

Oaks, acorns, and the geographical ecology of acorn woodpeckers

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Abstract

We investigated the geographical ecology of acorn woodpeckers (Melanerpes formicivorus) using 30 years of Audubon Christmas Bird Counts and data on the diversity and abundance of oaks. Spatial autocorrelation in acorn woodpecker population densities is not significantly greater than zero both in either the southwestern United States, where populations are often locally isolated, or along the Pacific Coast, where they are more evenly distributed. In both regions, the effective distributional limit of acorn woodpeckers is set not by the limits of oaks but by sites where oak diversity drops to a single species. This result is consistent with acorn production patterns in central coastal California demonstrating that variability in overall acorn production and the probability of acorn crop failure decline with increasing oak species number but drop most markedly when two, compared to one, species of oaks are present together. Along the Pacific Coast, acorn woodpecker densities increase and population variability decreases with increasing abundance and diversity of oaks; however, analyses indicate that overall population size in this region is primarily determined by resource abundance while population stability is determined by resource diversity. Comparable patterns are not obvious in the Southwest, where acorn woodpecker densities are much lower than along the Pacific Coast. This may be due to a combination of greater competition for resources and oak communities that differ both qualitatively and quantitatively in their productivity compared to those along the Pacific Coast.

Keywords

Acorn woodpeckers, acorns, Christmas bird counts, geographical ecology, spatial autocorrelation, oaks, Pacific Coast, United States.

INTRODUCTION

Acorn woodpeckers (*Melanerpes formicivorus* Swainson) are common and conspicuous residents of foothill and montane woodlands from northwestern Oregon, California, the American Southwest, and western Mexico through the highlands of Central America (Fig. 1) as far south as northern Colombia. They are notable for several reasons, including a close association with oaks (genera *Quercus* and *Lithocarpus*), the fruit of which constitutes a significant fraction of their diet (Koenig & Mumme, 1987; Koenig *et al.*, 1995). Throughout most of their range these birds are highly social and exhibit a unique method of storing acorns in specialized trees known as storage trees or granaries. Stored acorns are critical for winter residency and subsequent reproductive success (Hannon *et al.*, 1987; Koenig & Mumme, 1987). Acorns of all species of oaks may be stored and eaten.

Based on data from seven years of Audubon Society

Christmas bird counts, Bock & Bock (1974) reported several striking relationships between the geographical ecology of acorn woodpeckers and the diversity and abundance of oaks. Their central hypothesis was that the distribution and abundance of woodpeckers should be affected by the predictability of acorn crops, which in turn should increase as more species of oaks are present in an area. Related to this hypothesis, they documented the following patterns.

(1) The distributional limits of acorn woodpeckers appeared to coincide not with the limits of oaks *per se*, but rather with those points where oak species number drops to a single common species.

(2) An apparently linear relationship existed between oak abundance and the average abundance of acorn woodpeckers along the Pacific Coast (corresponding to the subspecies *bairdi*) but not in the Southwest (corresponding to the subspecies *formicivorus*).

(3) Along the Pacific Coast, there existed a nearly exponential relationship between woodpecker abundance and oak species diversity up to five species, beyond which the relationship was

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Figure 1 The distribution of acorn woodpeckers in North and Middle America (from Koenig *et al.*, 1995). Isolated populations also occur in northern Colombia. Birds are primarily resident throughout their range.

flat. No relationship between oak species number and mean woodpecker abundance in the southwestern United States was found.

Based on these results, Bock & Bock (1974) proposed that acorn woodpeckers along the Pacific Coast living in sites with fewer than five oak species are subject to random, frequent acorn crop failures acting in a catastrophic and densityindependent manner, but that birds living in areas with more species of oaks are limited in a density-dependent manner not by oak species numbers but by oak (and hence acorn) abundance. In contrast, they suggested that birds in the Southwest are always likely to be limited by density independent factors because the critical threshold of consistent yearly production of acorns is never achieved.

Here we reexamine the geographical ecology of acorn woodpeckers and extend the earlier results of Bock & Bock (1974). There are two reasons why such a reanalysis is appropriate. First, thanks to subsequent efforts by the Laboratory of Ornithology at Cornell University and the National Biological Service, 30 years of Audubon Christmas bird count data are now available. Such sample sizes allow more detailed and specific testing of the relationship between acorn woodpeckers and oak species number than was possible using the data painstakingly computerized by Bock & Bock (1974). Second, studies of acorn production at Hastings Reservation in central coastal California (Koenig *et al.*, 1994b) make it possible to examine the relationship between acorn production and oak species number in much greater detail than previously possible.

Specifically, we address the following questions.

(1) What is the relationship between oak species number and the probability of acorn crop failure?

(2) How spatially autocorrelated are acorn woodpecker population sizes? Are patterns of spatial autocorrelation in woodpecker populations similar to those exhibited by acorn production?

(3) What is the relationship of oak abundance and oak species number to the abundance and annual variability in acorn woodpecker populations?

(4) Is there support for the hypothesis that the factors limiting population size of acorn woodpeckers along the Pacific Coast are different from those in the Southwest? Are such differences related to different relationships between acorn woodpeckers and oak species numbers, as suggested by Bock & Bock (1974)?

METHODS

Acorn production and oak species number

Acorns of five species of oaks were censused each fall between 1980 to 1996 at Hasting Reservation, a 900-ha reserve located in the Santa Lucia Mountains of central coastal California. Visual counts were made on a total of 249 individual trees including eighty-seven Q. lobata Née, fifty-seven Q. douglasii Hook. & Arn., sixty-three Q. agrifolia Née, twenty-one Q. chrysolepis Liebm. Trees were located throughout the reserve, but all were within 3.5 km of each other. Details and justification of the these methods are presented in Koenig et al. (1994a). Additional information about the five species can be found in Koenig et al. (1994b) and Knops & Koenig (1997); one difference between the species important because of its potential role in affecting patterns of acorn production is that *Q. lobata*, *Q.* douglasii, and Q. agrifolia require 1 year to mature acorns ('1year species'), while Q. kelloggii and Q. chrysolepsis require 2 years to mature a crop of acorns ('2-year species').

Christmas bird counts

Data spanning 30 years from the winter of 1959-60 to 1988-89 were downloaded from the Christmas Bird Count (CBC) Database maintained by the National Biological Service (ftp:// ftp.im.nbs.gov/pub/data.cbc). Files were used as provided, except that counts that did not overlap in time and were within 3 min of both latitude and longitude were combined. Numbers of individual acorn woodpeckers reported during counts were divided by the total number of hours spent counting by groups in separate parties within a site to standardize for differential effort. Only counts conducted within the normal range of acorn woodpeckers (Oregon, California, Arizona, New Mexico, and Texas) and that reported acorn woodpeckers during at least one year were used in the analysis. Data were divided geographically into two regions corresponding to the U.S. range of the subspecies bairdi (Oregon and California along the 'Pacific Coast') and the U.S. range of the subspecies *formicivorus* (Arizona, New Mexico, and Texas in the 'Southwest'). In total, the data set included 2614 censuses conducted at 150 different sites for an average of 17.4 years per site.

For details and discussion of CBC data, see Bock & Root (1981) and Root (1988).

Statistical methods

Variation in acorn production

Annual variation in the total acorn crop at Hastings Reservation as a function of oak species number was estimated as follows. First, we calculated the mean log-transformed acorn crop for each species for each year. Correlations between pairs of species were calculated using these values. Second, we averaged mean values across all species included in a particular analysis, again for each year. Third, we calculated the overall coefficient of variation (CV) in the resulting mean values over the entire 17year length of the census. Fourth, we averaged CV values across all combinations of n species. The number of such combinations for n=1 to 5 is 5, 10, 10, 5, and 1, respectively.

We also compared the percentage of years in which an acorn crop failure occurred, where failures were defined as a year in which the log-transformed mean value (averaged across all species included in the analysis as per step 2, above) was <0.5. This cutoff was used because when the overall acorn crop was less than this, a substantial fraction of the acorn woodpecker population is forced to abandon their territories during the winter (Hannon *et al.*, 1987). However, the exact cutoff value is not critical to the conclusions.

Spatial autocorrelations

Spatial autocorrelation in acorn production on a global scale based on data from the literature is reported elsewhere (Koenig & Knops, 1997). Here we contrast results from that study with spatial autocorrelation in annual acorn woodpecker abundances as determined from the CBC database.

In order to test for spatial autocorrelation, we logtransformed CBC values to reduce the correlation between the mean and variance. Then, for each site, we performed a linear regression of year on the log-transformed values; values used in subsequent analyses were the residuals from these regressions. This procedure avoids spurious cross-correlations due to longterm changes in population size (Hanski & Woiwod, 1993; Koenig & Knops, 1998).

We then calculated Pearson correlation coefficients (r) and great-circle distances for all pairwise combinations of sites that were conducted simultaneously on at least four years. Positive r values indicate that the relative annual numbers of acorn woodpeckers counted at the two sites were similar at the two sites (that is, when a relatively large number were counted at site A, a relatively large number were also counted at site B), while negative r values indicate the converse.

This procedure yields two matrices, one with the distance between sites and the other with the correlation coefficients between the standardized annual numbers of the target species. We analyzed these data with modified correlograms following the procedure of Koenig & Knops (1998). In short, pairwise sites were divided into five distance categories based on whether the geographic distance between them was ≤ 100 km, >100-250 km, >250-500 km, >500-1000 km, or >1000 km apart. Within each distance category, randomization trials were conducted in which sets of correlation coefficients were chosen from the pool such that individual CBC sites were only used once. Once a complete set of correlations from non-overlapping pairwise combinations of sites was chosen, the mean *r* value for the trial is calculated and the number of positive and negative correlation coefficients present in the chosen set summed.

A total of 1000 trials was performed for each distance category; trials were checked to ensure that the set of pairwise combinations used was unique. Means were calculated from the set of mean *r* values generated by the randomization trials. Statistical significance was assessed based on the proportion of the 1000 trials yielding more positive than negative correlations; for example, if 990 trials yielded more positive than negative correlations, P = 0.01.

Oaks and acorn woodpeckers

We estimated the relative amount of each site covered by oaks based on the information reported in the published site description. Sites were divided into four categories roughly corresponding to <10%, 10-<20%, 20-<30%, and \geq 30% of the site covered by oaks. Oak species present at each site were determined from distributional data and maps published in Griffin & Critchfield (1972) and Miller & Lamb (1985). Only species of *Quercus* and *Lithocarpus* that normally grow as trees were included; hybrids and species normally growing as shrubs were not. Number of years species require to mature acorns was taken from Miller & Lamb (1985).

Several sources of error are inherent in this procedure. First, although we took into account known elevational differences between tree distributions and count sites whenever possible, we could not always be certain of the elevational range of particular count sites. A second problem is our decision to exclude shrub oaks. This was necessary primarily because the distributions of tree oaks are thoroughly mapped, whereas those of many shrubby forms are not. Also, our long-term studies of acorn woodpeckers suggest that these birds prefer to obtain acorns from the canopy whenever possible. In any case, these problems should not result in any differences between our results and those of Bock & Bock (1974), since they used an identical protocol.

Effects of oak species number and oak abundance on acorn woodpecker populations were determined by analysis of variance (ANOVA) so as to allow for the detection of nonlinear relationships.

RESULTS

Oak species number and acorn crop variability

A basic assumption of the analyses performed here and by Bock & Bock (1974) is that variability in acorn production declines with increasing number of species. Correlations between the mean annual acorn crop of the five species surveyed

Table I Spearman rank correlation coefficients of mean log-transformed annual acorn production by five species of oaks at Hastings Reservation between 1980 and 1996 (n = 17 years). Number of years species require to mature acorns is listed in parenthesis after each species. Comparisons between species that require different numbers of years to mature acorns are in boldface type.

	Q. lobata (1)	Q. douglasii (1)	Q. agrifolia (1)	Q. chrysolepis (2)
Q. douglasii (1)	0.87***			
Q. agrifolia (1)	0.37	0.59**		
Q. chrysolepis (2)	-0.25	-0.36	-0.03	
Q. kelloggii (2)	-0.07	-0.28	-0.23	0.49

P<0.01; *P<0.001; other P>0.05.

at Hastings Reservation (Table 1) indicate that mean annual crops of different species can be similar, sometimes significantly so, but that they are not completely synchronous. Thus, annual variability in the acorn crop on a community-wide basis should decline as more species are present in a site. This pattern is likely to be especially pronounced when species requiring different number of years to mature acorns are present in a site, as acorn crops are generally positively correlated between species requiring the same number of years to mature acorns (four of four correlations), but not between those requiring different numbers of years to mature acorns (zero of six correlations), a significant difference (Fisher exact test, *P*<0.01).

It follows that annual variability in overall acorn crop size and the probability of acorn crop failures should decline as more species of oaks are present, relationships that both hold using data on acorn production at Hastings Reservation (Fig. 2). However, the only statistically significant difference is between single species samples and samples including two or more species. Based on these results, we predict that annual variability in acorn woodpecker population size should be lower in sites containing more species of oaks and that the difference between sites containing one compared to two or more species of oak should be particularly pronounced.

Spatial autocorrelation of acorn woodpecker populations

Long-term population studies of acorn woodpeckers at Hastings Reservation indicate that reproductive success and juvenile survivorship are strongly dependent on the size of the acorn crop (W.D. Koenig, unpublished data). Furthermore, prior work has demonstrated that spatial autocorrelation in acorn production by species requiring the same number of years to mature acorns is significantly positive between sites up to 500–1000 km apart (Koenig & Knops, 1997). Consequently, to the extent that acorn woodpecker populations track acorn availability, their populations should be similarly spatially autocorrelated.

Results from analyses of the CBC data falsify this hypothesis; spatial autocorrelations between acorn woodpecker populations are not significantly greater than zero, even for sites <100 km apart (Fig. 3).

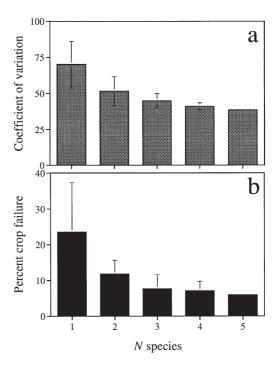


Figure 2 The (a) mean coefficient of variation in overall acorn abundance and (b) probability of crop failure, as defined by an overall mean log-transformed acorn crop <0.5 (see text) plotted against the number of species included in the analysis. Data based on 17 years of acorn production data on five species of oaks at Hastings Reservation, central coastal California. Each point represents the mean of all possible permutations of *n* species, where n=1 to 5. For each set of permutations, the log-transformed means of each species were themselves averaged to obtain the overall mean acorn crop for each year.

Acorn woodpeckers and oaks

Along the Pacific Coast, there are highly significant differences in the mean and CV of mean acorn woodpecker abundance as a function of oak abundance category (Kruskal–Wallis oneway ANOVAs; mean abundance: $\chi^2=33.9$, df=3, P<0.001; CV: $\chi^2=10.4$, df=3, P<0.02). In general, mean abundance increases and the CV of mean abundance decreases with

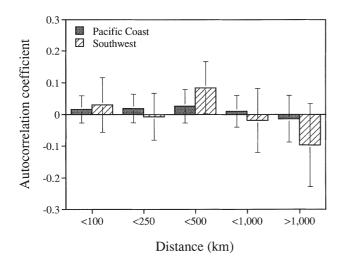


Figure 3 Modified correlograms of the mean $(\pm SD)$ autocorrelation coefficients between annual population densities of acorn woodpeckers divided according to region (Pacific Coast or Southwest) and distance between sites. None of the values are significantly different than zero.

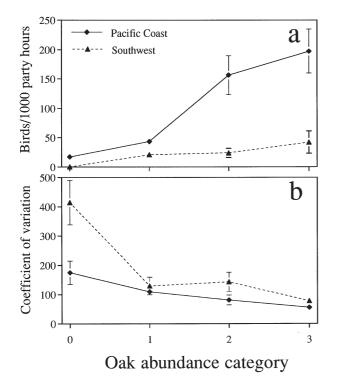


Figure 4 Mean $(\pm SE)$ density (a) and CV (b) of acorn woodpecker populations along the Pacific Coast and the Southwest plotted as a function of oak abundance within sites. Data based on Christmas Bird Counts conducted between 1959–60 and 1988–89.

increasing oak abundance (Fig. 4). Trends are similar in the Southwest, but differences between oak abundance categories are not quite statistically significant (mean abundance: $\chi^2 =$ 7.4, df = 3, *P* = 0.06; CV: $\chi^2 =$ 7.6, df = 3, *P* = 0.06).

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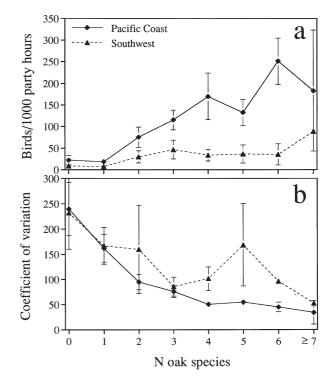


Figure 5 Mean (\pm SE) density (a) and CV (b) of acorn woodpecker populations along the Pacific Coast and the Southwest plotted as a function of oak species numbers present within sites. Data based on Christmas Bird Counts conducted between 1959–60 and 1988–89.

Along the Pacific Coast, these patterns are repeated in acorn woodpecker abundance versus oak species number (Fig. 5). Trends are strongly positive (mean) and negative (CV of the mean) and differences according to different numbers of oak species are both highly significant (Kruskal–Wallis one-way ANOVAs with localities containing five or more species of oaks lumped; mean abundance: $\chi^2=41.0$, df=5, P<0.001; CV: $\chi^2=23.6$, df=5, P<0.001). In contrast, acorn woodpecker population size and variability do not differ significantly with oak species number in the Southwest (mean abundance: $\chi^2=$ 5.7, df=5, P=0.34; CV: $\chi^2=4.7$, df=5, P=0.45). In both areas, acorn woodpeckers are rarely found in areas containing one species of oak.

Because the relationships between acorn woodpecker populations and both oak species number and oak abundance are similar, we performed two-way ANOVAs to disentangle their effects (Table 2). Along the Pacific Coast, oak abundance determines mean acorn woodpecker size but the number of oak species determines the CV in acorn woodpecker population size. In the Southwest, where acorn woodpecker population sizes are much lower and sample sizes smaller, the only significant effect detected was a barely significant effect of oak abundance on the CV of annual acorn woodpecker population size.

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Table 2 Results of two-way ANOVAs examining the effects of oak species number and oak abundance on the mean and CV of acorn woodpecker abundance as determined from CBC data. Sites with five or more species of oaks were combined. Oak abundance categories were 0–3 based on published description of the CBC site (see text). Interaction terms for all analyses were non-significant (ns; P>0.05).

	F-value	df	P-value
Pacific Coast			
Mean			
Oak species	1.30	5,82	ns
Oak abundance	6.15	3, 82	< 0.001
CV			
Oak species	3.22	5,82	= 0.01
Oak abundance	0.23	3, 82	ns
Southwest			
Mean			
Oak species	1.37	5, 16	ns
Oak abdundance	0.47	3, 16	ns
CV			
Oak species	0.29	5, 16	ns
Oak abundance	4.09	3, 16	< 0.05

DISCUSSION

The hypotheses that variability in annual acorn production and the probability of overall crop failure decline with increasing oak species diversity are verified by acorn production patterns at Hastings Reservation (Fig. 2). A major reason for this decline is the asynchrony between the crops of oak species that require different numbers of years to mature acorns. Unfortunately, few data from other sites are available. However, these results suggest that the acorn crops of oak species requiring the same number of years to mature acorns are positively correlated, sometimes significantly so, but those requiring different numbers of years are not (Table 1).

Species requiring the same number of years to mature acorns produce crops that are also spatially autocorrelated, both intraand inter-specifically, over large geographic areas up to 1000 km (Koenig & Knops, 1997). However, this widespread geographic synchrony in acorn production does not translate into comparable synchrony in acorn woodpecker populations (Fig. 3). The primary reason for this is likely to be the asynchrony in acorn production between different species of oaks, particularly those that require different numbers of years to mature acorns (Table 1). Because of this, sites that contain different oak species often have very different overall acorn crops, even when they are geographically close. Furthermore, acorn woodpeckers forced to abandon territories in the fall due to locally poor acorn crops may move to nearby areas where acorns are available (Hannon et al., 1987) further reducing spatial autocorrelation in population size.

As a result, populations of acorn woodpeckers throughout their U.S. range vary in size independently of each other and may act as metapopulations connected to each other by dispersal whose local persistence may depend on regional processes (Hanski & Gilpin, 1991). This has previously been proposed for acorn woodpeckers in the Southwest by Stacey & Taper (1992), where populations are often isolated in riparian or montane situations. Apparently, similar processes may be important along the Pacific Coast, where acorn woodpecker populations are typically more dense and more evenly distributed.

Along the Pacific Coast, acorn woodpeckers increase in overall density with increasing oak abundance (Fig. 4a) and with increasing oak species number (Fig. 5a). Patterns are similar in the Southwest but on a reduced scale: for example, sites in the Southwest containing seven or more species of oaks support densities of acorn woodpeckers roughly equal to those along the Pacific Coast containing only two species of oaks (Fig. 5a). Similarly, Southwestern sites with an estimated 30% + of oak woodland support densities of acorn woodpeckers roughly equal to those of Pacific Coast sites containing 10-20% of oak woodland.

Two-way ANOVAs including both oak species number and oak abundance indicate that these factors have very different effects on acorn woodpecker populations along the Pacific Coast (Table 2). Specifically, oak abundance appears to be the prime determinant of mean woodpecker population size while oak species number is the prime determinant of annual population variability. Thus, our analyses support the intuitively pleasing conclusion that mean population size is determined by resource (oak) abundance, while annual variability in population size is determined by resource variability, which is in turn inversely dependent on oak species number (Fig. 2). This pattern was not found in the Southwest (Table 2).

These findings are generally consistent with the assumptions and results previously reported by Bock & Bock (1974). First, our data support the assumption that overall acorn productivity is more stable and the probability of a crop failure lower when more species of oaks are present within a site (Fig. 2) due to asynchrony in acorn production between different species of oaks-especially those requiring different numbers of years to mature acorns (Table 1). The largest difference is found between one species of oak, for which the average probability of crop failure is 23.5% or nearly once per acorn woodpecker generation, and two species of oaks, for which the probability of crop failure is 11.8% or less than once every two generations. This sharp drop appears to determine the effective distributional limit of acorn woodpeckers, which are regularly found only in sites containing two or more species of oaks (Fig. 5a), as previously suggested by Bock & Bock (1974).

Our analyses also corroborate Bock & Bock's (1974) finding that populations of acorn woodpeckers are distinctly sparser in the Southwest than along the Pacific Coast independent of oak species number or oak abundance (Figs 4 and 5). Bock & Bock (1974) suggested that this difference might be due to different population regulation mechanisms acting in the two areas. Specifically, they suggested that most acorn woodpeckers living along the Pacific Coast are present in areas of high oak species number above a critical threshold of consistent yearly acorn production and are consequently limited in a densitydependent manner by oak abundance. In contrast, they suggested that birds in the Southwest are limited by density independent factors because the critical threshold of consistent yearly production of acorns is never achieved. These conclusions were based in part on the existence of a resource diversity threshold of five oak species along the Pacific Coast, which our analyses failed to detect (Fig. 4a). However, our results support the hypothesis that mean acorn woodpecker abundance at sites along the Pacific Coast is determined by oak abundance rather than oak species number (Table 2). In contrast, oak species number, but not oak abundance, determines annual variability in acorn woodpecker population size. Thus, acorn woodpecker populations are more dense where oaks are more abundant, but they are more stable from year to year where oak species diversity is greater. These patterns are precisely those predicted if oak abundance limits overall population size in a density-dependent manner.

In contrast, we found only weak effects of both oak species number and oak abundance on acorn woodpecker populations in the Southwest. One interpretation of this is that a critical threshold of consistent yearly production of acorns is never achieved, as suggested by Bock & Bock (1974). Unfortunately, neither our analyses nor the earlier ones of Bock & Bock (1974) shed much light on why this might be the case. The possibility that oaks in the Southwest are generally less productive than those along the Pacific Coast cannot be ruled out and may contribute to the observed patterns. Lower oak species diversity in the Southwest does not appear to be a factor, since oak species numbers are not notably lower than along the Pacific Coast. However, the relative occurrence of oaks of different types in the two regions may be important. Only 16% of twenty-five sites identified as being within the range of one of the oaks in the Southwest contained both species requiring one and two years to mature acorn crops, whereas 63% of 104 sites along the Pacific Coast contained species of both types, a highly significant difference (Fisher exact test, P<0.001). Because of the generally high synchrony between annual acorn crops of oaks within types requiring the same number of years to mature acorns (Table 1), this is likely to result in higher overall annual variability and an increased probability of acorn crop failure in the Southwest as well as a lower dependence of these demographic variables on oak species number.

These results confirm that along the Pacific Coast, the geographical ecology of acorn woodpeckers is strongly related to both the abundance and diversity of oaks and that the distributional limit of acorn woodpeckers is generally set by the presence of at least two common species of oaks. This latter relationship is also found in the Southwest, but otherwise the effects of either oak abundance or diversity are weak in this part of their range. Additional population data, especially from Mexico where oak species diversity can be very high, will be necessary in order to clarify the relationship between acorn woodpeckers and oaks in this region.

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REFERENCES

- Bock, C.E. & Bock, J.H. (1974) Geographical ecology of the acorn woodpecker: diversity versus abundance of resources. Am. Nat. 108, 694–698.
- Bock, C.E. & Root, T.L. (1981) The Christmas Bird Count and avian ecology. *Stud. Avian Biol.* 6, 17–23.
- Griffin, J.R. & Critchfield, W.B. (1972) The distribution of forest trees in California. USDA Forest Service Research Paper PSW-82.
- Hannon, S.J., Mumme, R.L., Koenig, W.D., Spon, S. & Pitelka F.A. (1987) Acorn crop failure, dominance, and a decline in numbers in the cooperatively breeding acorn woodpecker. J. anim. Ecol. 56, 197–207.
- Hanski, I. & Gilpin, M. (1991) Metapopulation dynamics: brief history and conceptual domain. *Biol. J. Linn. Soc.* 42, 3–16.
- Hanski, I. & Woiwod, I.P. (1993) Spatial synchrony in the dynamics of moth and aphid populations. J. anim. Ecol. 62, 656–668.
- Koenig, W.D. & Knopps, J.M.H. (1997) Patterns of geographic synchrony in growth and reproduction of oaks within California and beyond. Proceedings of a symposium on oak woodlands: ecology, management, and urban interface issues. (ed. by N.H. Pillsbury, J. Verner and W.D. Tietje), pp. 101–106. USDA Forest Service Gen. Tech. Rep. PSW-GTR-160.
- Koenig, W.D. & Knops, J.M.H. (1998) Testing for spatial autocorrelation in ecological studies. *Ecography* 21, 423–429.
- Koenig, W.D. & Mumme, R.L. (1987) Population ecology of the cooperatively breeding acorn woodpecker. Princeton University Press, Princeton.
- Koenig, W.D., Knops, J.M.H., Carmen, W.J., Stanback, M.T. & Mumme, R.L. (1994a) Estimating acorn crops using visual surveys. *Can. J. For. Res.* 24, 2105–2112.
- Koenig, W.D., Mumme, R.L., Carmen, W.J. & Stanback, M.T. (1994b) Acorn production by oaks in central coastal California: variation within and among years. *Ecology*, 75, 99–109.
- Koenig, W.D., Stacey, P.B., Stanback, M.T. & Mumme, R.L. (1995) Acorn woodpecker (*Melanerpes formicivorus*). *The birds of North America*, No. 194 (ed. by A. Poole and F. Gill). Academy of Natural Sciences, Philadelphia; American Ornithologists' Union, Washington, D.C.
- Knops, J.M.H. & Koenig, W.D. (1997) Site fertility and leaf nutrients of sympatric evergreen and deciduous species of *Quercus* in central coastal California. *Plant Ecol.* 130, 121–131.
- Miller, H. & Lamb, S. (1985) Oaks of North America, 327 pp. Naturegraph Publishers, Inc., Happy Camp, California.
- Root, T. (1988) Atlas of wintering North American birds, 312 pp. University of Chicago Press, Chicago, Illinois.
- Stacey, P.B. & Taper, M. (1992) Environmental variation and the persistence of small populations. *Ecol. Appl.* 2, 18–29.