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Influence of acorn woodpecker social behaviour on transport of coast live oak (*Quercus agrifolia*) acorns in a southern California oak savanna

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Summary

1. Many plant species depend upon animals for seed dispersal, yet animals disperse seeds in pursuit of their own social and behavioural agendas. Animal social behaviour affects where and how they forage, so it must also shape patterns of seed dispersal.

2. At Sedgwick Reserve, California, USA, we established a study population of *Quercus agrifolia* to determine patterns of acorn foraging by the acorn woodpecker (*Melanerpes formicivorous*). This cooperative breeder lives in social groups that defend territories surrounding arboreal seed caches (granaries), foraging communally within these territories.

3. We genotyped pericarp tissue of 568 acorns, as well as 285 adult *Q. agrifolia* trees, including all adults within 150 m of 16 focal granaries. After quantifying genotyping error, we identified a genetically reliable subset of 524 acorns. We assigned a source tree to each acorn and estimated the number of seed sources per granary and seed source sharing among granaries.

4. We found one to eight distinct seed-source genotypes per granary, and an effective source diversity ranging from 1.0 to 6.6 seed sources. Of all transport events, 96.5% involve source trees within 150 m of the granaries. For one granary, all sampled acorns were transported from five trees located more than 1.3 km away, with all source trees within 90 m of each other. No measure of seed-source diversity was associated with density of potential seed sources, and the pattern of acorn movement fits three traditional dispersal curves poorly.

5. Woodpecker groups rarely collected acorns from overlapping sets of maternal sources. Some pairs of neighbouring granaries shared maternal sources, and we identify those that were probably maintained by the same woodpecker group.

6. *Synthesis*. Territoriality of woodpecker groups restricts both the spatial area of foraging and the sharing of seed sources. This foraging behaviour limits distances and directions of acorn transport from oaks located within woodpecker territories. Dispersal agents with this type of social structure will create a high degree of local genetic structure. Extreme behavioural variations may result in anomalous long-distance dispersal events that increase genetic connectivity, but are likely to do so in an episodic and erratic fashion.

Key-words: assignment analysis, genotyping error, *Melanerpes formicivorous*, pericarp, probability of maternal identity, *Quercus agrifolia*, seed dispersal, social behaviour

Introduction

For the many tree species with vertebrate-dispersed seeds (Howe & Smallwood 1982; Tiffney 2004; Eriksson 2008; Galetti *et al.* 2008), the behaviour of the dispersal agent determines the patterns and characteristics of seed dispersal (Fleming & Heithaus 1981; Herrera 2002; Wang & Smith 2002; Muscarella & Fleming 2007). Many studies have shown how the handling and transport of seeds and fruits by vertebrates influence the fates of individual seeds (e.g., Loiselle & Blake 1999; Holbrook & Smith 2000; Levey & Sargent 2000; Wenny 2000; Poulsen *et al.* 2002; Gomez 2003; Jordano *et al.* 2007). Fewer studies have considered how social aspects of vertebrate behaviour, such as territoriality or mating systems, shape dispersal patterns of seeds (Russo, Portnoy & Augspurger 2006). Seba's short-tailed bats (*Carollia*

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perspicillata) defecate *Piper* seeds beneath social nocturnal roosts located an average of 38 m from *Piper* patches (Fleming 1981). Groups of spider monkeys (*Ateles paniscus*) defecate large clumps of seeds beneath sleeping trees (Russo & Augspurger 2004), their choice of which is territorial (Mitani & Rodman 1979; Lowen & Dunbar 1994; Russo, Portnoy & Augspurger 2006) and is also dependent on proximity to fruiting resources (Chapman, Chapman & McLaughlin 1989). Males of the Long-wattled Umbrellabird (*Cephalopterus penduliger*) congregate in display areas (leks), whereas females are largely solitary, maintaining non-overlapping home ranges; these differences in social behaviour create sex-specific dispersal patterns for seeds of the palm *Oenocarpus bataua* (J. Karubian, unpublished data).

Among seed-dependent vertebrates, the social behaviour of the acorn woodpecker (*Melanerpes formicivorus*) and its dependence on acorns for reproductive success are particularly well documented (Stacey & Bock 1978; Koenig & Mumme 1987; Koenig *et al*. 1995), yet relatively little is known about this species' foraging patterns (see Grivet, Smouse & Sork 2005; Koenig, Mcentee & Walters 2008), and even less is known regarding the impact of its unusual social behaviour on seed movement. Acorn woodpeckers are cooperative social breeders, heavily dependent upon acorns for survival and reproductive success (Bock & Bock 1974; Koenig & Mumme 1987). Each group defends an all-purpose territory of 3.5–9 ha, which includes its breeding tree, acorn-bearing oaks, and one or more 'granary' trees in which harvested acorns are stored, most commonly in holes made by the woodpeckers (MacRoberts & MacRoberts 1976; Gutierrez & Koenig 1978; Koenig & Mumme 1987). Within the territory, members of a group will defend granaries and acorn-bearing oaks against other conspecific groups and against heterospecific foragers (MacRoberts 1970). The net effect of territorial defence on acorn dispersal would appear to be that foraging bouts of acorn woodpeckers will radiate away from granary trees in numerous directions, to source trees within a local territory; but that the seeds from any particular source tree will tend to be dispersed directionally by the woodpeckers, towards the granary or granaries tended by the group. We predict that three specific aspects of acorn woodpecker social behaviour are likely to affect seed movement and contribute to this overall pattern. First, woodpeckers may forage from oaks located close to their granaries because foraging generally occurs well within the defended territory (Grivet, Smouse & Sork 2005; Koenig, McEntee & Walters 2008). Secondly, woodpeckers may occasionally forage from extraterritorial oaks, due to the non-saturated spatial array of woodpecker territories (Koenig, VanVuren & Hooge 1996). Thirdly, active defence of acorn-bearing oaks will result in little or no sharing of acorn sources maintained by different woodpecker groups (MacRoberts 1970), although birds may forage farther afield when an acorn crop is particularly poor (Koenig, McEntee & Walters 2008). Foraging-specific studies to date have supported these predictions (Grivet, Smouse & Sork 2005; Koenig, McEntee & Walters 2008), but have been limited by acorn or granary sample sizes, as well as by uncertainty in assignment of acorn sources. We note that the woodpeckers, like any seed predator, are likely to consume a significant portion of the seeds they move; unfortunately it is not yet known how frequently acorns handled by acorn woodpeckers escape consumption by being incidentally dispersed to other locations. Whatever this rate may be, we would expect the pattern of incidental seed dispersal to be largely coincident with that observed for seeds moved to granaries, and it is on the movement of these seeds that we focus.

Although acorn woodpeckers appear to be an ideal species for studying the impact of social behaviour on seed movement, a territorial dispersal agent can still be highly mobile, and direct observation cannot always document the full range of their movements or record all seed-source trees that are visited (Koenig, VanVuren & Hooge 1996). However, we can identify the outcome of dispersal through recent advances in seed genotyping, which utilize the genotype of maternally derived seed coat or pericarp tissue in the seed to identify the genotype of its maternal source directly (Godoy & Jordano 2001; Grivet, Smouse & Sork 2005; Jones *et al*. 2005; Jordano *et al*. 2007). With these techniques, we can increase the number of dispersal events observed and thereby enhance our ability to detect even rare events of long-distance dispersal. Despite these advantages, poor DNA quality from maternally derived tissue in the seed can prevent genetic identification, a problem encountered in pericarps of the sympatric *Quercus lobata* by Grivet, Smouse & Sork (2005). Jones *et al*. (2005) reported that only 14% of *c*. 5200 *Jacaranda copaia* seeds provided reliable maternal genotypes, and others have encountered similar problems, warning that poor maternal source assignment can yield misleading estimates of seed disperser behaviour (Garcia, Jordano & Godoy 2007). Genetic assay difficulties are fairly general, but maternal genotypes derived from seeds and fruits have nevertheless greatly expanded our ability to track dispersal events, and further advances in genotype analysis such as assessment of and correction for genotyping errors may allow us to evaluate and mitigate even these remaining problems.

Here, we examine the impact of acorn woodpecker behaviour on the movement of acorns within a population of coast live oak (*Quercus agrifolia* Née) in a southern California oak woodland. We sampled acorns from acorn woodpecker granaries, genotyped maternally derived tissue in each acorn and matched them to adult *Q. agrifolia*, mapped and genotyped at the same site. Before we began our analysis, we examined patterns of acorn genotyping error, accounted for common genotyping errors observed in our data set, and identified the best subset of samples for further analysis. Using these reliable seed genotypes, we pursued two primary analytical objectives. Our first was to assess the impact of woodpecker social behaviour on local patterns of seed movement, using both a seed pool structure approach (Grivet, Smouse & Sork 2005) and a maternity assignment analysis, to determine the distances and spatial orientations of maternal source trees around granaries. For this portion of the work, we also examined the degree to which woodpecker foraging was spatially restricted to the locality of each granary by fitting standard diffusive dispersal kernels to our seed movement distances, as well as testing whether either

the observed or effective number of seed-source trees per granary was influenced by the density of trees located within the territorial foraging range of acorn woodpeckers. Our second objective was to examine whether territoriality restricts the extent to which maternal source trees are sampled by more than one woodpecker group. We use the Grivet, Smouse & Sork (2005) probability of maternal identity (PMI) analysis to examine the probability that woodpeckers filling two different granaries sampled from the same source tree, and we introduce a new extension of that analysis that accounts for features of woodpecker social behaviour not adequately addressed by the original conceptualization of PMI. We also examine the spatial context of specific source tree sharing events to establish some criteria for determining whether source tree sharing by two granaries is indicative of maintenance of the granaries by the same woodpecker group.

Materials and methods

STUDY SITE

Our study site is located in the Figueroa Creek valley of Sedgwick Reserve, part of the University of California Natural Reserve System. Sedgwick Reserve is a 2380-ha research area managed by UC Santa Barbara and located in the Santa Ynez Valley, Santa Barbara Co., California (34°42′ N, 120°02′ W). The habitat is oak woodland, containing three oak species: California valley oak (*Q. lobata* Née) in the open valley, blue oak (*Quercus douglasii* Hook & Arn) in greater density on hillsides, and coast live oak (*Q. agrifolia* Née) in both the valley and on the hillsides (Tyler, Kuhn & Davis 2006). On the hillsides and hilltops, *Q. agrifolia* occurred in large densities, whereas on the valley floor it occurred in lowered densities, mostly clustered along the creek bed. Pollen and seed dispersal for *Q. lobata* at this site have been described extensively (Sork *et al.* 2002; Grivet, Smouse & Sork 2005; Austerlitz *et al.* 2007; Pluess *et al.* 2009). The sampling area was in Figueroa creek and the extended valley, similar to that for previous work with *Q. lobata* (Dutech *et al.* 2005; Grivet, Smouse & Sork 2005).

STUDY SPECIES

Quercus agrifolia is an evergreen, monoecious, wind-pollinated tree in the red-oak section (Lobatae) of the genus (Pavlik *et al.* 1991) and is susceptible to sudden oak death (Tyler, Kuhn & Davis 2006; Dodd *et al.* 2008). Flowering occurs in spring, with acorns maturing in late summer and autumn of the same year. Acorns are dispersed by gravity and several seed predator vertebrate species, including acorn woodpeckers (*Melanerpes formicivorus*), scrub jays (*Aphelocoma californica*) and small rodents. Seed production in *Q. agrifolia* varies temporally, with a large seed crop every 2 or 3 years (Koenig *et al.* 1994; Liebhold *et al.* 2004; V.L. Sork, pers. obs.).

Melanerpes formicivorus is a common bird species in California oak woodlands. The species breeds in cooperative groups containing one or more breeding males and females and several non-breeding helper adults, which all share a communal cavity nest (MacRoberts & MacRoberts 1976; Koenig & Mumme 1987). At our field site, almost all acorn woodpecker granaries are located in the thick bark of adult *Q. lobata* trees, with acorns cached inside woodpecker-created holes in the bark, cracks or other bark features. A woodpecker group will fill a primary granary and occasionally one or more auxiliary granaries as acorns become available each year, and will defend the granary/ies and the foraging territory surrounding it/them from other foragers (MacRoberts & MacRoberts 1976). The survival and reproductive success of the woodpeckers depend critically upon their caching a sufficient quantity of acorns to last into the breeding season (Koenig & Mumme 1987). Acorn woodpecker reproductive success does not increase during years of increased acorn production, but decreases when overall acorn crops across all species are unusually low at a site (Koenig & Mumme 1987). Acorn woodpeckers can fly up to 10 km day^{-1} (Koenig, VanVuren & Hooge 1996), with typical foraging ranges being substantially smaller unless acorns are scarce (Koenig, McEntee & Walters 2008). A recent direct observational study revealed that 94% of all acorns and 83% of all source trees in a central California oak woodland were located within 150 m of the granary, as well as a low amount of shared usage of source trees between woodpecker groups (Koenig, McEntee & Walters 2008).

FIELD METHODS

In the autumn of 2006, we collected *Q. agrifolia* acorns from 16 granaries. Prior to the production of acorns, we marked a rectangular *c.* 0.5-m^2 area within each granary and removed all old acorns and pericarp fragments. After woodpeckers had begun caching acorns within this cleared sector, we collected from 8 to 50+ *Q. agrifolia* acorns per granary, depending upon availability. We genotyped 8–12 acorns per granary from six granaries and 38–50 acorns from the remaining 10 granaries.

In the autumn, winter and spring of 2007–08, we sampled leaves from all *Q. agrifolia* adults within 150 m of each granary, a distance which includes more than 80% of potential acorn source trees, based on studies of *Quercus* at two sites (Grivet, Smouse & Sork 2005; Koenig, McEntee & Walters 2008). This sample of 198 adults yielded a mean number of *Q. agrifolia* adults within 150 m of granaries (20.6 ± 4.5 for 16 granaries) that was similar to that of *Q. lobata* (17.4 ± 1.4), although the *Q. agrifolia* has much greater variation in density from granary to granary than *Q. lobata* (CV = 0.88 and 0.34, respectively). We sampled an additional set of 87 adults located along Figueroa Creek and the slopes and hilltops around the canyon, but the entire valley population was not genotyped.

DNA EXTRACTION AND GENOTYPING

We ground adult leaf and acorn pericarp samples, using a Retch tissue grinder (Haan, Germany) and tungsten ball, and extracted DNA via the QIAgen DNEasy Plant Mini Kit (Germantown, MD, USA). Pericarp samples are very tough and dry, so we soaked the samples overnight in extraction buffer before grinding.

We genotyped 10 microsatellite loci, which were originally developed for *Quercus rubra* (Aldrich *et al.* 2002): quru-GA-0C11, -0C19, -0E09, -0I01, -0M05, -0M07, -1C06, -1C08, -1F02 and -1G13. We labelled primers with Hex, Fam, Tet or Pet fluorescence (Applied Biosystems, Carlsbad, CA, USA). We did not dilute pericarp DNA extracts prior to PCR amplification. We amplified loci in multiplex, using the QIAgen multiplex PCR mix. We PCR-amplified, following a touchdown profile that we optimized for *Q. agrifolia*'s suite of loci within pericarp DNA extracts. The PCR profile consisted of 15 min of hot-start at 95 °C, two cycles of denaturing at 94 °C for 30 s, annealing at 60 °C for 1 min, and extension at 72 °C for 35 s, 18 cycles of denaturing at 93 °C for 30 s, annealing from 59 to 50 °C for 1 min 30 s, respectively, and extension at 70 °C for 45 s, and 20 cycles of denaturing at 92 °C for 30 s, annealing at 50 °C for 1 min 30 s, and extension at 70 °C for 1 min, with a final extension at 72 °C for 5 min. The relatively long denaturing and annealing times are in accordance with QIAgen's hotstart *Taq* protocols. We assigned base

pair genotypes on an Applied Biosystems ABI 3730 capillary sequencer at the Gonda Core facility at UCLA (http://www.genoseq.ucla.edu).

ASSESSMENT OF AND CORRECTION FOR GENOTYPING ERROR

As noted previously, maternally derived seed tissue extracted from field samples can exhibit high rates of genotyping error, due to degraded DNA quality. We considered the potential effects of genotyping error in three ways. First, we measured genotyping error by estimating rates and types of errors through repetition of the extraction, amplification and genotyping steps with three subsets of pericarp samples: 'good' samples that amplified well across all loci, 'poor' samples that amplified poorly across two or more loci, and a randomly selected subset of samples. To expand the coverage of this analysis, all pericarps were candidates in this analysis, including those from granaries that were excluded from the final data set due to low sample size. We then compared genotypes from the original run and each rerun. We found two basic types of genotyping errors: non-amplifying or 'null' alleles (Pemberton *et al.* 1995), in which a seed from a seed source with a heterozygous genotype at a locus appeared to be a homozygote of one of the seed-source alleles, e.g. a seed scored 160/160 when the seed-source genotype was 160/164; and genotype incompatibilities, in which the size of microsatellite allele(s) at a locus in the seed did not match the seed-source allele sizes and were also not consistent with the presence of a null allele, e.g. a scored 160/164 or 162/162 when the seed-source genotype was 160/166. Secondly, we compared adult genotypes for potential sources of ambiguity in assignment, paying particular attention to assignment ambiguities that could occur when accounting for genotyping errors. Thirdly, we considered the extent to which failure to account for genotyping error could bias our estimates, by re-running our assignment analyses without accounting for errors.

SEED POOL STRUCTURE USING PMI ANALYSES

To characterize the degree of acorn source diversity within and among granaries, we calculated the PMI (Grivet, Smouse & Sork 2005) from the relative representations of acorn sources within granaries. PMI is the probability that two randomly drawn acorns from the same granary come from the same acorn source tree, and its reciprocal $N_{em} = 1/\text{PMI}$ is an estimate of the effective number of maternal sources, an ecological analogue to the effective number of alleles in population genetics (Kimura & Crow 1964). PMI is calculated from genotype tallies; for the gth granary containing n_g acorns, x_{gk} acorns come from each of K identified sources, the PMI estimator q_{gg} for granary g is

$$q_{gg} = \sum_{k=1}^{K} \left(\frac{x_{gk}}{n_g}\right)^2. \qquad \text{eqn 1}$$

A proportional estimator structured like q_{gg} is biased, particularly at small sample sizes (Nei & Roychoudhury 1974), so we used an additional PMI estimator q^*_{gg}, which adjusts q_{gg} by applying a correction factor (Nielsen, Tarpy & Reeve 2003) for the effective number of 'types' in a population:

$$q^*_{gg} = \frac{q_{gg}\cdot(n_g-1)\cdot(n_g-2)+3-n_g}{(n_g-1)^2}. \qquad \text{eqn 2}$$

We preferentially report values of q^*_{gg} and its reciprocal $N^*_{em} = 1/q^*_{gg}$ in the text. Note that this adjusted index yields estimates similar to those of r_{gg} used previously (Grivet, Smouse & Sork 2005), but N^*_{em} is more numerically stable and a slightly better estimator (Nielsen, Tarpy & Reeve 2003).

To determine the degree to which local availability of acorn source trees affects acorn source diversity within granaries, we regressed N^*_{em} and K_g, the absolute number of distinct source genotypes observed within a granary, against the number of *Q. agrifolia* trees found within 50, 100 and 150 m of each granary.

OVERLAP IN SEED SOURCES AMONG GRANARIES USING PMI

Using PMI overlap analysis, we calculated the shared maternal identity between the gth and hth granaries (Grivet, Smouse & Sork 2005). PMI overlap q_{gh} is the probability that two randomly drawn acorns from *different* granaries (g and h) come from the same acorn source tree. As for q_{gg}, the PMI overlap estimator q_{gh} is calculated from genotype tallies as

$$q_{gh} = \sum_{k=1}^{K} \frac{x_{gk}\cdot x_{hk}}{n_g\cdot n_h}. \qquad \text{eqn 3}$$

There is unavoidable variation in seed-source representation within finite samples; this estimator is not biased for small sample sizes, because the acorns are drawn from separate collections.

Our PMI overlap estimator q_{gh} characterizes the relative degree of acorn source usage among granaries (Grivet, Smouse & Sork 2005), but it may not capture some important features of seed movement by acorn woodpeckers. If the overall degree of seed source sharing between two neighbouring granaries is high, one could reasonably conclude that these represent primary and auxiliary granaries within the territory of a single woodpecker group (Koenig & Mumme 1987). However, if the relative proportion of each shared seed-source tree is low within either the gth or the hth granary (that is, if either or both of x_{gk}/n_g or x_{hk}/n_h are low for each shared seed source k in eqn 3), then the PMI overlap estimator composed of the summed term values will also be low. It would be preferable to have a pairwise measure that is less sensitive to source-specific sharing and more sensitive to the overall degree of sharing between granaries. We introduce the pooled PMI (PPMI) estimator q^0_{gh} that expresses the probability that two seeds drawn from separate seed caches g and h are from *any* source within the total set of seed sources shared between the two seed caches:

$$q^0_{gh} = \frac{y_{gh}\cdot y_{hg}}{n_g\cdot n_h}, \qquad \text{eqn 4}$$

where y_{gh} and y_{hg} are jointly defined for a pair (or more) of seed caches to be the total number of seeds within a seed cache belonging to sources common to the pair:

$$y_{gh} = \sum_{\substack{k=1,\\ x_{gk}>0 \text{ and } x_{hk}>0}}^{K} x_{gk} \qquad \text{eqn 5}$$

and similarly for y_{hg} summing over x_{hk}. As defined here, q^0_{gh} may differ from q_{gh} when there is more than one shared seed source between seed caches; otherwise it is identical to q_{gh}. We consider the utility of the PPMI estimator q^0_{gh} more fully with a specific example from our data set below.

ACORN SOURCE TREE MATCHING AND ANALYSIS OF ACORN MOVEMENT

We assigned acorn pericarp genotypes directly to potential source trees. We assumed that adult source trees were genotyped correctly

from leaf tissue, consistent with our observation that a very low percentage ($<<1\%$) of adult genotypes differed when regenotyped. We allowed for two types of genotyping errors in pericarps: non-amplifying 'null' alleles (Pemberton *et al.* 1995) and incompatible genotypes between pericarp and a potential seed-source tree. Based on our assessments of genotyping error due to null alleles (1.7% in randomly regenotyped pericarps, see Results), we allowed a 2% chance that a null allele occurred at a locus when the genotype of a pericarp and potential source tree differed as described above. We allowed for any number of null-allele mismatches between pericarp and potential source tree, with the 2% probability multiplied across all such loci, resulting in 0.04% probability of a match between pericarp and potential seed-source tree with two null-allele mismatches, etc. We also allowed a maximum of one incompatible mismatched locus between pericarp and potential source tree, with the single incompatibility treated as missing data in the pericarp. When missing data occurred at a pericarp locus, either because of failure to amplify or because of our treatment of a genotype incompatibility, the probability of a match with a potential seed-source tree was calculated from the population frequencies of the allele(s) at the potential seed-source tree locus. We jointly evaluated the impact of these errors and missing data on pericarp-source tree matches within a likelihood framework, and chose the assignment with the strongest support using an R-language program (D.G. Scofield, unpublished data).

After these assignments, we examined the distances of acorn movements from source trees to granaries. To determine whether acorn movement by acorn woodpeckers occurred in a diffusive manner (a regular decrease in frequency as distance increases) and is thus similar to pollen and seed dispersal patterns observed in many other systems (e.g., Burczyk, Adams & Shimizu 1996; Clark *et al.* 1998; Bullock & Clarke 2000; Greene & Calogeropoulos 2002), we fit within-granary frequencies of movement distances to several common diffusive dispersal kernel functions: a negative exponential (Austerlitz *et al.* 2004), an exponential power (Clark *et al.* 1998) and an inverse power (Clauset, Shalizi & Newman 2009). We then evaluated the degree to which the observed distribution of movement distances was fit by the diffusive dispersal models. We found that acorns from one granary represented an extreme outlier with respect to movement distances (granary 140, mean distance 1378.0 ± 14.4 m), so we also fit the dispersal functions to a data subset without acorns from this granary (maximum distance 372 m in the data subset). We also assessed the relative degree of spatial isolation of woodpecker foraging by examining how frequently acorn woodpeckers transported acorns to a granary other than the granary physically closest to the source tree.

To test whether woodpecker groups having territories with fewer *Q. agrifolia* trees would forage farther afield, we regressed the number of unassigned acorns and unassigned acorn genotypes against the number of oaks within 50, 100 and 150 m of each granary, with the expectation that the number of unassigned acorns and genotypes within a granary would be negatively related to the number of neighbouring oaks.

Results

POPULATION GENETIC CHARACTERISTICS OF *Q. AGRIFOLIA* AT SEDGWICK

Of the 285 *Q. agrifolia* adults in the Sedgwick population that we genotyped for all 10 polymorphic microsatellite loci, we achieved complete 10-locus genotypes for 275, with eight trees missing one locus, one tree missing two loci and one tree missing four loci. Heterozygosity per locus in adult trees was high overall at $H_E = 0.702 \pm 0.037$, with a mean effective number of alleles per single locus of $A_e = 4.13 \pm 0.53$ (for allele frequencies and locus-specific measures of allelic and genotypic diversity, see Table S1 in Supporting Information). The

Table 1. Genotyping error analysis for *Quercus agrifolia* pericarps from acorn woodpecker granaries. Pericarp genotypes were classified as 'good' if all 10 loci gave strong and unambiguous readings and 'poor' if some or all loci gave weak or unresolvable readings. Persistent null alleles are those that were null on repeated runs, while unstable null alleles were null in at least one run and non-null in another run. Mismatched non-null alleles had different estimates of allele sizes between different genotyping runs

	Random resample ($N = 42$)			Good pericarps ($N = 38$)			Poor pericarps ($N = 48$)		
Locus, % genotyping error	Any mismatch	Any null	Both null	Any mismatch	Any null	Both null	Any mismatch	Any null	Both null
0C11	2.4	2.5	0	0	0	0	6.3	8.3	2.1
0C19	4.8	4.8	0	0	0	0	18.8	20.8	2.1
0E09	1.2	0	0	0	0	0	12.5	13.5	2.1
0I01	6.0	4.8	0	1.3	0	0	24.0	25.0	2.1
0M05	0	0	0	0	0	0	15.6	16.7	4.2
0M07	0	0	0	0	0	0	13.5	16.7	4.2
1C06	0	0	0	0	0	0	6.3	8.3	2.1
1C08	7.1	2.4	0	3.9	0	0	53.1	54.2	4.2
1F02	2.4	2.4	0	0	0	0	10.4	12.5	2.1
1G13	0	0	0	0	0	0	12.5	14.6	2.1
Any mismatch	20/2.4%			4/0.5%			166/17.3%		
Persistent null-allele mismatch	0/0%			0/0%			26/2.7%		
Unstable null-allele mismatch	14/1.7%			0/0%			157/16.4%		
Incompatible mismatches	6/0.7%			4/0.5%			9/0.9%		

estimated inbreeding coefficient was $F = 0.021 \pm 0.018$, which was not significantly different from 0, entirely compatible with a lack of inbreeding in adults.

ASSESSMENT OF GENOTYPING ERROR AND SELECTION OF DATA SET

Our direct assessment of genotyping error (Table 1) indicated four classes of genotyping errors: (i) persistent null-allele mismatches, which are null alleles that remained consistently null during regenotyping; (ii) unstable null-allele mismatches, which appeared null in one genotyping run and non-null in another; (iii) incompatible mismatches, which were mismatches that were not consistent with the pattern for null alleles; and (iv) missing data, in which no alleles at a locus amplified sufficiently for detection. In our random sample of 42 regenotyped pericarps, the occurrence of null alleles is 1.7% (at five separate loci), with incompatible mismatches occurring about half as often, 0.7% (at three loci). In our sample of 38 'good' pericarps with strong initial genotypes, no null alleles were observed, while incompatible mismatches were observed about as often as in the random sample, 0.5% (at two loci). In our collection of 48 'poor' pericarps, persistent null alleles occurred in 2.7% of loci, while unstable null alleles occurred in 16.4% of loci. Incompatible mismatches at 0.9% were nearly as rare as in the good samples, suggesting that the majority of genotyping errors in pericarps involves null alleles. In the poor pericarp group, the genotyping error was spread across all 10 loci, and the loci with the highest error rates (0I01 and 1C08) also had the highest rates in the random and good pericarp samples (Table 1). In this study, we classified only 8.7% of the total number of acorns genotyped as poor. After excluding the 48 seeds with poor genotypes, we had a final data set of 524 acorns collected from 16 granaries.

The initial seed-source assignment, which does not take into account genotyping error, resulted in 388 acorns (74% of 524) with assigned seed sources. By allowing for null-allele mismatches, we were able to assign source trees to 66 additional pericarps, indicating the utility of our method for correcting assignment problems created by null alleles in degraded DNA. By allowing for a single locus with an incompatible genotype mismatch (see above), we were able to assign just two additional pericarps to source trees, consistent with our observation of greater rarity of incompatible mismatches in comparison to null-allele mismatches (Table 1). Overall, we were able to assign seed sources to 456 acorns, which is 87.0% of our total sample.

We examined the genotypes of adult trees to determine the degree to which ambiguity in acorn assignment might occur among these potential acorn sources. One pair of adults differed at two loci in a manner that could cause ambiguity in assignment with error handling; however, no pericarps were assigned to either of these adults. Additionally, four pairs of adults differed at three of the 10 loci, but none was a source of acorns sampled in this study. Thus, these 10 loci provided sufficient genetic resolution to identify unambiguously unique seed-source trees for all pericarps.

LOCAL PATTERNS OF ACORN MOVEMENT

Of the 524 total acorns genotyped, we assigned 456 (87.0%) to one of 46 *Q. agrifolia* adult trees (Fig. 2), with 68 acorns from nine unique sources unassigned to genotyped adult trees in our data set. The absolute number of unique acorn sources within each granary (K_g) varied from 1 to 8, with mean $K_g = 3.9 \pm 0.5$. The relative representation of each source varies widely from granary to granary (Fig. 1). The effective numbers of acorn sources ($N^*_{em} = 1/q^*_{gg}$) varied from 1 to about 6, with mean $N^*_{em} = 2.35 \pm 0.37$/granary (Table 2).

The mean movement distance ± SE among all assigned acorns was 92.4 ± 7.7 m, and was 69.5 ± 1.9 m if we exclude the eight long-distance movements (> 1 km); median distance was 53.6 m both with and without the eight long-distance movements. The shortest distance that acorn woodpeckers moved an acorn was 10.5 m for granary 10, while the longest was 1449 m for granary 140. Most movement was short-distance: the mean movement distance for 12 of 16 granaries was < 100 m, and three of the remaining four granaries had mean distances of < 128 m (Table 2), with 96.5% of all assigned acorns collected from trees within 150 m of the granary.

Granary 140, in contrast to others, contained acorns that had been transported from five separate source trees > 1320 m away, which is about 1 km further than any other distance we observed (Fig. 3). Notably, all five source trees were within 90 m of each other (Fig. 2). Four acorns from granary 140, all from a single seed source, could not be assigned to

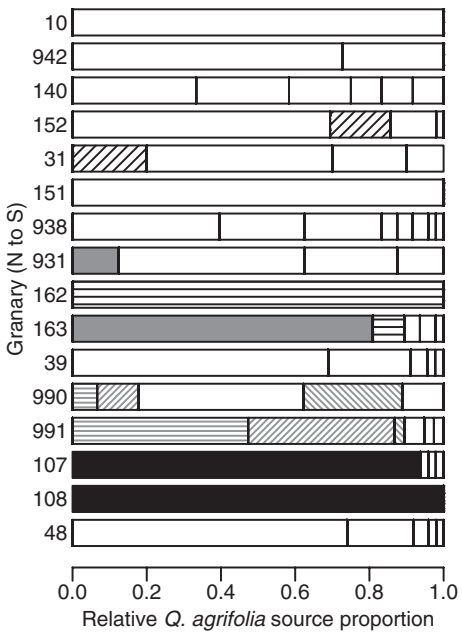

Fig. 1. Unique *Quercus agrifolia* acorn source proportions, as determined from pericarps, listed by granary. The number of vertical divisions indicates the number of seed sources identified. Filled or cross-hatched patterns indicate proportions from acorn sources shared across more than one granary; white boxes indicate acorn sources unique to one granary. Granaries are ordered from north to south.

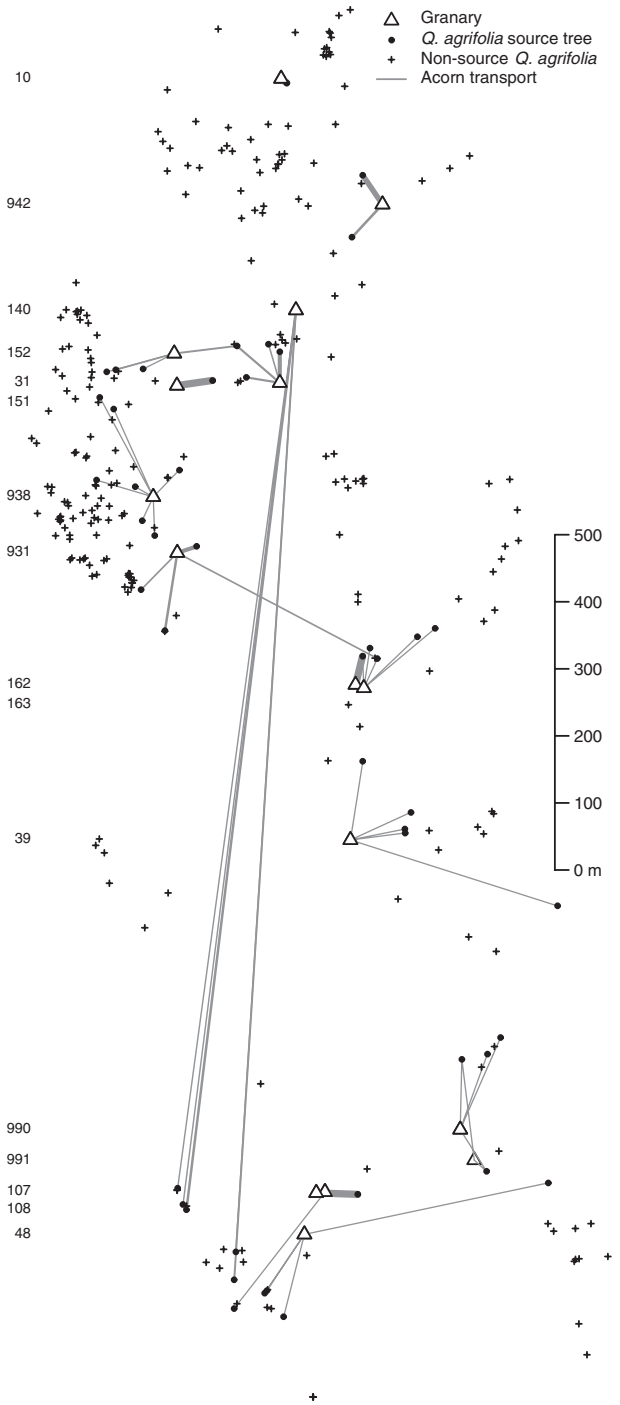

Fig. 2. Movement of *Quercus agrifolia* acorns by acorn woodpeckers at Sedgwick Reserve. *Quercus agrifolia* source trees with genotypes are shown; those without genotypes are not included in the figure. Granary designation is indicated on the left, at its relative north–south position. Line width is proportional to the fraction of acorns in each granary from the indicated adult source tree.

their source tree (Table 2). There is no ambiguity in the assignments for granary 140; all pericarps had complete 10-locus genotypes with no missing data, as did all assigned adult source trees (data not shown). Although these acorns were transported an unusually long distance in comparison to other seed sources assigned within our data set, it is possible that at least some of the 68 acorns from nine unique seed sources that we were unable to assign also represent long-distance dispersal events; in any event they were all transported at least 150 m, as we genotyped all seed sources within 150 m of a sampled granary. We will further discuss the observations for granary 140 below.

Using the source-tree designations and movement distances calculated from the assigned acorns, we determined how frequently acorns were transported to the nearest granary, after excluding granary 140. Out of 448 assigned source-to-granary acorn movements, just 48 (11%) had at least one granary closer to the source tree than the observed granary. After excluding acorn movements for which the closer granary was presumed to be maintained by the same woodpecker group as the observed granary (see below for a discussion of these three granary pairs), the remaining 26 acorns (5.8%) were moved a mean of 189.0 ± 40.1 m, roughly twice the mean distance to the nearest granary and the mean distance of all acorn movements, and 2.7 times the mean distance of all acorn movements after excluding granary 140. Acorn transport events that do not result in the acorn being moved to the nearest granary or a granary maintained by the same bird group are clearly uncommon both in frequency and in distance.

Using the movement distances calculated from the assigned acorns, we fit three dispersal curves to summarize distance patterns to each of two data sets: a full data set containing all acorn movements, and a subset excluding the long-distance acorn movements observed in granary 140. For each data set, both the negative exponential and inverse power curves had significant parameter estimates, but parameters for the exponential power curve were not significantly different from 0 (Table 3), and thus its fit could not be distinguished from that of the negative exponential. Akaike Information Criterion (AIC) values favoured the negative exponential curve. Most significantly, regardless of the parameter estimates, the fits of these diffusive dispersal models to our observed data sets all produced similar log-likelihoods and AIC values. These models were largely indistinguishable, despite large sample sizes, and they all fit the data poorly (Table 3; Fig. 3).

Because diffusive dispersal models fit our data poorly, we performed a more straightforward analysis of the effects of local seed-source density by regressing the observed number of genotypes per granary (K_g) against the number of *Q. agrifolia* trees within 50, 100 and 150 m of each granary. We found a significant relationship between K_g and the number of *Q. agrifolia* within 50 m ($r^2 = 0.26$, d.f. = 14, $P = 0.04$), but other regressions of K_g against *Q. agrifolia* number were not significant (≤ 100 m: $r^2 = 0.10$, $P = 0.22$; ≤ 150 m: $r^2 = 0.08$, $P = 0.28$), nor was there a relationship between the effective number of source trees (N^*_{em}) and the number of *Q. agrifolia* nearby, at any distance (≤ 50 m: $r^2 = 0.11$, $P = 0.29$; ≤ 100 m: $r^2 = 0.02$, $P = 0.81$; ≤ 150 m: $r^2 = 0.01$, $P = 0.90$).

The 68 acorns from nine unique seed sources that we were unable to assign to any of the genotyped adult trees within our field site (Table 2) presumably represent nine seed-source trees visited by woodpeckers maintaining sampled granaries but nei-

Table 2. Probability of maternal identity (PMI) analysis for *Quercus agrifolia* pericarps from *Melanerpes formicivorus* granaries, with the number of pericarps genotyped per granary (N_g), number of unique genotypes per granary (K_g), two estimators of PMI, given by eqns 1 and 2, and the effective number of acorn sources derived from the reciprocal of each PMI estimator. Also shown is the mean dispersal distance of acorns assigned to source trees, and the number of pericarps and genotypes that remained unassigned to genotyped adult source trees ($N_{g\text{-un}}$, $K_{g\text{-un}}$). Granaries are listed in north-to-south order

Granary	N_g	K_g	q_{gg}	q^*_{gg}	N^q_{em}	N^*_{em}	Distance ± SE (m)	$N_{g\text{-un}}$	$K_{g\text{-un}}$
10	12	1	1.000	1.000	1.00	1.00	10.5	0	0
942	44	2	0.603	0.595	1.66	1.68	56.5 ± 1.0	0	0
140	12	6	0.222	0.164	4.50	6.60	1378.0 ± 14.4	4	1
152	49	4	0.524	0.514	1.91	1.95	64.6 ± 2.8	0	0
31	10	4	0.340	0.283	2.94	3.75	56.1 ± 4.9	0	0
151	47	1	1.000	1.000	1.00	1.00	53.6	0	0
938	48	8	0.259	0.244	3.87	4.12	71.4 ± 4.5	1	1
931	8	4	0.344	0.277	2.91	4.00	96.5 ± 37.0	0	0
162	9	1	1.000	1.000	1.00	1.00	43.8	0	0
163	47	5	0.665	0.658	1.50	1.52	53.5 ± 2.6	0	0
39	45	5	0.527	0.517	1.90	1.94	105.4 ± 7.2	0	0
990	45	5	0.298	0.283	3.36	3.55	126.9 ± 3.8	5	1
991	38	6	0.385	0.369	2.60	2.71	31.5 ± 4.7	19	4
107	48	4	0.880	0.878	1.14	1.14	52.6 ± 3.7	2	2
108	12	1	1.000	1.000	1.00	1.00	61.9	0	0
48	50	5	0.582	0.574	1.72	1.74	127.1 ± 10.4	37	1
G = 16	N = 524	K = 55	0.584	0.583	1.71	1.71	92.4 ± 7.7	68	9

ther located nor genotyped in our study. The number of unassigned acorns varied widely among granaries, with 10 granaries having no unassigned acorns and two granaries (991 and 48), both located in the southern portion of the study area, having 19 and 37 unassigned acorns, respectively. Neither the number of unassigned acorns nor number of distinct unassigned genotypes ($N_{g\text{-un}}$ and $K_{g\text{-un}}$, respectively, in Table 2) were predictable from the number of nearby source trees at 50, 100 and 150 m (d.f. = 14 for all non-significant regressions, data not shown).

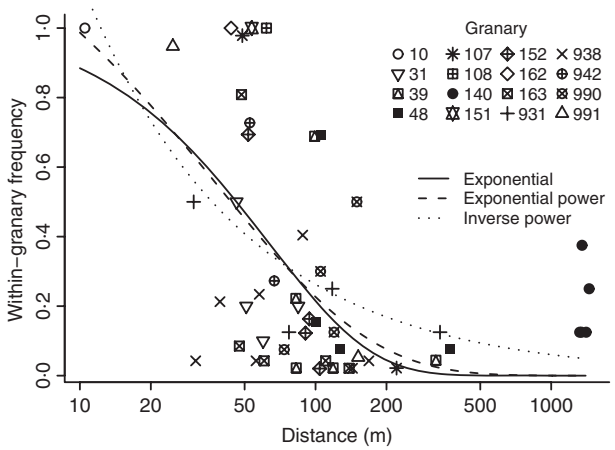

Fig. 3. Pairwise distance–frequency plots of acorn movement distances and fits of dispersal curves to movement distances. The y-axis is within-granary frequency of acorns, such that all frequencies within a granary sum to 1. Note that the *x*-axis is log-scale. See the text and Table 3 for details of curve fits.

SEED SOURCE SHARING BETWEEN GRANARIES

Five pairs of granaries share acorns from the same maternal source tree (Fig. 1, Table 4). Three of these pairs (162–163, 990–991, 107–108) were closely situated (Table 4) and thus may represent granaries maintained by the same woodpecker group. For two pairs, 162–163 and 107–108, the relative degree of overlap apparent in genotype tallies (low and high, respectively; Fig. 1) is reflected in the value of the PMI pairwise overlap measure q_{gh} (0.085 and 0.938; Table 2). For the 990–991 granary pair, despite the shared usage of three acorn sources, forming a respective total of 44% and 90% of collected acorns from each granary (Fig. 1), q_{gh} for the pair was only 0.082, which is similar to that for the two much more widely separated granary pairs (31–152 and 163–931) that appear to share acorn sources incidentally (Table 2). In contrast, our PPMI measure q^0_{gh} shows a much greater degree of overlap for the 990–991 granary pair (q^0_{gh} = 0.398), while producing overlap estimates identical to q_{gh} for the other pairs (Table 2).

Based on our spatial analysis (Table 4), inter-granary distance is less than or approximately equal to mean granary-source distance for our three hypothesized single-group granary pairs (162–163, 990–991, 107–108) and greater than mean granary-source distance for the two apparently incidental granary pairs (152–31, 931–163). For incidental granary pairs, one would expect disjoint territories with sources located between granaries, resulting in greater distance between incidental granaries than between each granary and the shared source. We could not perform this analysis for one of the shared sources for granary pair 990–991, because the acorns with the shared genotype could not be assigned to a source tree.

Table 3. Curve fits for dispersal distance data sets. Data sets included the full set of dispersal distances (maximum 1449 m), and a subset which excluded the extreme long-distance dispersal events observed for granary 140 (maximum 372 m). Criteria shown are negative log-likelihood (−lnLik) and Akaike Information Criterion (AIC) values for the curve fits, with the lowest (strongest) value for each indicated in bold type; dispersal kernel parameter estimates (α and β); and model-predicted mean dispersal distance (δ). Dispersal kernels include the negative exponential (Austerlitz *et al.* 2004), exponential power (Clark *et al.* 1998) and inverse power (Clauset, Shalizi & Newman 2009). Inverse power curves with decay parameter estimates $\alpha \leq 2$ have infinite moments. A non-significant parameter estimate is indicated by NS. Model fits included a multiplicative scaling parameter (not shown)

Dispersal curve	Data set	−lnLik	AIC	$\alpha \pm$ SE	$\beta \pm$ SE	δ (m)
Negative exponential	Full	6.04	**18.1**	63.5 ± 16.9	–	63.5
	Subset	6.25	18.5	63.5 ± 17.3	–	63.5
Exponential power	Full	**5.92**	19.8	38.3 ± 57.2 **(NS)**	0.66 ± 0.56 **(NS)**	88.9
	Subset	6.13	20.3	38.7 ± 58.2 **(NS)**	0.66 ± 0.57 **(NS)**	88.3
Inverse power	Full	6.20	18.4	1.64 ± 0.13	–	∞
	Subset	6.94	19.9	1.66 ± 0.14	–	∞

Table 4. Probability of maternal identity statistics and assigned-source distances for all granary pairs sharing at least one acorn source tree, with the overlap in source trees measured by q_{gh} (eqn 4), q^*_{gg} and N^*_{em} when both granaries are near each other and analysed as a single pool, q^0_{gh}, the pooled pairwise overlap measure (eqns 4 and 5), distance between the members of a granary pair, and distances from each member of the granary pair to each shared source tree

Granary pair	q_{gh}	Pooled q^*_{gg}	Pooled N^*_{em}	q^0_{gh}	Distance between (m)	Distance to common source(s) (m)
152, 31	0.033	–	–	0.033	163.4	94.1, 84.4
931, 163	0.101	–	–	0.101	343.5	337.4, 48.5
162, 163	0.085	0.509	1.97	0.085	13.3	43.8, 47.5
990, 991	0.082	0.200	5.01	0.398	50.1	105.0, 151.7; 73.6, 24.8
107, 108	0.938	0.902	1.11	0.938	13.1	48.9, 61.9

Discussion

ACORN MOVEMENT AND ACORN WOODPECKER SOCIAL BEHAVIOUR

The pattern of *Q. agrifolia* acorn transport to granaries provides strong evidence for the impact of the social behaviour of acorn woodpeckers. The low number of trees sampled by woodpecker groups when filling a granary is (at least in part) a consequence of territoriality, which restricts foraging to a small spatial area. Overall, each woodpecker group foraged from relatively few *Q. agrifolia* trees within this restricted area, as was found for *Q. lobata* at the same study site (Grivet, Smouse & Sork 2005) and for multiple species of oaks at Hastings Reserve in Carmel Valley, California, USA (Koenig, McEntee & Walters 2008).

Within this foraging area, the diversity of acorns brought by acorn woodpeckers to their granaries does not appear to depend in any straightforward way upon the diversity or proximity of local source trees. Acorn woodpecker foraging patterns were poorly fit by standard diffusive dispersal curves (Fig. 3, Table 3), and we were unable to detect a linear relationship between either the number of observed maternal source trees (K_g) or the effective number of maternal source trees (N^*_{em}),and local density of *Q. agrifolia* around granaries, with the exception of K_g vs. the number of *Q. agrifolia* within 50 m of the granary. Taken together, these results indicate that while the frequency of woodpecker foraging does decrease with distance, it does not do so in a convincingly diffusive manner; rather, our data indicate a severe reduction in foraging frequency at about 150–200 m distance for most granaries (Fig. 3) and not a gradual reduction with distance as is found with diffusive dispersal.

Our results indicate that acorn woodpecker territoriality both confines foraging to closely restricted areas and mediates gathering of acorns within a foraging area. Within territories, woodpecker usage of acorn source trees is complex, and we were able to detect only a rough general pattern of decreased usage with distance with little relationship to local acorn source-tree availability. Other factors may influence usage of acorn sources within territories, as acorn woodpeckers do not forage from different *Quercus* species according to local species abundance, and always include some portion of insects and tree sap in their diet (MacRoberts & MacRoberts 1976; Koenig & Mumme 1987; Rosas-Espinoza *et al.* 2008). Outside the territory, woodpeckers are likely to restrict their foraging even with low local tree density, unless acorn production is so low that woodpeckers are forced to forage farther afield (Koenig, McEntee & Walters 2008).

Territoriality also restricts the sets of trees sampled by woodpecker groups to be largely non-overlapping, and our genetic evidence is entirely consistent with direct observational

evidence of foraging (MacRoberts & MacRoberts 1976; Koenig & Mumme 1987; Koenig, McEntee & Walters 2008). The resolution of our genetic data set allows us to examine in more detail the five granary pairs that share acorns from at least one source tree (Table 4), as this sharing among granaries may be particularly helpful in understanding the interaction between acorn transport and woodpecker territoriality. These granary pairs can be divided into two groups: a 'dual-granary' group, containing three granary pairs (162–163, 990–991 and 107–108) that show a relatively high amount of source and/or foraging area overlap, and thus appear to represent paired granaries within the territory maintained by a single woodpecker group; and an 'incidental' group, containing two granary pairs (152–31, 931–163), each of which shows little source and/or spatial overlap in foraging areas and which appear to share source trees incidentally.

We base this distinction between dual-granary and incidental granary pairs on four sets of observations. First, members of dual-granary pairs are found within about 50 m of each other, well within our observed mean foraging distance, while members of incidental granary pairs are at least 150 m apart, at least 60 m beyond our observed mean foraging distance (Table 4). Secondly, dual-granary pairs are generally closer to each other than they are to their shared source tree(s). In contrast, distances between incidental granary pairs are often greater than between their shared source tree (Table 4). The relative rarity of acorn transport to the closest granary that is not also maintained by the same bird group provides further support for these observations. Thirdly, two of the dual-granary pairs have markedly higher PPMI (q^0_{gh}) estimates than do the other granary pairs (Table 4). Fourth, the spatial extents of seed sources used around each member of a dual-granary pair overlap (Fig. 2). This is true for all three dual-granary pairs, including the pair with low PPMI (162–163; Fig. 2). Similar dual and incidental granary pair types appear to explain earlier observations of *Q. lobata* source sharing at both Sedgwick and Hastings (Grivet, Smouse & Sork 2005; D.G. Scofield, V.R. Alfaro, D. Grivet, V.L. Sork, unpublished data), with the latter buttressed by direct observations of acorn woodpecker territory structure and granary usage (W. D. Koenig, personal communication). Thus, the 16 granaries are probably maintained by 13 distinct woodpecker groups. The size of our data set and its spatial and genetic resolution allow us to suggest definitive groupings, even without direct observational data on the woodpeckers. In sum, using genetic data from acorns alone, we established the occurrence of general patterns of acorn source tree sharing that appear to reflect important details of acorn woodpecker population structure at our site, and also established the occurrence but relative rarity of acorn transport events that fall outside these general patterns.

LONG-DISTANCE TRANSPORT – A NOTABLE EXCEPTION TO THE GENERAL PATTERN

The woodpecker group maintaining granary 140 showed an unusual pattern of acorn transport that was not observed by any other group – all acorns that we sampled came from multiple trees located within 90 m of each other more than 1.3 km away (Fig. 2). Their behaviour is noteworthy because it illustrates a rare event for this system – long distance, directed movement – while maintaining the overall pattern of a spatially confined foraging area. We can only speculate as to the reasons for this situation. A large *Q. lobata* granary collapsed near the foraging area 1–2 years prior to the current study (V. L. Sork, pers. obs.). Given that partial or complete granary failures occur with some regularity and, when severe, can lead to territory abandonment (Koenig & Mumme 1987), one possible scenario involves relocation of the resident bird group to an existing, but abandoned, granary without co-occurring relocation of the foraging territory, perhaps due to the presence of other bird group territories in the vicinity of the newly occupied granary. Whatever the underlying reason for the disjoint locations of the granary and the foraging territory, it seems unlikely that the observed situation could persist indefinitely and that as time progresses, the woodpecker group would be expected to establish a more local territory. One would anticipate that such occasional extreme relocations, however, would result in saltational dispersal events for the oaks that could be consequential in moving plant genetic diversity across the landscape over longer time periods.

GENOTYPING ERROR IN MATERNALLY DERIVED SEED TISSUE

Before closing, we want to comment on the problem of genotyping error in dispersed seeds due to DNA quality, which often declines as the seed ages in its dispersed location, be it an acorn woodpecker granary, embedded within animal faeces or beneath the soil. As time since removal from the source tree increases, the number of genotyping errors observed in maternally derived seed tissue (in terms of mismatches with respect to original seed-source genotype) will increase. Our results emphasize the preponderance of null-allele errors under these conditions (Table 1) and underscore the benefits of allowing for such errors during assignment analyses. As we did observe some variation among loci in the occurrence of null genotyping error (Table 1) (Pemberton *et al.* 1995), different systems may exhibit different error profiles. We also found during our regenotyping analysis that while most samples provided consistent genotypes, some samples (8%) provided inconsistent genotypes with much higher occurrence of null alleles (Table 1). Depending on sample sizes and study design, it is preferable to drop such poor samples from the data set on the basis of genetic inconsistency. Another issue not immediately apparent from our regenotyping efforts is that fully 13% of the remaining acorns with consistent genotypes were assigned to a source tree because we conservatively accounted for genotyping error, especially null alleles, during assignment. Future studies should address the possibility of cryptic genotyping error during assignment analyses. For studies using maternally derived tissue from older seeds, our findings offer some good rules for deciding when to include samples in the final data set.

Conclusions

The social behaviour of acorn woodpeckers restricts both the distance and the variety of directions in which they transport acorns away from oak trees. Woodpecker foraging decisions are based on patterns more complicated than simple local seed-source density and appear to vary locally on a granary-by-granary basis. Future work should explore more elaborate foraging models based on conditions specific to particular foraging territories. The observations we report here are probably general for acorn woodpeckers, but seed dispersers with different social systems may well show different, although equally idiosyncratic, patterns of seed movement (Krijger *et al*. 1997; J. Karubian, unpublished data; Russo, Portnoy & Augspurger 2006). The important point is that seed dispersal patterns will probably make sense only in light of the foraging behaviour of the animal vectors.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Allele counts for 10 microsatellite loci of 285 sampled *Quercus agrifolia* adults at Figueroa Creek, Santa Ynez Valley, California, USA.

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