Acorn harvesting by acorn woodpeckers: annual variation and comparison with genetic estimates

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ABSTRACT

Questions: (1) How does the effort that birds invest in harvesting acorns, including the distance the acorns are moved – a key factor affecting population structure of the trees – covary with the size of the acorn crop? (2) How well are harvest patterns, previously inferred by indirect, genetic methods, matched by data from direct observations of harvesting?

Organisms: The acorn woodpecker (*Melanerpes formicivorus*), a cooperatively breeding species that is highly dependent on acorns, which are stored in specialized storage trees known as granaries.

Methods: We observed acorn harvesting over 4 years at Hastings Reservation in central coastal California, a period over which acorn crops varied considerably in size.

Results: Birds harvested 94% of acorns from a small number of trees located within 150 m of their granary. The distances travelled by birds to harvest acorns and the number of trees from which acorns were harvested were both greater in a poor acorn year than when the crop was good. Birds did not necessarily prefer the species of acorn that was most abundant. The distance birds travelled to harvest acorns, harvesting overlap among groups, and the number of trees from which acorns were harvested generally matched the findings of Grivet *et al.* (2005), indicating that an indirect genetic approach can be effective when direct observation of seed dispersal is difficult.

Keywords: acorn woodpecker, caching behaviour, dispersal, foraging strategy, *Melanerpes formicivorus*, oaks, seed movement.

INTRODUCTION

Propagule dispersal plays a key role in determining the spatial structure of plant populations, and thus is important to population persistence, demography, and geographical ecology. Unfortunately, tracking seed movement is challenging, as it requires either following the physical movement of seeds from point of production to point of fall or

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retrospectively retracing dispersed seeds back to their maternal source (Gómez, 2003). The latter approach can sometimes be accomplished using molecular methods (Dow and Ashley, 1996; Godoy and Jordano, 2001; Grivet *et al.*, 2005), but validation of these techniques has rarely been attempted. Such validation is particularly difficult in the case of animal-dispersed seeds because it entails following dispersers and then locating the seeds they move (Levey and Sargent, 2000; Holbrooke *et al.*, 2002).

Here we present the results of a 4-year study in which we followed the movement of acorns being harvested and stored by a common avian seed predator in California oak woodlands, the acorn woodpecker (*Melanerpes formicivorus*). This species, a permanent resident that lives in family groups, is critically dependent on acorns (Hannon *et al.*, 1987; Koenig and Mumme, 1987) that they store in structures known as storage trees or granaries (Koenig *et al.*, 1995). With an estimated 7.3×10^6 acorn woodpeckers in California (Koenig *et al.*, 1995), each storing an average of 325 acorns per year (Koenig and Mumme, 1987), this species harvests about 2.4×10^9 acorns in California in an average year. Thus, although a high proportion of the acorns harvested are eventually consumed, acorn woodpeckers are nonetheless a major dispersal vector, and thus a potentially significant factor in oak demography.

Our aim is to quantify the spatial patterns of acorn harvesting by acorn woodpeckers. These data will allow us to compare observed patterns with those expected based on energetic considerations and to compare our data with the results of Grivet and colleagues' (2005) genetic, seed pool structure approach, thus yielding a unique comparison between direct and retrospective methods of quantifying seed dispersal parameters.

Acorn woodpecker groups in our study area defend territories 3.5–9.0 ha in size (MacRoberts and MacRoberts, 1976), values corresponding to circles with radii of 106 to 169 m, respectively. Thus, we expected that the majority of acorns would be harvested within a relatively short distance of granaries and that the overall spatial pattern of acorns harvested would show a leptokurtic distribution as found in other studies of vertebrate seed dispersal (Westcott and Graham, 2000; Godoy and Jordano, 2001; Gómez, 2003). However, most territories are not bounded on all sides by other groups and birds sometimes foray considerably farther to obtain food and search for reproductive vacancies, so more distant seed dispersal is possible (Koenig *et al.*, 1996).
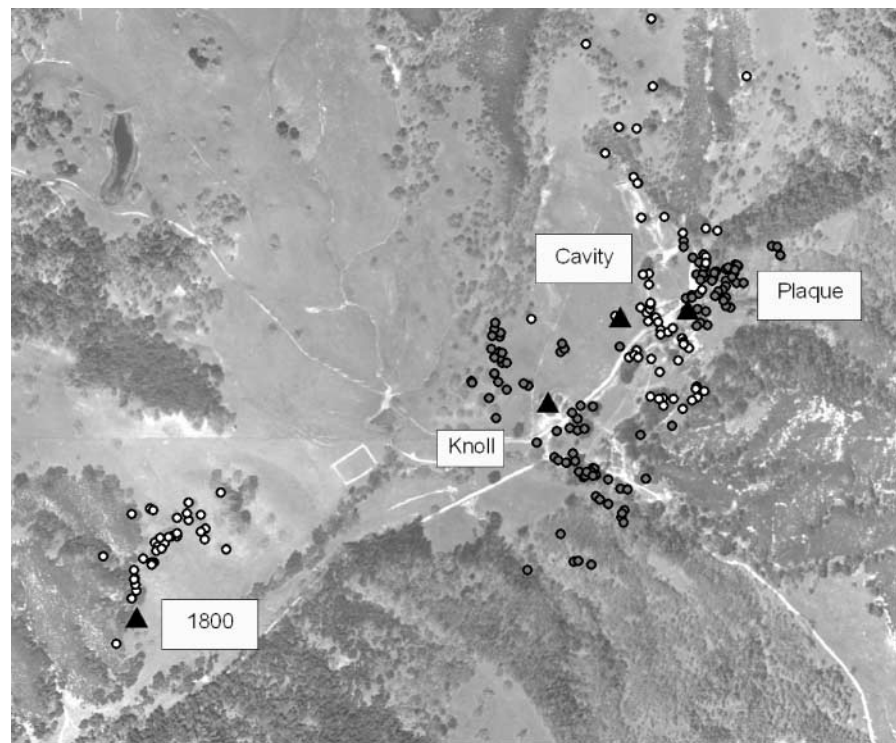
METHODS

Field observations

Acorn woodpeckers live in permanently territorial family groups of between 2 and 15 individuals (Koenig and Mumme, 1987; Koenig *et al.*, 1995). Territories typically contain one or more centralized storage sites in which group members communally store acorns harvested from surrounding trees when acorns mature in September until they are no longer present on the trees, which is usually in December, although in some cases acorns can remain on a few trees through the winter. We observed harvesting activity in 2002 (18 October to 14 November), 2004 (4 October to 20 December), 2005 (14 September to 19 November), and 2007 (13 October to 4 December) at Hastings Reservation, central coastal California (Table 1). Four family groups of acorn woodpeckers were observed in each of the 4 years of the study (Fig. 1). During watches, two observers communicating via two-way radios recorded as many acorns as possible harvested by birds in the focal group. Acorns, which are harvested one at a time, are taken directly to and stored in the group's storage area. The individuals harvesting acorns were not identified, but the size and composition of groups was known

Table 1. Sample sizes and relative size of the acorn crop (mean number of acorns counted per 30 s; N trees) during the 4 years of the study

	Year				
Variable	2002	2004	2005	2007	Total
No. of watches	23	40	38	24	125
Hours of observation	23	114	89	27	253
No. of acorns harvested	601	1579	797	591	3568
No. of trees	23	75	113	45	—
Acorn crop					
Q. lobata ($N = 85$)	42.0	46.7	2.0	61.9	—
Q. douglasii ($N = 56$)	36.8	39.1	2.6	50.4	—
Q. agrifolia ($N = 63$)	19.9	18.1	6.1	9.8	—

1 km

Fig. 1. Aerial photo of the study site, Hastings Reservation in central coastal California. The four focal groups are designated by black triangles. Trees from which birds harvested acorns are designated by small grey (Plaque, Knoll) and white (Cavity, 1800) circles.

from ongoing demographic studies. Harvest trees and granaries were tagged and their locations recorded using GPS units.

The foraging ranges of groups based on the trees from which acorns were harvested were estimated from minimum convex polygons using Hawth's analysis tools for ArcGIS (Beyer, 2004). Analyses were made for each group × year separately and across years by combining trees used by the same group across all years of the study.

Virtually all trees within the foraging ranges of the groups observed were oaks of three species: valley oak (*Quercus lobata*), blue oak (*Q. douglasii*), and coast live oak (*Q. agrifolia*). The relative size of the acorn crop of these species during each of the 4 years was determined by visual surveys conducted in September during which two observers counted as many acorns as possible during 15 s (30 s total) on 202 marked trees (85 *Q. lobata*, 55 *Q. douglasii*, and 62 *Q. agrifolia*) distributed throughout the study site (Koenig *et al.*, 1994a, 1994b). All *Q. lobata* within the study area were marked as part of a separate study, and thus the number of trees from which birds harvested acorns could be compared with the total number of trees of this species growing within the foraging ranges of the focal groups.

Harvesting effort

We gathered four measures of harvesting effort:

1. *Harvesting distance*. Calculated as the distance between where an acorn was harvested and the granary in which it was stored. Values presented are for both individual acorns and for individual trees, the latter reducing pseudoreplication due to birds or groups disproportionately harvesting from particular trees. An increased harvesting distance is assumed to represent greater effort.
2. *Foraging range*. Minimum convex polygons calculated using individual trees from which acorns were harvested. An increased foraging range is assumed to represent greater effort.
3. *Rate of acorn storage*. Calculated as the number of acorns observed being harvested divided by the duration of the watch and the number of individuals present in the group as known from demographic surveys. Differences among years were tested using a generalized linear model (GLM) including 'year' and 'group' as random factors. Increased harvesting rate is assumed to indicate a combination of increased acorn availability and greater effort.
4. *Number of harvest trees*. We expected birds to expend greater effort harvesting acorns, indicated by the use of a larger number of trees, in poor acorn years versus good acorn crop years.

In general, we expected harvesting effort to be focused on trees close to the granary and on species producing the largest acorn crop within a year. We also expected the effort expended harvesting to be greatest in the year when the acorn crop was poor, because more effort would presumably be required to find acorns.

Comparison with indirect genetic methods

Three of the four groups we studied were adjacent to each other, while the fourth was separated by two territories from the other three (Fig. 1). Given this distribution of focal

territories, we expected detectable overlap in trees from which birds harvested acorns only among the three adjacent territories (Plaque, Cavity, and Knoll). Thus, overlap was estimated by the number of trees used by more than one of these groups divided by the total number of trees used by all three groups for harvesting during the course of a single season. More formally, we quantified overlap by the probability of maternal identity (PMI), defined as the probability that two randomly harvested acorns, one from the gth and hth groups, were harvested from the same tree. The PMI values across granaries of the three adjacent territories were calculated following Smouse and Robledo-Arnuncio (2005) and applied in an identical context by Grivet *et al.* (2005, equations 3a and 3b), where the average PMI across all pairs of granaries is represented by $\bar{r}_{gh}$ (equivalent to $\bar{q}_{gh}$).

We also calculated the mean PMI within groups representing the probability that two acorns harvested at random by the same group were from the same tree, again following the equations in Grivet *et al.* (2005, equations 2a and 2b). Values for the two alternative PMI derivations ($\bar{q}_0$ and $\bar{r}_0$) were almost identical, but because our observed PMI values were generally less than 0.40, we used $\bar{r}_0$, which is less biased than $\bar{q}_0$, to estimate the effective number of trees from which acorns were harvested (Smouse and Robledo-Arnuncio, 2005).

Calculations were made for trees of all three species combined and for *Q. lobata* alone. These latter values allowed for a direct comparison with Grivet *et al.* (2005), whose analyses were restricted to this species.

RESULTS

The acorn crop differed considerably over the 4 years of the study, being fair to poor in 2005 and good to very good in the other 3 years (Table 1). The relative productivity of the three oak species also differed among years. For example, compared with the other two species, *Q. agrifolia* was best in 2005 and worst in 2007.

During the 4 years of the study, we observed 3568 acorns harvested by birds from the four focal groups (Table 1). Overall, 94% of harvested acorns and 83% of trees from which acorns were harvested came from trees <150 m from the granary. Some overlap in harvesting occurred, primarily in the poor acorn year of 2005. Overall, nine trees (6.7%) were used by birds from adjacent groups in the same year, eight in 2005, and one in 2007.

Year to year differences

The distance birds travelled to harvest acorns, measured as the mean distance to individual trees from which acorns were harvested, differed significantly among both years and groups (GLM including year and group: year, $F_{3,547} = 32.4$, $P < 0.001$; group, $F_{3,547} = 24.7$, $P < 0.001$), with a significantly greater mean distance to harvest trees in 2005 than in the other 3 years ($P < 0.001$ for 2005 vs. each of the other years; LSD *post-hoc* tests; Table 2). Histograms of the distance between granaries and harvest trees during the 4 years reveal the expected leptokurtic distribution in all years (Fig. 2). Foraging range size also differed significantly among years (GLM: year, $F_{3,12} = 4.2$, $P = 0.03$), with 2005 having significantly higher foraging ranges than the other 3 years ($P \leq 0.02$ for 2005 vs. each of the other years). The mean rate of acorn storage also differed significantly among years (GLM including year and group: year, $F_{3,367} = 16.4$, $P < 0.001$; group, $F_{3,367} = 5.7$, $P = 0.001$), with 2002 having significantly higher ($P < 0.05$ for 2002 vs. each of the other years) and 2005

Table 2. Annual differences in distance from granaries to harvest trees, foraging range of groups considering trees from which acorns were harvested, and rate of acorn harvesting (mean ± standard deviation)

Variable	Year				Total
	2002	2004	2005	2007	
Distance (m) of acorn harvesting (no. of acorns)	48 ± 28 (607)	65 ± 35 (1579)	96 ± 90 (797)	63 ± 26 (591)	69 ± 53 (3568)
Distance (m) of acorn harvesting (no. of trees)	51 ± 27 (81)	64 ± 39 (190)	126 ± 122 (189)	64 ± 29 (94)	83 ± 83 (554)
Foraging range (ha) ($N = 4$ groups)	0.4 ± 0.3	1.4 ± 1.0	7.0 ± 5.8	1.1 ± 0.4	2.4 ± 3.8
Rate of acorn harvesting (acorns per bird per hour) (no. of watches)	2.0 ± 2.2 (70)	1.3 ± 1.5 (118)	0.6 ± 0.8 (113)	1.5 ± 1.3 (73)	1.3 ± 1.6 (374)

Note: Distance of acorn harvesting and foraging ranges based on combining multiple acorns harvested within individual watches. For both the distance birds flew to harvest acorns (on a per-acorn or per-tree basis) and home range, 2005 values were significantly greater than values for the other 3 years (ANOVAs, LSD *post-hoc* tests). Rate of acorn harvesting was significantly different among the 4 years (ANOVA, LSD *post-hoc* tests), with 2005 significantly lowest, 2002 significantly highest, and 2004 and 2007 being indistinguishable.

significantly lower ($P < 0.001$ for 2005 vs. each of the other years) storage rates than the other two years (LSD *post-hoc* tests; Table 2).

In 3 of 4 years birds harvested a higher proportion of *Q. lobata* acorns and from a higher proportion of *Q. lobata* trees than either of the other species (Fig. 2). However, despite widely differing productivity of the three species over the 4 years of the study (Table 1), birds harvested acorns from a relatively equitable mix of the species in all years (Fig. 2b). Thus, even in 2007, when the relative productivity of *Q. agrifolia* was very low, 27% of acorns and 22% of trees from which acorns were harvested were of this species.

The proportion of individual *Q. lobata* from which birds harvested acorns differed depending on how the data are viewed. Considering only trees within the foraging ranges of birds within a particular year, birds harvested acorns from all or nearly all trees (77–100%) in the good years and only 23% of trees in 2005, the poor acorn year (Fig. 3). However, basing foraging ranges on all trees used for harvesting across all 4 years of the study, the proportion of *Q. lobata* from which acorns were harvested was small in the good years (5–10%) and relatively high (22%) in the poor year (2005).

Seed pool structure

On average, 16.6 trees (all oak species combined) and 6.5 trees (*Q. lobata* alone) were used for harvesting (mean maternal richness; Table 3). A high proportion of acorns were harvested from a small number of trees in all years, albeit less so in 2005. Averaged across groups, the proportion of acorns harvested from the single tree most heavily used in a particular year ranged from 23 to 70% and the proportion of acorns harvested from the top four trees ranged from 49 to 100%. Birds concentrated their harvesting efforts on the fewest trees in 2002 and on the most trees in 2005.
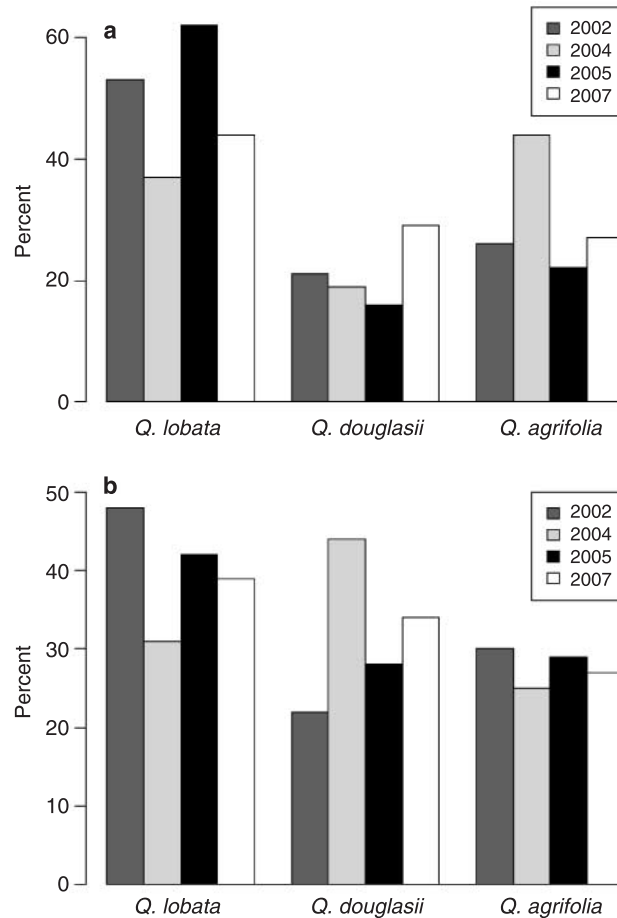
Fig. 2. Annual differences in the overall percentage of the three species of acorns harvested measured on a per-acorn (a) and a per-tree (b) basis.

Mean PMI values ($\bar{r}_0$) ranged from 0.11 to 0.33 and neither it nor its inverse, the effective number of trees from which acorns were harvested ($N_{em} = 1/\bar{r}_0$), exhibited a consistent pattern *vis-à-vis* the overall acorn crop, with values being relatively low ($\bar{r}_0$; high for N_{em}) in the good acorn years of 2002 and 2004 but showing the opposite trend in 2005 (a poor acorn year) and 2007 (a good acorn year). However, considering *Q. lobata* alone, $\bar{r}_0$ values were lowest (N_{em} highest) in the poor year of 2005, with values for the other three good acorn years being considerably higher ($\bar{r}_0$; lower for N_{em}).

DISCUSSION

Acorn harvesting and foraging strategies of acorn woodpeckers

Acorn woodpeckers usually harvested acorns from trees located close to their granaries. Overall, 94% of acorns and 83% of trees from which acorns were harvested came from trees
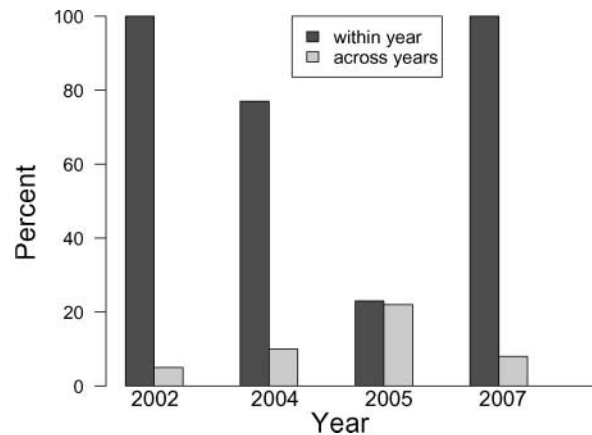
Fig. 3. Annual differences in the mean percentage of *Q. lobata* trees within the foraging range of groups from which acorns were harvested. 'Within year' considers only the foraging range for that year; 'across years' considers trees within the foraging range of all 4 years combined.

Table 3. Seed pool structure including the mean number of trees from which acorns were harvested (mean maternal richness), the average probability of maternal identity ($\bar{r}_0$), the effective number of trees harvested by a group (N_{em}), and the mean overlap between trees harvested by adjacent groups ($\bar{r}_{gh}$) for all species of oaks combined and for *Q. lobata* only

Variable	Hastings					Grivet *et al.* (2005)
	2002	2004	2005	2007	Mean	2002
All species						
No. of acorns	601	1579	797	591	—	—
Mean maternal richness	5.8	18.8	30.3	11.5	16.6	—
$\bar{r}_0$	0.330	0.262	0.124	0.112	0.207	—
$N_{em} = 1/\bar{r}_0$	3.03	3.82	8.08	8.95	5.97	—
$\bar{r}_{gh}$	0.000	0.000	0.002	0.000	0.001	—
Q. lobata only						
No. of acorns	318	579	493	262	—	215
Mean maternal richness	2.8	5.8	12.8	4.5	6.5	4.3
$\bar{r}_0$	0.655	0.541	0.175	0.288	0.415	0.474
$N_{em} = 1/\bar{r}_0$	1.53	1.85	5.70	3.47	3.14	1.95
$\bar{r}_{gh}$	0.000	0.000	0.004	0.000	0.001	0.007

Note: Number of granaries = 4 (Hastings) and 17 (Grivet *et al.*, 2005), with the exception of $\bar{r}_{gh}$ at Hastings, which is based on three contiguous territories (see text).

located less than 150 m away from storage sites. This harvesting behaviour distinguishes acorn woodpeckers from blue jays (*Cyanocitta cristata*) in the eastern USA and the European jay (*Garrulus glandarius*), both of which have been found to transport acorns much longer distances (in the case of blue jays a mean of 1.1 km) before caching them in the ground (Darley-Hill and Johnson, 1981; Gómez, 2003).
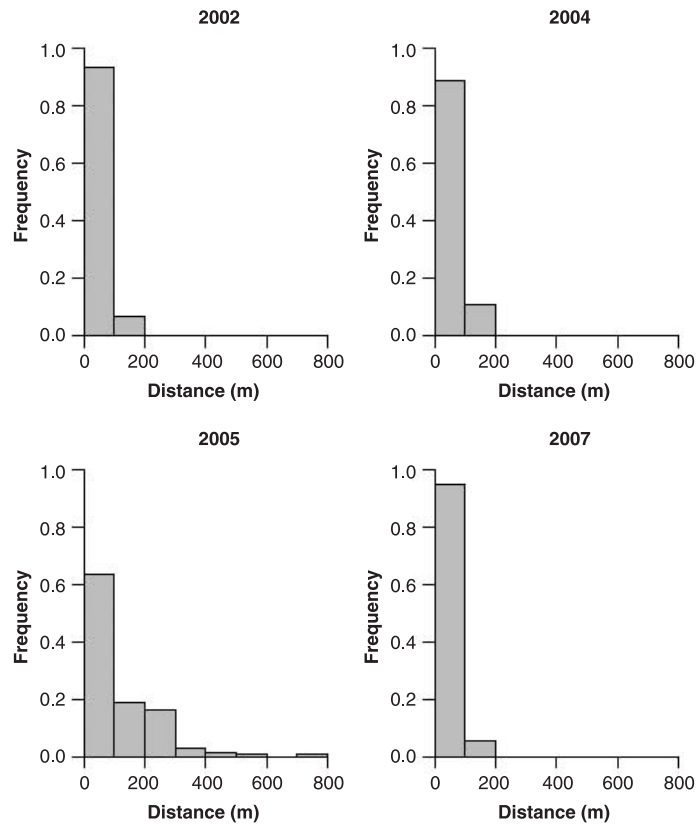
Fig. 4. Frequency distribution of the distance between acorns harvested by acorn woodpeckers and the granaries in which they were stored for each of the 4 years of the study. The maximum distance birds were observed to travel to harvest acorns was 102 m in 2002, 171 m in 2004, 796 m in 2005, and 130 m in 2007.

As expected, birds harvested acorns from a greater number of trees and over larger distances in the poor acorn year compared with good acorn years. Within the foraging ranges of birds in good years, acorns were harvested from nearly all trees. However, considering the larger area over which acorns were harvested during the 4 years of the study, birds harvested acorns from only a small proportion of potential trees in good crop years but from a much larger fraction in the poor crop year. The overall rate of acorn storage was, as expected, lowest during the poor acorn crop year.

These results suggest that the effect of incidental dispersal of acorns by acorn woodpeckers during the process of harvesting acorns on the genetic structure of oak populations is unlikely to be large. The majority of acorns harvested were taken within the normal foraging ranges of the birds, and harvesting overlap (birds from two groups taking acorns from the same tree) was uncommon. Given the strong territoriality of this species (MacRoberts and MacRoberts, 1976; Mumme and de Quieroz, 1985), such restricted movement and limited overlap is not surprising.

Other than the wider area and greater proportion of trees from which birds collected seeds in the poor acorn year of 2005, the patterns of acorn harvesting that emerged from

this study were not generally those predicted based solely on energetic considerations. For example, we found no evidence that birds preferred to harvest and store *Q. agrifolia* acorns, despite acorns of this species yielding more energy on average than acorns of the other two species in the study area (Koenig and Benedict, 2002). Other factors besides energy are apparently important in determining the acorns harvested by acorn woodpeckers. One possibility is tannin content, although previous work suggests that tannins do not have a strong effect on overall digestive efficiency in this species (Koenig and Heck, 1988; Koenig, 1991), and neither do they interact with the length of acorn storage in a way that is likely to influence harvesting preferences (Koenig and Faeth, 1998).

Seed pool structure and a comparison with Grivet *et al.*

Within groups, birds harvested acorns from the greatest number of trees, both in total (mean maternal richness) and weighted by the number of acorns harvested from different individuals (N_{em}), in the poor acorn year of 2005. The probability of maternal identity ($\bar{r}_0$), or the probability of two random acorns harvested by a group coming from the same tree, averaged 0.21 (range 0.11–0.33). As expected, there was little overlap in maternal identity across territories; that is, groups generally did not harvest acorns from trees being used by another group.

Grivet *et al.* (2005) sampled a relatively small number of acorns (215) from a large number of granaries (17), encompassing most or all trees used for acorn storage within a single valley. In contrast, our sampling encompassed a large number of acorns (3568) from few territories (4). Despite the different methodology, the quantitative results of the two studies are similar, particularly when restricted to *Q. lobata*, the species studied by Grivet *et al.* (2005), and considering that the acorn crop during one of the years of our study was much poorer than the year during which Grivet *et al.* conducted their study.

Based on visual surveys at the two study sites, which are 215 km apart, the acorn crop of *Q. lobata* in 2002 was very good in both localities (mean number of acorns counted per tree in 30 s = 42.0 [Hastings Reservation] and 36.8 [Sedgwick Reserve]), so acorns of this species were readily availability at both study sites that year (W. Koenig and J. Knops, unpublished data). Restricting our analyses to *Q. lobata*, the mean number of trees from which acorns were harvested was 51% higher at Hastings (6.5) than at Sedgwick (4.3), but this was primarily due to the poor acorn year of 2005 when the number of trees used for harvesting at Hastings was high. Excluding 2005, mean maternal richness for *Q. lobata* at Hastings was 4.4, almost identical to Grivet and colleagues' value of 4.3. The PMI values calculated by Grivet *et al.* were well within the range of values we observed at Hastings, as was the effective number of *Q. lobata* mothers harvested by the birds, which was 2.0 at Sedgwick and ranged from 1.5 to 5.7 (mean = 3.1) at Hastings. Grivet *et al.* estimated that 97% of acorns were harvested within 150 m of a granary, while we found that 94% of acorns were harvested within 150 m of a group's granary facilities.

In this particular system, quantifying seed dispersal by other vectors and measuring pollen flow would be needed to determine the relative importance of acorn woodpeckers to overall dispersal distance, and thus population structuring, in *Q. lobata* and other California oaks. However, these results support Grivet and colleagues' conclusion that a seed pool approach can provide a good approximation of seed movement, and that such an approach can be effective when direct observation of seed dispersal is difficult. Our

results thus provide a basis for conducting future studies to estimate this critical parameter in trees and other taxa that produce animal-dispersed propagules.

ACKNOWLEDGEMENTS

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