

Mast-producing trees and the geographical ecology of western scrub-jays

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We analyzed the relationship between population abundance and variability of western scrub-jays *Aphelocoma californica* based on 48 yr of Audubon Christmas Bird Counts and the resources on which they depend as indexed by the diversity and abundance of mast-producing oaks and pines and, for California, estimates of acorn production based on a statewide survey. In general, populations of *A. c. californica* along the Pacific coast were related to oaks, with populations being more abundant and more stable in areas with more oak species and greater oak abundance. In contrast, populations of *A. c. woodhouseii* in the Great Basin were correlated with pines/conifers, again with higher abundance and greater stability with increased number of pine species and greater abundance of pines/conifers. The presumed driver of these patterns is increased resource abundance with greater habitat abundance and increased resource stability with increasing species diversity due to asynchrony in seed production among different species of trees. Asynchrony in acorn production is particularly high among oaks that require different number of years to produce acorns, but we failed to confirm that populations with access to both types were more stable than those with access to only one type after controlling for oak diversity. However, we did find a strong positive correlation between overall mean scrub-jay abundance in California and overall acorn production one year earlier, suggesting that acorns benefit scrub-jay populations primarily by increasing reproductive success the following year. These patterns demonstrate the strong dependence between population dynamics and resource stability as well as how different these relationships can be within closely related taxa.

Scrub-jays (*Aphelocoma* spp.) are widely distributed and familiar birds found in a broad range of lowland and lower montane arid habitats including brush, chaparral, oak, piñon pine (*Pinus edulis* and *P. monophylla*), juniper (*Juniperus* spp.) riparian woodland, and tropical deciduous forest (Peterson and Vargas B. 1993, AOU 1998, Curry et al. 2002). Over the wide geographic range of the genus (Fig. 1), congeners differ considerably in morphology and are behaviorally complex, making it a model not only for studies on morphological evolution (Pitelka 1951, Peterson 1992, Bardwell et al. 2001), but also for studies of behavioral ecology (Woolfenden and Fitzpatrick 1984, Peterson and Burt 1992, Burt and Peterson 1993, Carmen 2004), spatial memory (Vander Wall and Balda 1981, Balda and Kamil 1989, Balda et al. 1997, Bednekoff et al. 1997), and cognition (Emery and Clayton 2001, Raby et al. 2007).

Given their wide morphological variation it is not surprising that scrub-jays are also complex systematically. Although historically divided into as many as 14 subspecies (Pitelka 1951), two disjunct populations, the Island scrub-

jay *A. insularis* on Santa Cruz Island off the coast of California and the Florida scrub-jay *A. coerulescens* of central Florida, are now considered separate species. The remaining populations of what is currently known as the western scrub-jay *A. californica* consist of three groups: *A. c. californica* (the California scrub-jay) from northwestern USA to Baja California, Mexico; *A. c. woodhouseii* (Woodhouse's scrub-jay) from northwestern Nevada to north-central Mexico; and *A. c. sumichrasti* (Sumichrast's scrub-jay) in south-central Mexico. However, these groups may be separate species (Delaney et al. 2008), helping to make this taxon one of continuing phylogenetic as well as behavioral interest (Peterson 1991, 1992, MacDonald et al. 1999).

Here we focus on the habitat relationships of the western scrub-jay, which vary along subspecific lines in conjunction with morphological differences in bill size and shape (Peterson 1993, Bardwell et al. 2001). Specifically, *A. c. californica* is largely associated with oak woodlands and oak-pine woodlands, while *A. c. woodhouseii* is found in both oak and oak-piñon pine-juniper woodlands and *A. c. sumichrasti*

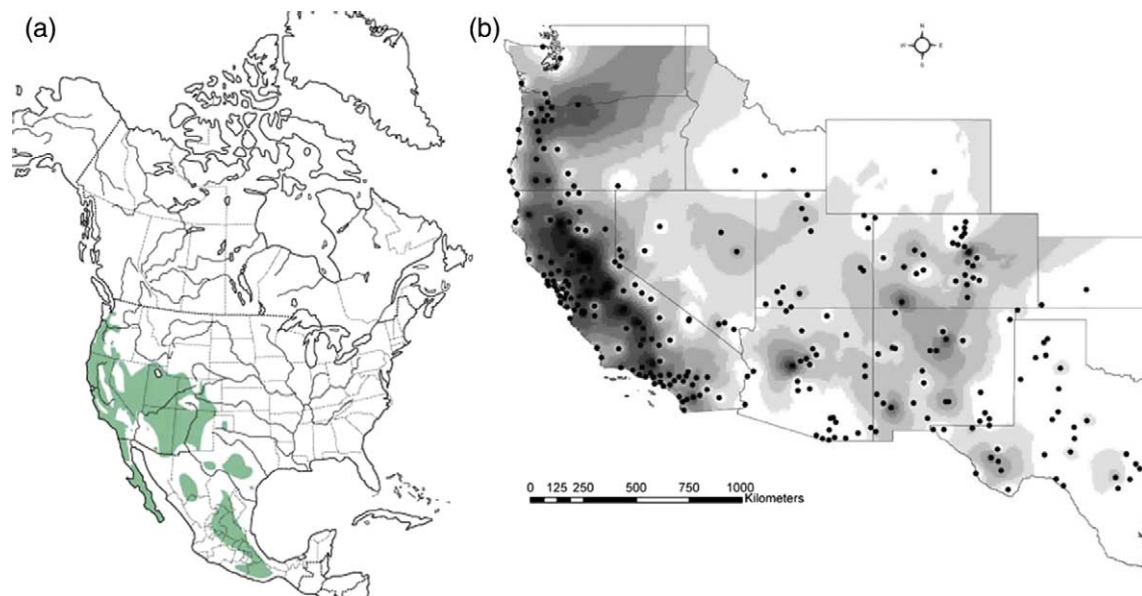


Figure 1. (a) The geographic distribution of western scrub-jays. Birds are resident throughout their range. *Aphelocoma c. californica* includes birds along the west coast from Washington through southern Baja including California except for the eastern mountains. *Aphelocoma c. woodhouseii* includes interior birds from southeastern Oregon and eastern California to Texas and central Mexico. *Aphelocoma c. sumichrasti* ranges from Tlaxcala in central Mexico south to Oaxaca and west-central Veracruz. From Curry et al. (2002), with permission. (b) The western USA with locations of the CBC sites used in the analysis marked. The degree of shading represents the average density of western scrub-jays; in general, densities are relatively high for *A. c. californica* and low for *A. c. woodhouseii*.

is often found in open or cut forests of oaks and pines (Curry et al. 2002). These generalizations, along with several studies of individual populations (Carmen 2004), suggest that the nuts of mast-producing trees, particularly oaks and pines, are key to the distributional ecology of this species. However, exceptions exist, particularly among some populations in peripheral parts of its range, where birds occupy habitats lacking mast-producing trees and nonetheless appear to be relatively common and successful (Peterson and Vargas B. 1993, Curry et al. 2002).

Given this variability, the primary question we address here is the extent to which the abundance and variability of western scrub-jay populations is concordant with oak and pine species diversity, and the extent to which patterns differ between the two major groups (*A. c. californica* and *A. c. woodhouseii*) for which data are available. We are able to further investigate the relationship between western scrub-jays and oaks in California due to detailed distributional data from the California Gap Analysis Project (Davis et al. 1998), and look specifically at the scrub-jay's relationship with acorn abundance, one of its major food resources, with data from a statewide acorn survey (Koenig and Knops 1997).

These analyses parallel in part those conducted earlier by Bock and Bock (1974) and Koenig and Haydock (1999) on the geographical ecology of the acorn woodpecker *Melanerpes formicivorus*, another mast-dependent western species. Analyzing earlier data from Hastings Reservation in central coastal California, Koenig and Haydock (1999) showed that variability in acorn production and the probability of an overall acorn crop failure declined with the number of oak species, a pattern attributable to asynchrony in acorn production by different oaks, particularly those requiring one year to mature acorns (1-yr

species) compared to those requiring two years to mature acorns (2-yr species) (Koenig and Knops 2002). These authors went on to show that increased oak species diversity correlated with decreasing annual variability in numbers of acorn woodpeckers on the Pacific coast, presumably because of lower annual variability of the acorn crop. This decline was greatest between areas with one and two species of oaks, suggesting that this was the main factor limiting acorn woodpeckers in this area to sites with at least two species of oaks.

Specific questions we address here include: 1) what is the relationship between western scrub-jay population abundance and variability to the diversity and abundance of oaks and pines? 2) How do these relationships differ between *A. c. californica* and *A. c. woodhouseii*, the two major groups of scrub-jays found in the USA? A priori, we predicted that populations of *A. c. californica*, which are generally dependent on acorns, should be more closely dependent on oaks while those of *A. c. woodhouseii*, which feed heavily on pine nuts, should be more closely tied to pines. 3) Are populations of western scrub-jays in California affected by the availability of oak species differing in the number of years they require to mature acorns? Because acorn production of the two different types of species (1-yr and 2-yr) are uncorrelated, we predicted that populations living in sites with access to both types of species should be relatively denser and less variable from year to year than populations living in sites with access to acorns of only one type of species. 4) Can we detect a relationship between acorn crop productivity and western scrub-jay abundance? Scrub-jays are well known to harvest and store acorns in the fall (DeGange et al. 1989, Carmen 2004) and thus a good acorn crop could potentially increase populations in at least three ways: by attracting immigrants from areas of poor

acorn productivity, by increased overwinter survival, and by increased reproductive success the next spring. If either of the first two of these mechanisms is important we would potentially expect a positive correlation between mast abundance in year x and bird abundance the same winter (year x). If a good acorn crop results primarily in increased reproductive success the next spring we would predict a positive correlation between mast abundance in year x and bird abundance the following winter in year $x+1$.

Methods

Bird abundance and distribution

Our source of data for western scrub-jay distribution and abundance was the Christmas Bird Count (CBC) Database maintained by the National Audubon Society. CBC counts involve up to 100 or more people counting all the birds they can during a single day within the last two weeks of December within a 24 km diameter circle (total area ca 452 km²). Counts included in the analysis were conducted over the 48 yr from the winter of 1959–1960 through 2006–2007. Files were used as provided, except that counts not overlapping in time and located within 3 min of both latitude and longitude were assumed to have been conducted at the same site and combined. Numbers of individual scrub-jays reported were standardized for effort by dividing by the total number of hours spent counting by groups in separate parties within a site to yield “birds per party hour” (BPPH). We then calculated the mean and coefficient of variation (CV; $SD/mean \times 100$) using BPPH values across all years each count was performed for an estimate of overall relative abundance and variability at that site. Only sites with at least 10 yr of data and reporting western scrub-jays during at least one year were used in the analysis. Since western scrub-jays are a relatively noisy and easily detected species, we are confident that CBC numbers generally provide good estimates of its relative abundance. Data were divided geographically into two regions corresponding to the USA range of *A. c. californica* (California, Oregon, and Washington) and that of *A. c. woodhouseii* (all other populations from Nevada through Texas; Curry et al. 2002). In total, we analyzed 10 223 censuses conducted at 478 sites for an average of 21 yr per site. For further details and discussion of CBC data see Bock and Root (1981) and Root (1988).

Overall, populations of *A. c. californica* neither increased nor decreased over the 48 yr of the study (linear regression of birds per party hour = 0.003 [yr]–3.484, $F_{1,5222} = 1.4$, $p = 0.24$). In contrast, populations of *A. c. woodhouseii* increased significantly (birds per party hour = 0.042 [yr]–7.891, $F_{1,4997} = 4.4$, $p < 0.001$). However, this trend is unlikely to have affected the results of the analyses conducted here.

Oak and pine diversity and abundance

We used two sources for data on tree distributions and abundance. First, for all sites we compiled data on overall estimated amount of each site covered by oaks and by conifers (necessitated because estimates are not made

for pines separately) based on the published CBC site descriptions. For some analyses, sites were then divided into five categories corresponding to 0, >0–5, >5–10, >10–20, and >20% of the site estimated to be covered by oaks and conifers, respectively. Next we determined the number of oak (*Quercus* and *Lithocarpus*) and pine (*Pinus*) species present at each site based on distributional data and maps in Griffin and Critchfield (1972) and USGS (2008). Because they are not included in these compilations, hybrids and species that normally grow as shrubs were not included. We then analyzed the relationship between the mean western scrub-jay abundance across all years and the mean CV among years for sites containing a given number of oak or pine species or a given abundance of oaks and conifers, combining sites with six or more species of oaks and those with five or more species of pines.

Number of years species require to mature acorns was taken from Miller and Lamb (1985). In general, oaks in the subgenus *Leucobalanus* (white oaks) fertilize and mature acorns in a single season (1-yr species) while those in the subgenus *Erythrobalanus* (black or red oaks) mature acorns the year following fertilization (2-yr species). There are exceptions, however, including at least one common California species, the coast live oak *Q. agrifolia*, which is a 1-yr species despite being in the *Erythrobalanus* subgenus.

The above values are subject to several sources of error, including problems associated with the published estimates of oak and conifer abundance, the use of an estimate for coniferous forest in general rather than pine forest in particular, and uncertainty with respect to whether a particular site encompasses the range of a given oak or pine species. We thus conducted a second set of analyses, using only the California data, for which we extracted detailed data on oak and pine abundance and distribution from the California Gap Analysis Project (Davis et al. 1998). The California Gap data are estimated to be 80% accurate (with 95% confidence) at a spatial resolution of 1 km², corresponding to 0.2% of the area encompassed by the CBC count circle. For each California CBC site, we determined the probable presence of each of California’s acorn-producing species, including shrub forms but not hybrids (*Quercus agrifolia*, *Q. berberidifolia*, *Q. chrysolepis*, *Q. cornelius-mullerii*, *Q. douglasii*, *Q. durata*, *Q. engelmannii*, *Q. garryana*, *Q. john-tuckeri*, *Q. kelloggii*, *Q. lobata*, *Q. sadleriana*, *Q. vaccinifolia*, *Q. wislizeni*, and *Lithocarpus densiflorus*) as well as the area within the site encompassed by all oaks combined. Similarly, for pines, we determined the probable presence of each of California’s 18 species (*Pinus albicaulis*, *P. attenuata*, *P. balfouriana*, *P. contorta*, *P. coulteri*, *P. flexilis*, *P. jeffreyi*, *P. lambertiana*, *P. longaeva*, *P. monophylla*, *P. monticola*, *P. muricata*, *P. ponderosa*, *P. quadrifolia*, *P. radiata*, *P. sabiniana*, *P. torreyana*, and *P. washoensis*), as well as the overall area within the site encompassed by all pines combined. We then conducted analyses identical to those above investigating the relationship between and mean annual and mean CV among years of western scrub-jay populations as a function of oak and pine species diversity and oak and pine abundance, measured as the proportion of the CBC circle in which oaks or pines occurred. Categories for oak and pine abundance were 0, >0–20, >20–40, 40–70, and >70%.

These analyses yielded three datasets: one for *A. c. californica* in California only based on the Gap data using oak and pine abundance, one covering the entire range of *A. c. californica* based on our estimates of tree distributions and published data on oak and conifer abundance, and a third covering the range of *A. c. woodhouseii* based on our estimates of tree distributions and published data on oak and conifer abundance. We refer to these as the “CA Gap”, “*californica*”, and “*woodhouseii*” data, respectively. For simplicity, we will refer to both the analyses involving pine abundance (CA Gap data) and conifer abundance (*californica* and *woodhouseii* data) as “pine/conifer” abundance.

Although we graphed mean bird abundance and mean CVs against the categories of oak and pines as described above, statistics were based on Spearman rank correlations between mean abundance and CV vs the non-categorized variables of oak (pine) species number and oak (pine/conifer) abundance within the CBC site. This yielded a statistical estimate of the overall relationship (positive or negative) between these independent variables and western scrub-jay population size and variability, and was performed using all data and excluding sites with no species of oaks (pines). In order to estimate the combined effects of the independent variables, we conducted multiple regressions of scrub-jay abundance and mean variability on oak species number, oak abundance, pine species number, and pine/conifer abundance. Regressions rather than some other multivariate technique were used in order to again provide estimates of the overall relationship (positive or negative) of each factor considering each of the other factors. Differences among sites containing oaks of different types (only one type [either 1-yr or 2-yr] vs both 1-yr and 2-yr species) were determined by general linear models including total number of oak species and oak abundance as covariates.

Relationship between bird abundance and the acorn crop

Starting in autumn 1994, two of us (WDK and JM HK) surveyed the acorn crop of the major species of California acorn-producing trees (*Q. agrifolia*, *Q. chrysolepis*, *Q. douglasii*, *Q. engelmannii*, *Q. kelloggii*, *Q. lobata*, *Q. wislizeni*, and *Lithocarpus densiflorus*) at 18 sites throughout California as part of the California Acorn Survey. The survey, which currently includes 1032 individually-marked trees in 47 populations, involves a visual survey of acorn abundance: in brief, two observers count as many acorns as they can in different parts of permanently marked trees in a 15 s period. These values are added and log-transformed to yield an index of the acorn crop for that tree. Further methodological details of the visual survey technique can be found in Koenig et al. (1994a); details concerning sample sizes and site locations are available from the authors on request.

For the analyses conducted here, we averaged the acorn crop index for all trees surveyed each year from 1994 to 2007 as an overall index of the state’s acorn crop for that year; no attempt was made to weight different species beyond the different samples sizes represented in the survey. We also performed analyses dividing 1-yr and 2-yr species in order to test whether populations of scrub-jays were more

closely related to acorn production by one or the other set of species. Values were correlated with the overall mean abundance of western scrub-jays based on all CBC surveys conducted in California both the subsequent winter (year x) and the winter one year later (year $x+1$). In all cases we computed correlations including all years and excluding 2005, the year when West Nile virus, an emergent disease to which scrub-jays are highly susceptible, became widespread in California and significantly impacted western scrub-jay populations (Koenig et al. 2007).

Results

The mean abundance and relative variability of scrub-jay populations measured by the coefficients of variation (CV) for all three datasets are plotted as a function of oak species diversity and oak abundance category in Fig. 2. In the majority of cases, mean abundance of *californica* populations were positively related and mean CV inversely related to increasing oak species diversity and oak abundance whether or not sites with no oaks were included. In contrast, populations of *A. c. woodhouseii* did not vary linearly with increasing oak species number, the patterns being either not significant or yielding opposite trends depending on whether sites with no oaks were or were not included. For example, populations of *woodhouseii* tended to be larger and less variable overall as oak species diversity increased including all sites, but were smaller and more variable as oak species diversity increased when sites with no oaks were excluded. This indicates that the overall pattern was due to a difference between populations with and without access to oaks rather than an effect of oak species diversity per se.

Relationships of scrub-jay populations with pines (Fig. 3) were very different than those with oaks. For *woodhouseii*, population size increased and mean CV’s generally decreased with increasing pine species number and pine/conifer abundance, although there were no significant relationships with pine species diversity when sites with no pines were excluded. For *californica*, however, relationships with pines/conifers were either not significant or negative, indicating that populations decreased in abundance and increased in variability with increasing pine species or pine/conifer abundance.

Increasing diversity will potentially correlate with increasing abundance, and abundance of oaks is likely to be inversely related to abundance of pines/conifers. Consequently, we performed multiple regressions of all four variables of oak species number, oak abundance, pine species number, and pine/conifer abundance, on the mean and mean CV of scrub-jay abundance. Results confirm the importance of oaks to *A. c. californica* and of pines to *A. c. woodhouseii* (Table 1). Using the CA Gap data, oak species number, but not oak abundance, was significant, correlating positively with mean abundance and negatively with mean CV. In the *californica* analysis, oak species number was again the most important explanatory variable, but in addition, oak abundance was positively related and pine/conifer abundance inversely related to mean abundance. For *woodhouseii*, neither oak species number nor oak abundance was significant; rather, mean abundance increased and CV

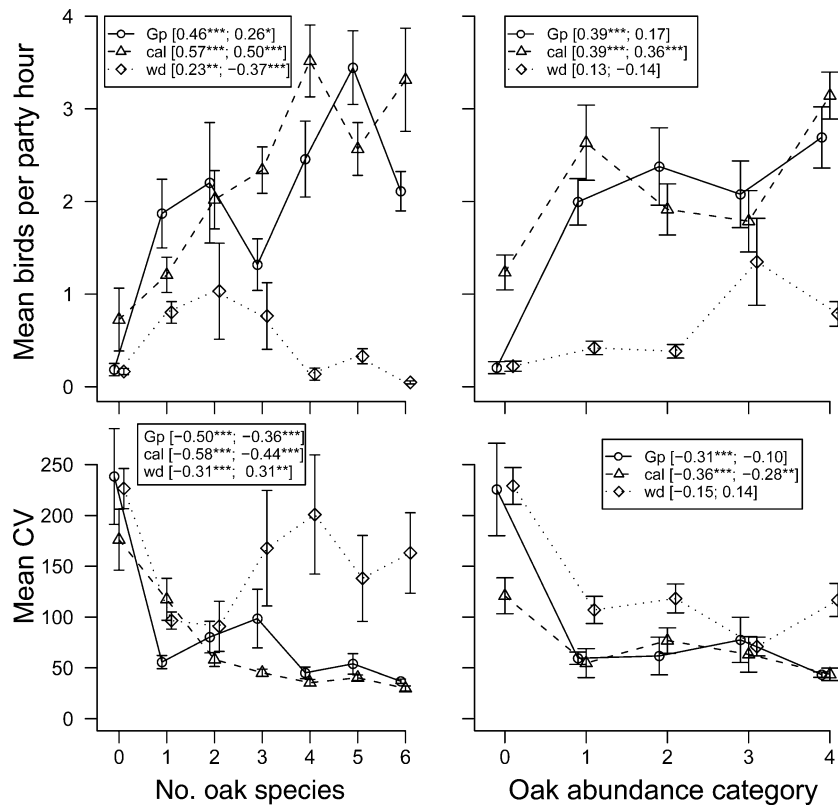


Figure 2. Mean (+SE) density (top) and CV (bottom) of western scrub-jay populations plotted as a function of number of oak species (left) and oak abundance category (right) within sites for California only (Gp; the Gap data), for *A. c. californica* (cal), and for *A. c. woodhouseii* (wd), the latter two datasets being based on estimates of oak species number at individual CBC sites. Values are Spearman rank correlations; the first value includes all data, the second excludes sites with no oak species. * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

decreased with increasing pine/conifer abundance. In addition, mean CV decreased with increasing number of pine species.

The relationships between mean abundance and variability of scrub-jay populations as a function of what types of oaks (1-yr species, 2-yr species, or both types) were present are summarized in Table 2; analyses were performed only for the two *A. c. californica* datasets since oaks did not significantly correlate with populations of *A. c. woodhouseii*. Differences controlling for oak species number and oak abundance were not significant in any of the tests. However, there were clear differences in scrub-jay population dynamics at sites with the different types of oaks, with sites containing only 2-yr species of oaks harboring much lower bird abundance and greater variability than sites with either just 1-yr species or both types of oaks. Comparisons in scrub-jay numbers and population variability between sites with only 1-yr vs only 2-yr species of oaks (again controlling for total oak species number and oak abundance) were significant in all but one case (Table 2).

We found no significant relationship between the overall mean acorn crop and the overall mean abundance of western scrub-jays in California the following winter (Fig. 4, top). However, there was a highly significant positive relationship between the acorn crop and mean bird abundance in year $x+1$ (Fig. 4, bottom), strikingly so when excluding 2005, a year when populations of western scrub-jays were significantly reduced due to West Nile virus

(Koenig et al. 2007). Based on the much higher densities of birds living in areas with 1-yr vs 2-yr species of oaks (Table 2), we would expect that the acorn crop of 1-yr species should be more important to producing this relationship than the acorn crop of 2-yr species; this was indeed the case (Fig. 5).

Discussion

Western scrub-jays use a complex range of habitats throughout their considerable geographic range and are ecologically plastic, assuming the ecological characteristics of the regions they live rather than being distributed only within the areas in which their preferred ecological regimes are present (Rice et al. 2003). However, the majority of populations inhabit oak and piñon-juniper woodlands, and with some notable exceptions, acorns or pine nuts are important to the species' ecology (Curry et al. 2002).

Our analyses confirm that in general, both the mean abundance and annual variability of populations of this species as measured by CBC data are dependent on oaks and pines, and furthermore, that relative density of this species in California is directly related to the overall size of the acorn crop the prior year, suggesting that the primary mechanism linking the acorn crop to scrub-jay populations is increased reproductive success the following spring. However, the two forms of western scrub-jay covered by

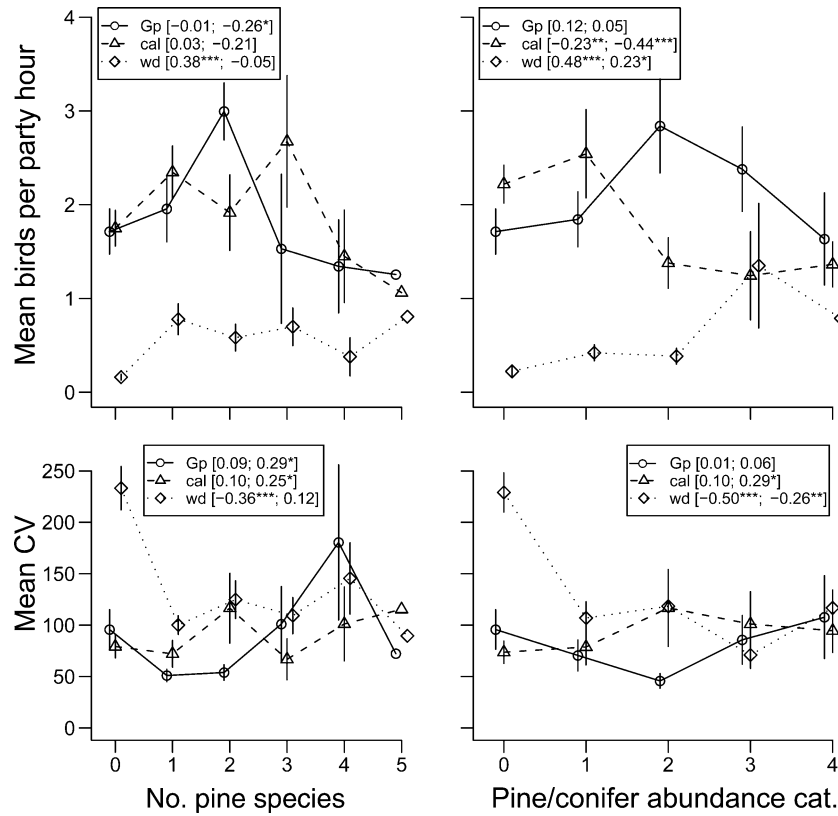


Figure 3. Mean (+SE) density (top) and CV (bottom) of western scrub-jay populations plotted as a function of number of pine species (left) and pine/conifer abundance category (right) within sites for California only (Gp; the Gap data), for *A. c. californica* (cal), and for *A. c. woodhouseii* (wd). Values are Spearman rank correlations; the first value includes all data, the second excludes sites with no pine species. * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

our analyses, *A. c. californica* and *A. c. woodhouseii*, corresponding to populations along the west coast of the USA and the interior states, respectively, exhibit distinct differences in their relationships to these tree taxa. *Aphelocoma c. californica* is generally correlated with oaks and oak species diversity, with mean abundance increasing and variability decreasing with increasing oak species and, to a lesser extent, oak abundance. Pines/conifers either had no

significant relationship to populations of this form or were inversely related to mean abundance. These results are consistent with the dependence of this form on oak woodlands throughout its range on the Pacific coast.

In contrast, *A. c. woodhouseii*, which generally inhabits oak-piñon-juniper woodlands in the Great Basin, exhibited variable relationships with oak species number and oak abundance that were not significant in multivariate analyses.

Table 1. Results of multiple regressions examining the effects of species number and abundance for oaks and for pines/conifers on the mean abundance and mean CV of western scrub-jays as determined by the CBC data. Significant values are highlighted in bold face.

	Mean abundance			CV of abundance		
	β_{stan}	t-value	p-value	β_{stan}	t-value	p-value
<i>CA gap</i>						
Oak species	0.32	2.3	0.02	-0.46	-3.4	0.001
Oak abundance	0.06	0.4	0.7	0.08	0.5	0.6
Pine species	-0.29	-2.0	0.052	0.03	0.2	0.8
Pine abundance	0.22	1.4	0.2	0.02	0.1	0.9
<i>californica</i>						
Oak species	0.40	5.2	<0.001	-0.42	-5.0	<0.001
Oak abundance	0.22	2.9	0.004	-0.10	-1.2	0.22
Pine species	0.07	0.8	0.4	0.13	1.3	0.2
Conifer abundance	-0.28	-3.2	0.002	0.04	0.4	0.7
<i>woodhouseii</i>						
Oak species	-0.08	-0.9	0.4	-0.07	-0.7	0.5
Oak abundance	0.03	0.3	0.8	0.01	0.03	1.0
Pine species	0.15	1.7	0.1	-0.23	-2.6	0.009
Conifer abundance	0.26	2.9	0.004	-0.23	-2.6	0.009

Table 2. Mean \pm SD (n sites) abundance and CV as a function of whether oaks present in the CBC site are only 1-yr species, only 2-yr species, or both type of species. Statistical tests are by general linear models with oak type entered as a fixed factor and both number of oak species and oak abundance included as covariates.

	CA gap data			<i>californica</i> data		
	Mean abundance	Mean CV	n sites	Mean abundance	Mean CV	n sites
1-yr species only	2.2 \pm 1.5	51 \pm 20	24	1.7 \pm 1.4	91 \pm 103	42
2-yr species only	0.8 \pm 1.0	142 \pm 139	11	0.8 \pm 0.9	127 \pm 126	14
Both types	2.6 \pm 1.5	47 \pm 27	60	2.7 \pm 1.4	41 \pm 15	61
Comparison of sites with one type vs both types						
F-value	3.7	3.0	—	0.3	2.3	—
DF	1,91	1,91	—	1,113	1,113	—
p-value	0.06	0.09	—	0.6	0.13	—
Comparison of sites with 1-yr species only vs 2-yr species only						
F-value	5.6	9.2	—	6.2	1.9	—
DF	1,31	1,31	—	1,52	1,52	—
p-value	0.02	0.005	—	0.02	0.17	—

Rather, mean abundance increased with increased pine/conifer abundance, while mean annual variability decreased with increasing pine/conifer abundance and increasing pine

species diversity. Thus, populations of this form are generally correlated with pines and (possibly) other conifers rather than oaks.

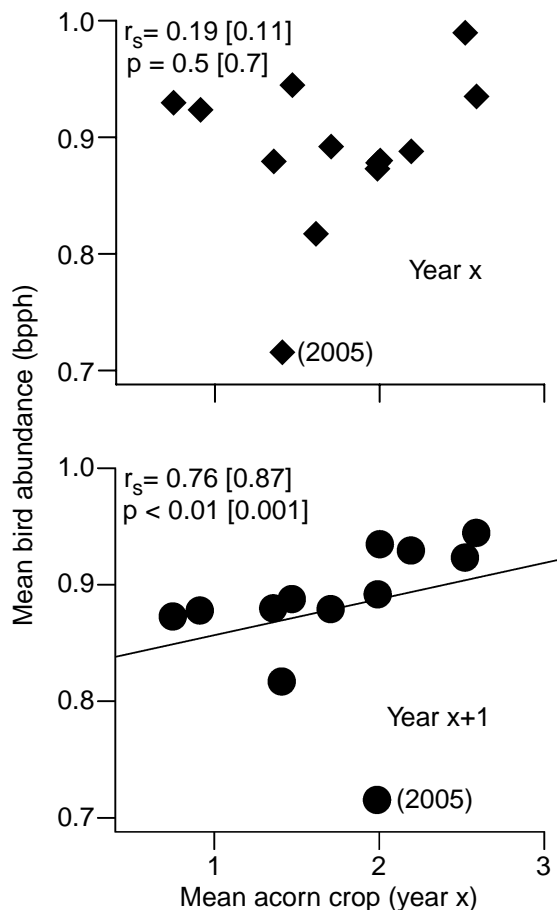


Figure 4. Relationship between the overall mean acorn crop of oaks in California (based on log-transformed means of counts of all trees included in the California Acorn Survey) and the overall mean abundance of western scrub-jays in California during winter (year x, top) and one year later (year x + 1, bottom). Years included (for the birds) are 1995–2007 (top) and 1996–2007 (bottom). Labeled in both cases is 2005, the year West Nile virus became widespread in California. Listed are Spearman rank correlations and p-values for all years and (in brackets) excluding 2005.

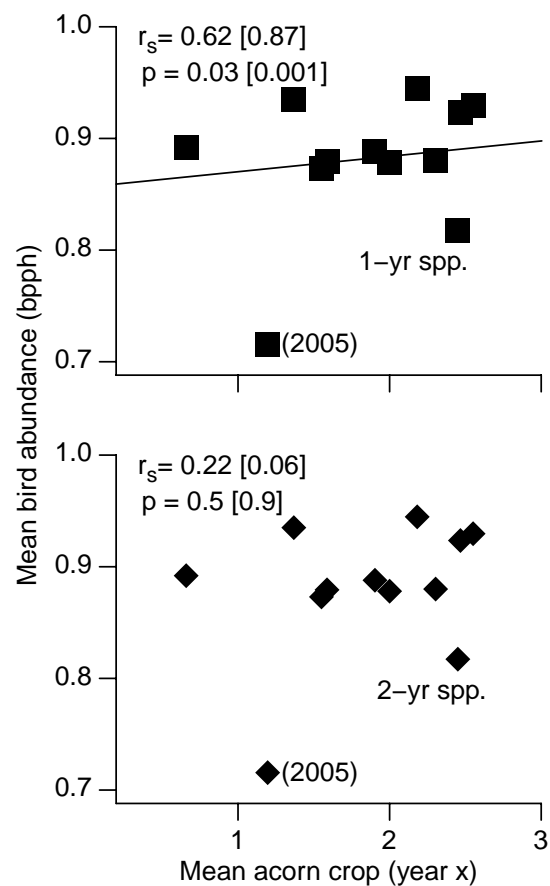


Figure 5. Relationship between the overall mean acorn crop of 1-yr oaks (top) and 2-yr oaks (bottom) in California (based on log-transformed means of counts of all trees of the appropriate type included in the California Acorn Survey) and the overall mean abundance of western scrub-jays in California during winter one year later (year x + 1). Years included (for the birds) are 1995–2007 (top) and 1996–2007 (bottom). Labeled is 2005, the year West Nile virus became widespread in California. Listed are Spearman rank correlations and p-values for all years and (in brackets) excluding 2005.

These differences in the factors influencing the population dynamics of western scrub-jays correspond not only to habitat preferences but to morphological and behavioral differences between the forms, at least some of which have been shown to be adaptive. Peterson (1993), for example, documented differences in bill shapes of western scrub-jays that were closely associated with habitat use, with populations living in oak woodlands generally exhibiting short, hooked bills while populations in piñon-juniper woodlands have long, pointed bills. These different bill shapes have been shown to be more efficient at exploiting the main food resources (acorns vs pine nuts) used by the two forms, and thus are adaptations to their respective environments (Bardwell et al. 2001).

In general, differentiation between the two northern forms of western scrub-jay, as well as a third form (*A. c. sumichrasti*) not studied here, are sufficiently great that they are plausibly considered separate species (Delaney et al. 2008). Our results support this assertion with respect to the habitat characteristics important to *A. c. californica* and *A. c. woodhouseii*. They also suggest other differences; for example, populations on the Pacific coast are denser (mean abundance = 1.9 ± 1.6 birds per party hour ($n = 138$) for *californica* vs 0.5 ± 0.7 birds per party hour ($n = 144$) for *woodhouseii*; Mann-Whitney U-test, $z = 7.7$, $p < 0.001$) and less variable than interior populations (mean CV = $85 \pm 100\%$ [$n = 138$] for *californica* vs $157 \pm 126\%$ [$n = 144$] for *woodhouseii*; Mann-Whitney U-test, $z = 8.3$, $p < 0.001$), differences that parallel those found for coastal vs interior forms of the mast-dependent acorn woodpecker *Melanerpes formicivorus* (Koenig and Haydock 1999). Differences between *A. c. californica* and *A. c. woodhouseii* also parallel differences found between sibling species of the plain titmouse found primarily in oak and pine-oak woodlands along the Pacific slope (the oak titmouse *Baeolophus inornatus*) compared to those inhabiting piñon-juniper woodlands in the Great Basin (the juniper titmouse *B. ridgwayi*) (Cicero 2000a, b).

A notable characteristic of both pines and oaks is highly variable seed production from year to year (Koenig and Knops 2000). In oaks, different species are often not highly synchronized in their seed production, with particularly great asynchrony exhibited by species maturing acorns in one vs two years (Sork et al. 1993, Koenig et al. 1994b, Koenig and Haydock 1999). Although less is known about production of pine seeds across communities, not all pines mature cones in the same number of years (Preston 1961) and it is highly likely that there is asynchrony in seed production among different species as well, even when they require the same amount of time to mature cones. Thus, overall variability in annual availability of nuts is expected to decrease with increasing number of species of nut-bearing trees. Such decreasing variability has previously been shown to influence population abundance and variability in the acorn woodpecker, in which populations were particularly sensitive to oak species diversity along the Pacific coast, with populations being limited to sites with two or more species of oaks, after which population abundance increased and annual variability decreased with increasing numbers of species (Koenig and Haydock 1999). In multivariate analyses, these authors found that, along the Pacific coast, mean population size of acorn woodpeckers

was determined primarily by resource abundance as indexed by oak abundance, while annual variability in population size was determined primarily by resource variability as indexed by oak species diversity.

Similarly, populations of *A. c. californica* increase in abundance and decrease in annual variability with increasing oak species diversity and increasing oak abundance. In a few cases these patterns were only shown when sites with no oaks were included, indicating that the main difference was due to the presence or absence of oaks, not the number of oak species or oak abundance per se. However, in several cases these patterns remained even when excluding sites with no species of oaks.

Unlike the pattern found in acorn woodpeckers, the main cause of these relationships appears to be oak species diversity rather than oak abundance, as in most cases only the former remained significant in multivariate analyses. Furthermore, western scrub-jays do not appear to be inordinately affected by the difference between sites with one vs two species of oaks. Using the CA Gap data, for example, populations in areas with a single oak species do relatively well in terms of both high density and low variability compared to sites with 2–3 species of oaks (Fig. 2), again contrasting with earlier findings with acorn woodpeckers.

Overall, however, *A. c. californica* populations appear to be strongly influenced by oak species diversity and are only moderately affected by oak abundance per se, with larger and more stable populations being found in association with more oak species. Such effects are particularly cogent in light of current environmental challenges such as global climate change, which threatens to significantly decrease the range of several California oak species over the next several decades (Kueppers et al. 2005), and emerging forest pathogens. Notable among the latter is sudden oak death (SOD), a recently introduced disease caused by the water mold *Phytophthora ramorum*, which threatens to significantly decrease oak species diversity in coastal areas of California where both of the major acorn-producing species (*Quercus agrifolia* and *Lithocarpus densiflorus*) are highly susceptible (Rizzo et al. 2002, Rizzo and Garbelotto 2003). Estimates based on CBC data suggest that between 20 and 30% of *A. c. californica* populations within the current range of *Q. agrifolia* could be lost by a disease sweep of this oak species, along with often considerably higher proportions of other oak (although not necessarily acorn)-dependent birds including acorn woodpeckers, oak titmice, Nuttall's woodpeckers *Picoides nuttallii*, and Hutton's vireos *Vireo huttoni* (Monahan and Koenig 2006, 2007).

With asynchrony in acorn production being particularly great between oak species requiring different numbers of years to mature acorns, we predicted that scrub-jay populations with access to both 1-yr and 2-yr species would be denser and show less annual variability than those with access to only a single type of oak. These predictions were not met: annual variability among scrub-jay populations with access to both types of oaks was less, but not significantly so, than among those with access to only one type after controlling for oak species diversity and abundance. However, there were significant differences between sites, with those containing only 2-yr species of oaks harboring scrub-jay populations that were considerably

less abundant and more variable than sites containing only 1-yr species of oaks.

One hypothesis for this difference in scrub-jay density is that acorn production is lower or more variable among years by 2-yr species of oaks. This is not supported by current data: based on data from the California Acorn Survey, there is no significant difference in mean productivity or mean CV among years between 1-yr and 2-yr species, either overall or when species of different types within the same site are contrasted in paired comparisons (Koenig and Knops unpubl.). Alternatively, the difference could be incidental to habitat preferences of the birds that correspond to oaks of the different types. In California, 1-yr species of oaks, particularly *Q. agrifolia*, *Q. lobata*, and *Q. douglasii*, predominate in coastal and lowland areas, to which western scrub-jays are particularly partial, whereas 2-yr oak species, including *Q. kelloggii*, *Q. chrysolepis*, *Q. wislizeni*, and *Lithocarpus densiflorus* tend to predominate in higher montane forests and in more interior sites in which *A. c. californica* is less characteristic and where competitors such as the Steller's jay (*Cyanocitta stelleri*) are more abundant. More study of this issue is clearly warranted.

Also remaining to be studied are populations of *A. c. sumichrasti* in Mexico, where diversity of oaks is high, as well as the relationship between populations and the resources on which they depend among both island scrub-jays and the Florida scrub-jay, although considerable work on the latter population at Archbold Biological Station confirms that it is heavily dependent on oaks and acorns (DeGange et al. 1989, Reynolds et al. 2003, Shawkey et al. 2004). Particularly intriguing would be if there were a relationship between the pattern of dependence of these forms on resources and their social behavior, as predicted by work indicating that cooperative breeding may be facilitated by highly variable and unpredictable resources (Emlen and Vehrencamp 1985, Rubenstein and Lovette 2007). Given the wide variability in social behavior within the genus, with cooperative breeding occurring not only among the Florida scrub-jay and the Mexican jay *A. ultramarina* but also in at least one population of *A. c. sumichrasti* in Oaxaca (Peterson and Burt 1992, Burt and Peterson 1993), there is clearly much to be done to understand how resource abundance and diversity affects the ecology and behavior of this intriguing genus.

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