductive traits for which resources are being partitioned, acorn size and number are not characters that are directly competing with each other, or if they are, then the allocation choice between them comes late, leading to a situation in which they may be positively correlated, even if resources are being directly divided between them (de Jong 1993).

In terms of other traits among which resources may be partitioned, one is growth. Among the trees with relatively complete data, there was a significant tendency for radial growth to correlate negatively with acorn size, suggesting a possible trade-off. However, a comparable inverse relationship is observed between radial growth and the size of the acorn crop that is due to confounding weather factors rather than a direct phenotypic trade-off (Knops et al. 2007). Whether the inverse relationship between radial growth and acorn size is the result of a similar confound remains to be determined.

A less ambiguous trait potentially involved in trade-offs is future reproduction. Based on the 28 years of acorn production data used in this study, the mean lag-one temporal autocorrelation among the acorn crops of valley oaks in our study is $r = -0.28 \pm 0.02$, with autocorrelations for 78 (91%) of 86 trees being negative (binomial test, $P < .001$). Given the lack of autocorrelation in relevant weather factors in this study area (between 1980 and 2007 the lag-one autocorrelation in annual rainfall was $r = 0.03$ [$P = .9$], and that for mean maximum early spring temperatures in March and April, the key time for flowering and pollination in valley oaks, was $r = 0.06$ [$P = .8$]), this suggests that the major trade-offs in resource allocation made by this species are between current and future reproduction, followed by a second possible division, albeit indirectly, between growth and reproduction.

Thus, contrary to the trade-offs hypothesis, it does not appear that the allocations of resources between acorn size and number directly compete with each other, although given that the study was focused on phenotypic correlations, it is possible that the observed results may be due to unmeasured environmental factors that are masking a trade-off between the underlying genetic basis of these traits. This caveat aside, our results suggest that factors other than the resources available to individual trees or present in different years determine the relationship between seed size and number. Controlled studies investigating the genetic basis of seed size variation, such as can be performed in more tractable systems (Paul-Victor et al. 2007), would be desirable, albeit logistically difficult in this long-lived species.

Trees such as the oaks studied here presumably have nutritional reserves on which they can draw and expend only a small proportion of their net annual assimilation on reproduction (Harper et al. 1970; Boucher and Nash 1990; Callaway and Nadkarni 1991). They thus qualify as "capital breeders," storing energy that can be mobilized for reproduction in future years, a situation creating a mechanical linkage between current and future reproduction (Stearns 1989). As such, it is, at least in retrospect, not surprising that a primary life-history trade-off in the system appears to be between current and future reproduction. In contrast, within years, trees are apparently capable of investing simultaneously in both larger seeds and

larger acorn crops with no resource switching. To the extent that the strongly negative lag-one autocorrelation between acorn crops is a key feature of masting behavior (Koenig et al. 1994*a*, 2003; Kelly and Sork 2002), these patterns also suggest a link to the highly variable annual seed production defining this evolutionarily interesting and ecologically important phenomenon.

Our results do not indicate the existence of a significant relationship between acorn size and tree age, at least to the extent that the latter is correlated with DBH. However, valley oaks are long lived, and the oldest trees in our population are estimated to be on the order of 500 years old. It is thus not possible to conclusively reject the possibility that a trade-off between seed size and lifetime reproductive output exists, as was found in an interspecific comparison performed by Moles et al. (2004), or that seed predation selects for smaller seeds and thus counters the presumed advantages of larger acorns, as found in *Quercus ilex* by Gomez (2004).

Despite the challenges they present, studies of life-history variation in long-lived species such as oaks deserve greater attention, both theoretically and empirically. As demonstrated here, such species may exhibit complex and surprising patterns of life-history covariation quite different from those observed in many of the shorter-lived species that have been more thoroughly studied to date.

Acknowledgments

We thank R. Drobek, J. McEntee, E. Moran, D. Morin, B. Piculell, J. Stahl, and A. Tucillo for shelling and weighing acorns and R. Karban, P. Klinkhamer, R. Wesselingh, and an anonymous reviewer for their comments. Support was provided by the University of California's Hastings Reservation and Integrated Hardwoods Range Management Program and by the National Science Foundation.

Literature Cited

Aarssen, L. W., and C. Y. Jordan. 2001. Between-species patterns of covariation in plant size, seed size and fecundity in monocarpic herbs. Ecoscience 8:471–477.

Abrahamson, W. G., and J. N. Layne. 2002. Relation of ramet size to acorn production in five oak species of xeric upland habitats in south-central Florida. American Journal of Botany 89:124–131.

Aniszewski, T., M. H. Kupari, and A. J. Leinonen. 2001. Seed number, seed size and seed diversity in Washington lupin (*Lupinus polyphyllus* Lindl.). Annals of Botany 87:77–82.

Boucher, V. L., and T. H. Nash III. 1990. The role of the fruticose lichen *Ramalina menziesii* in the annual turnover of biomass and macronutrients in a blue oak woodland. Botanical Gazette 151: 114–118.

Callaway, R. M., and N. M. Nadkarni. 1991. Seasonal patterns of nutrient deposition in a *Quercus douglasii* woodland in central California. Plant and Soil 137:209–222.

Cattelino, P. J., C. A. Becker, and L. G. Fuller. 1986. Construction and installation of homemade dendrometer bands. Northern Journal of Applied Forestry 3:73–75.

de Jong, G. 1993. Covariances between traits deriving from successive allocations of a resource. Functional Ecology 7:75–83.

Gomez, J. M. 2004. Bigger is not always better: conflicting selective pressures on seed size in *Quercus ilex*. Evolution 58:71–80.

Greene, D. F., and E. A. Johnson. 1994. Estimating the mean annual seed production of trees. Ecology 75:642–647.

Harper, J. L., P. H. Lovell, and K. G. Moore. 1970. The shapes and sizes of seeds. Annual Review of Ecology and Systematics 1:327–353.

Henery, M. L., and M. Westoby. 2001. Seed mass and seed nutrient content as predictors of seed output variation between species. Oikos 92:479–490.

Jakobsson, A., and O. Eriksson. 2000. A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. Oikos 88:494–502.

Kelly, D., and V. L. Sork. 2002. Mast seeding in perennial plants: why, how, where? Annual Review of Ecology and Systematics 33: 427–447.

Kennedy, P. G., N. J. Hausmann, E. H. Wenk, and T. E. Dawson. 2004. The importance of seed reserves for seedling performance: an integrated approach using morphological, physiological, and stable isotope techniques. Oecologia (Berlin) 141:547–554.

Knops, J. M. H., and W. D. Koenig. 1994. Water use strategies of five sympatric oaks in central coastal California. Madroño 40:290–301.

———. 2000. Annual variation in xylem water potential in California oaks. Madroño 47:106–108.

Knops, J. M. H., W. D. Koenig, and W. J. Carmen. 2007. A negative correlation does not imply a trade-off between growth and reproduction in California oaks. Proceedings of the National Academy of Sciences of the USA 104:16982–16985.

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

Koenig, W. D., J. M. H. Knops, W. J. Carmen, M. T. Stanback, and R. L. Mumme. 1994*b*. Estimating acorn crops using visual surveys. Canadian Journal of Forest Research 24:2105–2112.

Koenig, W. D., D. Kelly, V. L. Sork, R. P. Duncan, J. S. Elkinton, M. S. Peltonen, and R. D. Westfall. 2003. Dissecting components of population-level variation in seed production and the evolution of masting behavior. Oikos 102:581–591.

Leishman, M. R. 2001. Does the seed size/number trade-off model determine plant community structure? an assessment of the model mechanisms and their generality. Oikos 93:294–302.

Leith, H. 1975. Modeling the primary productivity of the world. Pages 237–263 *in* H. Leith and R. H. Whittaker, eds. Primary productivity of the biosphere. Springer, New York.

McComb, A. L. 1934. The relation between acorn weight and the development of one year chestnut oak seedlings. Journal of Forestry 32:479–484.

Moles, A. T., D. S. Falster, M. R. Leishman, and M. Westoby. 2004. Small-seeded species produce more seeds per square metre of canopy per year, but not per individual per lifetime. Journal of Ecology 92:384–396.

Morgan, M. T. 1998. Female fertility per flower and trade-offs between size and number in *Claytonia virginica* (Portulacaceae). American Journal of Botany 85:1231–1236.

Parciak, W. 2002. Environmental variation in seed number, size, and dispersal of a fleshy-fruited plant. Ecology 83:780–793.

Paul-Victor, C., L. Turnbull, and B. Schmid. 2007. Genetic basis of the seed size/seed number trade-off in *Arabidopsis thaliana*. Paper presented at the Ecological Society of America/Society for Ecological Restoration International joint meeting, August 5–10, San Jose, CA. http://eco.confex.com/eco/2007/techprogram/P3900.HTM.

Pavlik, B. M., P. C. Muick, S. Johnson, and M. Popper. 1991. Oaks of California. Cachuma, Los Olivos, CA.

Pease, C. M., and J. J. Bull. 1988. A critique of methods for measuring life history trade-offs. Journal of Evolutionary Biology 1:293–303.

Schaal, B. A. 1980. Reproductive capacity and seed size in *Lupinus texensis*. American Journal of Botany 67:703–709.

Smith, C. C., and S. D. Fretwell. 1974. The optimal balance between size and number of offspring. American Naturalist 108:499–506.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman, San Francisco.

Stearns, S. C. 1989. Trade-offs in life-history evolution. Functional Ecology 3:259–268.

Tripathi, R. S., and M. L. Khan. 1990. Effects of seed weight and microsite characteristics on germination and seedling fitness in two species of *Quercus* in a subtropical wet hill forest. Oikos 57: 289–296.

van Noordwijk, A. J., and G. de Jong. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. American Naturalist 128:137–142.

Vaughton, G., and M. Ramsey. 1998. Sources and consequences of seed mass variation in *Banksia marginata* (Proteaceae). Journal of Ecology 86:563–573.

Venable, D. L. 1992. Size-number trade-offs and the variation of seed size with plant resource status. American Naturalist 140:287–304.

Waring, R. H., and B. D. Cleary. 1967. Plant moisture stress: evaluation by pressure bomb. Science 155:1248–1254.

Warne, R. W., and E. L. Charnov. 2008. Reproductive allometry and the size-number trade-off for lizards. American Naturalist 172: E80–E98.

Westoby, M., E. Jurado, and M. R. Leishman. 1992. Comparative evolutionary ecology of seed size. Trends in Ecology & Evolution 7:368–372.

Wilbur, H. M. 1977. Propagule size, number, and dispersion pattern in *Ambystoma* and *Asclepias*. American Naturalist 111:43–68.

Wolf, L. L., F. R. Hainsworth, T. Mercier, and R. Benjamin. 1986. Seed size variation and pollinator uncertainty in *Ipomopsis aggregata* (Polemoniaceae). Journal of Ecology 74:361–371.

Wulff, R. D. 1986. Seed size variation in *Desmodium paniculatum*. I. Factors affecting seed size. Journal of Ecology 74:87–97.

Natural History Editor: Henry M. Wilbur

Left, a valley oak at the edge of Antelope Valley near the southern edge of its range. *Right*, valley oak acorns. In a good crop year, a single tree can produce upwards of 50,000 acorns. Acorns in such good years are larger, not smaller, than acorns produced in poor acorn years. Photographs by Walt Koenig.