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Granary-Site Selection by Acorn Woodpeckers in the Willamette Valley, Oregon

Abstract

The acorn woodpecker is among the most common primary cavity nesting bird of the Oregon white oak woodlands. In most of their range, acorn woodpeckers are dependent on granaries for acorn storage, yet little is known about their selection of granary sites. We compared habitat characteristics within 12 m of granary and non-granary trees at 20 acorn woodpecker colonies in Benton County, Oregon during the winter of 2001. Compared to non-granaries, granary plots consistently had greater oak basal area and shorter shrub height, and granary trees were of larger diameter. Within each of the 20 sites, oak basal area was greater near granary than non-granary trees. This, together with the selection for larger diameter granaries, suggests acorn woodpeckers are more likely to locate granaries in the immediate area of high acorn production. Increased acorn production in the vicinity of granaries is likely beneficial to the birds because minimal effort is expended in caching maximum forage. Our results shed light on granary selection at the spatial scale of the immediate area surrounding granaries and suggest factors associated with acorn woodpecker distribution at the landscape scale.

Introduction

The acorn woodpecker (*Melanerpes formicivorus*) is highly specialized for living in oak (*Quercus* spp.) communities, and its range is limited by the distribution of oak woodlands and diversity of oak species (Bock and Bock 1974). The demography of acorn woodpeckers is similarly affected by acorn mast and the ability to store it (Koenig et al. 1995). The central feature of acorn woodpecker territories is the storage tree, or granary. Acorn woodpeckers gather acorns directly from the tree and drill small holes in granaries in which to store them for the winter (MacRoberts 1970, MacRoberts and MacRoberts 1976, Koenig and Mumme 1987). Typically, each home range will contain one primary granary tree, and often one or more secondary granaries with fewer storage holes (Koenig et al. 1995). Granaries are defended from competitors and are reused each fall (Koenig et al. 1995).

Why specific trees are chosen as granaries is unknown. It is probably energetically beneficial for the birds to center their activities, and consequently their granaries, on the highest quality microhabitats within their home range (Pyke et al.. 1977). Proximity to acorn production may be important to granary-site selection due to increased caching efficiency and acorn quantity. Larger diameter trees may provide many advantages including greater mast production and a greater volume of dead and decaying wood, which may be beneficial for the construction of granaries and cavities. Avoidance of predation and competitors for acorns may also play a role on granary location. Granaries in areas with low ground cover height may be indicative of a safer site with lower terrestrial competition and predation. Although many tree species and human structures may be used as granaries (Koenig et al. 1995), oaks may be more attractive as granary sites than other tree genera. As large expanses of suitable habitat decline (ODFW 2005), particularly in the northern edge of their range (e.g., Ryan and Carey 1995), more attention to granary-site selection may be necessary to ensure viable acorn woodpecker populations.

Our objectives were to compare tree and surrounding habitat characteristics between granary and non-granary trees for a population of acorn woodpeckers at the northern fringe of their range. We examined the selection of granaries at the spatial scale of the immediate ($\leq$15 m) area surrounding the granary within colonies of acorn woodpeckers. Such information will aid management of oak woodlands and savannas, threatened vegetation types in Oregon (ODFW 2005).

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Study Sites

We conducted the study within Benton County of western Oregon (Figure 1). This portion of the Willamette Valley is mostly flat, low elevation (~100 m) and dominated by agricultural and suburban uses. The climate is mild with wet winters and warm, dry summers (Franklin and Dyrness 1973).

We sampled habitat characteristics from 20 acorn woodpecker colonies chosen from those identified by Doerge (1979) and unpublished Oregon Department of Fish and Wildlife surveys, and by searching oak woodlands from nearby roads with binoculars (Figure 1). All were dominated by Oregon white oak (*Quercus garryana*) and were near modified grasslands, including fields of grass

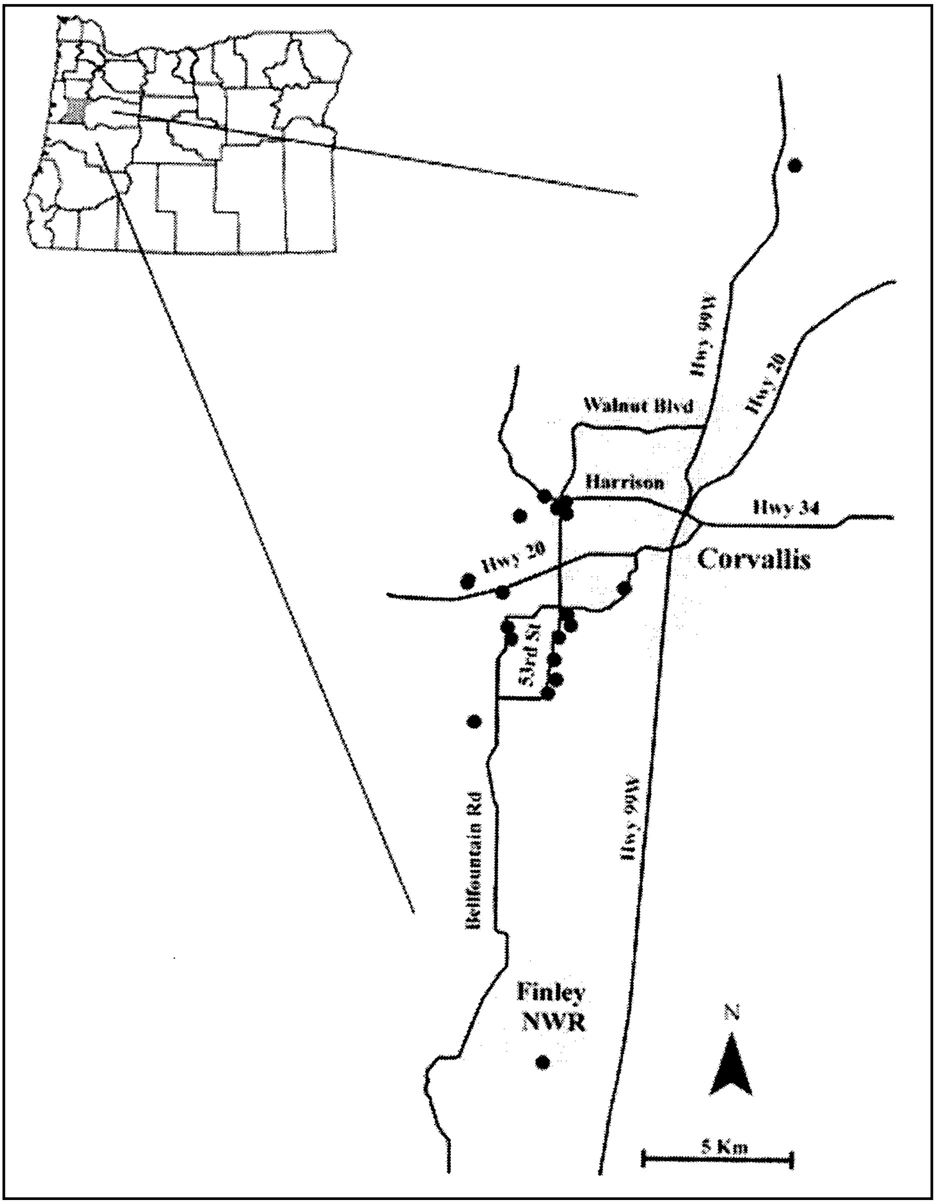

Figure 1. Location of acorn woodpecker study sites (n=20) within Benton County, Oregon. Acorn woodpecker sites are indicated by a solid circle. Inset indicates location of Benton County (shaded) within Oregon.

seed crops. Douglas-fir (*Pseudotsuga menziesii*), giant sequoia (*Sequiadendron giganteum*), and bigleaf maple (*Acer macrophyllum*) were the only other trees present.

Methods

We located granaries by walking through acorn woodpecker colonies and searching with binoculars for the birds and their granaries during the winter months (January-April) of 2001 when the trees lacked leaves and the woodpeckers were actively feeding upon cached acorns. We recorded the position of the main granary (defined below) or the center of storage activity when there was no obvious main granary.

We defined the foraging range of each woodpecker group by the location of the main granary. Following Koenig and Mumme (1987), we defined the main granary as the largest consistently guarded cache, and a primary foraging range as the area within a 50-m radius from the main granary. We considered 50 m as our operational definition of the primary foraging range because it contained all granaries in most colonies. Three non-granary trees and three granary trees within the primary foraging range were selected for measurement by randomly selecting a universal transverse mercator (UTM). The random UTM was selected using a random distance (δ) weighted towards the exterior (to give equal probability for the entire foraging range) according to

$$\delta = 50\sqrt{\chi_1}\,,$$

and a random angle (α) was generated according to

$$\alpha = 360\chi_2\,,$$

where χ_1 and χ_2 were randomly generated numbers between 0 and 1. Therefore, δ was the distance in meters from the main granary, and α was the bearing (in degrees east of true north) from which the distance was measured. The nearest tree or snag $\geq$20 cm diameter at breast height (dbh) was selected if within 5 m of the random location. We continued to select random locations until we had located three granary and three non-granary trees.

We described characteristics of granary and non-granary trees and the area surrounding them. At each of the randomly selected granary and non-granary trees (hereafter referred to as "reference tree"), we recorded tree type (oak, conifer, deciduous non-oak), whether the tree was alive or dead, and dbh. We measured dbh of all oak trees $\geq$20 cm dbh within 12 m of the reference tree (granary or non-granary) and added these measurements to estimate oak basal area. We used 12 m because acorns are usually gathered from within that distance of the granary (Nicpon 1995; E. Johnson, personal observation). We chose 20 cm dbh as the minimum size to include because oaks rarely produce mast until achieving this size (Goodrum et al.1971, Peter and Harrington 2002). Shrub height in the immediate area of the granary and non-granary trees was estimated by measuring the maximum height within four 1-m-diameter circles, with each center 3 m from the reference tree in each of the four cardinal directions (Higgins and Barker 1982).

We calculated mean dbh (reference trees), oak basal area, and shrub height for the three granary and three non-granary plots in each of the 20 colonies. We then computed the difference between the mean values for granary and non-granary plots within each site (χ^*), and used these 20 differences (granary–non-granary) in paired t-tests (Proc Means; SAS Institute 1998). We report the mean difference, its associated SE, and the *P*-value, the probability of the observed data given the null hypothesis of no difference ($\chi^* = 0$). We also report the mean and SE of habitat characteristics of granary and non-granary plots with all sites pooled, rather than paired by site, and we qualitatively compared these results with those from the paired differences.

Results

Oregon white oak was by far the most abundant tree species in our sites and other tree species were relatively uncommon or absent from the plots. All of the randomly selected granary trees were living oaks, although we observed granaries in bigleaf maple and giant sequoia within the study sites. Granaries were also observed in a utility pole and on the side of a house. The randomly selected non-granary trees were white oak (87%), Douglas fir (5%), and big-leaf maple (8%). Two of the non-granary trees were snags.

The predominant difference between granary and non-granary plots was oak basal area, which was consistently much higher in granary plots. Oak basal area was almost twice as great at granary (50.1 ± 4.1 m^2/ha) than at non-granary (27.2 ± 3.0 m^2/ha) plots (Figure 2A), with an average differ-

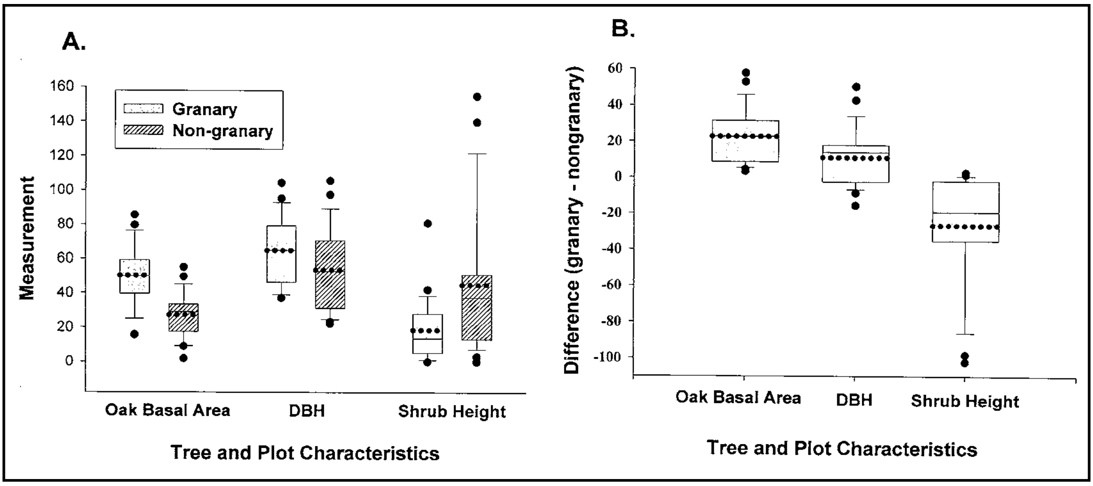

Figure 2. Box-and-whisker diagrams of oak basal area (m^2/ha), dbh (cm) of randomly selected granaries or non-granaries, and shrub height (cm) at 20 acorn woodpecker sites, Benton County, Oregon. Oak basal area and shrub height were sampled from within 12-m of the granary or non-granary tree; DBH is that of the reference tree. The median and mean are shown as the solid and dotted line, respectively, within the box, and the box contains the 25th to 75th percentile of observations. The error bars indicate the 10th and 90th percentile. Outlying points are shown as filled circles. (A) Comparison of the distribution among the mean values from 3 plots at each of the 20 sites. The y-axis is the unit of measurement as indicated above for each variable. (B) Differences (granary – non-granary plots) of dbh (reference trees), oak basal area, and shrub height were computed from the mean values of the 3 granary and 3 non-granary plots within each site.

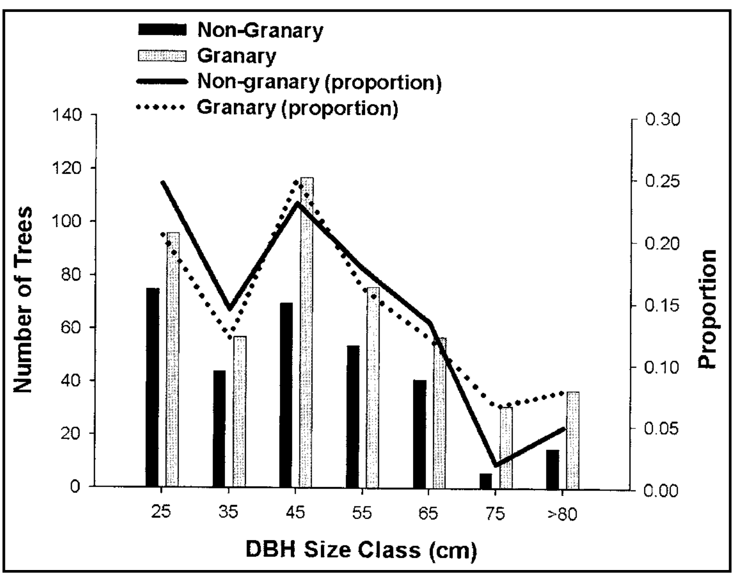

Figure 3. Diameter at breast height (dbh) distribution of Oregon white oak trees within 12-m sample plots surrounding granary and non-granary reference trees. The mid-point of the interval class is shown on the x-axis; 20 cm dbh was the smallest tree included in the samples. The number of trees, pooled from the 3 12-m plots from each of the 20 sites is shown on the histogram.

ence within sites (χ^*) of 23.0 ± 3.5 m^2/ha (P<0.001; Figure 2B). Although the basal area of oaks overlapped between granary and non-granary plots when considering all sites pooled (Figure 2A), there was no overlap within any particular site (Figure 2B). Patterns of diameter distribution of Oregon white oaks was similar between the pooled granary and non-granary plots, with few very large (>80 cm dbh) trees within the sample plots (Figure 3). Shrub height was shorter in granary (18.5 ± 4.3 cm) than non-granary (45.0 ± 9.5 cm) plots, with an average paired difference of -26.0 ± 7 cm (P=0.001; Figure 2). Diameter at breast height of reference trees was greater at granaries (64.7 ± 4.7 cm) than non-granaries (53.5 ± 5.5 cm); the paired difference was 11.3 ± 3.8 cm (P=0.008; Figure 2). The differences were greater in all of these characteristics when comparing granary and non-granary plots within a site (Figure 2B) than among sites (Figure 2A).

Shrub height was negatively correlated with oak basal area (-0.62, $P = 0.0035$), as expected for oak savanna habitats where oak was the dominant over-story cover.

Discussion

We found that granaries were generally the larger oak trees with low surrounding shrub height and were consistently associated with areas of greater basal area of Oregon white oak. We speculate that this is because of acorn production, reflecting the importance of acorns to the bird's demography, particularly for winter survival and spring reproduction (Koenig et al. 1995). Although insects are a critical part of the acorn woodpecker's diet, availability of acorn mast drives their demography in most populations (Koenig et al. 1995).

If acorn woodpeckers are behaving in a manner consistent with optimal foraging theory (Pyke et al. 1977), granaries should be located centrally in the major acorn-producing area within the home range. This would allow for minimal expenditure of energy per acorn. If this is true, habitat directly around the granaries is expected to have greater acorn production relative to other portions of the home range. Our findings of a greater difference of oak basal area between the granary and non-granary plots within a site than the pooled means across all sites, suggest that woodpeckers selected the granary location with the greatest basal area within its home range more than it selected a specific basal area. Oregon white oak acorn production generally increases as basal area increases (Goodrum et al. 1971), but as Peter and Harrington (2002) documented for acorn production of Oregon white oaks, *per capita* production is greatest when stand density is low and oaks are at least 60-80 yr. In northwestern California, Raphael (1987) demonstrated that acorn woodpeckers were positively associated with tanoak (*Lithocarpus densiflora*) canopy volume and mast production. Indeed, all of the granary plots we sampled had greater basal area of oaks than non-granary plots within the same site. The mean basal area that we observed within sites was greater than that reported by Peter and Harrington (2002), suggesting that trees were not at maximum *per capita* production. As Peter and Harrington (2002) point out, there is a need for a better understanding of the trade off of *per capita* and stand-level acorn production to guide effective management.

Because the Oregon white oak is the only native oak species in Benton County and the predominate species in the Willamette Valley, acorn woodpeckers likely experience a great deal of fluctuation in forage availability. Acorn production may be more consistent in areas of greater oak species diversity because of the asynchronous annual masting among different oak species. This led Bock and Bock (1974) to hypothesize that oak diversity may limit the distribution of acorn woodpeckers. Acorn production by Oregon white oak is cyclical (Sudworth 1967, Coblentz 1980), with high yields of acorn crops occurring every 3-6 years (Ryan and Carey 1995). During years of low acorn production, acorn woodpeckers in the Willamette Valley likely experience a great deal of winter mortality, although we are unaware of demographic data to evaluate this hypothesis. Consequently, acorn production probably limits population size in the Willamette Valley, as it does in other regions (Hannon et al. 1987, Koenig and Mumme 1987; Koenig et al. 1995).

Competition for acorns and predator avoidance may also be important influences in granary-site selection. Competition for nesting cavities and acorns, as well as predation comes from both terrestrial and aerial sources (Neff 1928, Troetschler 1976, Koenig et al. 1995, Nicpon 1995). This may lead to the selection of sites that are more defensible, less desirable for competitors and predators, and that have greater escape opportunities. Our finding of lower shrub height near granaries was consistent with this hypothesis; however, it is possible this finding was partially due to the negative correlation with oak basal area. Although correlated, shrub height was clearly dependant upon vegetation management of the site (e.g. mowing & grazing) rather than simply under-story suppression (E. Johnson, pers. obs.).

Because the acorn woodpecker is highly dependent upon the presence of masting oaks, management of these trees is likely to greatly affect the birds that depend upon them. The oak woodland-savanna vegetation in the Willamette Valley has declined in area to less than 15% of its pre-settlement extent (Pacific Northwest Ecosystem Consortium 1998) due to conversion to agriculture, succession to a Douglas-fir dominated forest, and unprecedented urban and suburban development (Towle 1983, Cambell 2004, Vesely and Tucker 2004). Further, most of white oak woodlands have high density of oaks

(Vesely and Tucker 2004). Although such stands may have a high basal area, they result in low acorn production (Peter and Harrington 2002) and thus presumably fewer beneficial granary locations. Our sample included only sites in which acorn woodpeckers foraged. In these sites, tree density was moderate and contained a large number of mid-size trees (40-80 cm dbh; Figure 3). The relative role of acorn production versus stand structure, *per se*, in acorn woodpecker foraging ecology is not known. Thinning dense stands to create larger diameter and more productive masting trees (Peter and Harrington 2002) will likely benefit acorn woodpeckers by creating potential granary sites with high acorn production, but the trade-off with lower basal area will need to be addressed. Our findings can be used as a basis for stand density management for acorn woodpeckers, although the relationship of size distribution and stand density on acorn woodpecker foraging ecology requires research conducted at larger spatial scales.

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